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GLOBAL SPREAD OF INSECT-ASSOCIATED FUNGI ON EXOTIC PLANTATION PINES

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ABSTRACT

During the course of the 20th Century, plantation forestry in the tropics and Southern Hemisphere has grown dramatically. This growth is associated with increased demand for wood and paper products and also with restrictions on the felling of native forests. Thus, huge industries have been established based on extensive areas planted to highly productive exotic pine species. An important reason for the success of exotic pine plantation forestry is that those tree species have been separated from the insect pests and diseases that feed on them in their place of origin. Pine-infesting insects have gradually begun to appear on trees previously separated from these pests. These accidental introductions have, in many cases, occurred despite outstanding quarantine restrictions. An aspect of the introduction of pine-infesting insects that is not commonly appreciated, is the fact that many live in association with fungi that are also detrimental to trees. These associations range from being relatively casual (e.g. *Fusarium circinatum* with cone and shoot-feeding insects) to highly specific (e.g. *Amylostereum areolatum* with the wood wasp *Sirex noctilio*). The identity of these fungal associates and the structure of their populations, provide clues to the origin of the introduced insects. This knowledge also has important implications for pest and disease avoidance in the future.

INTRODUCTION

The global demand for timber and pulp products during the 20th Century has lead to a rapid growth in the number of plantations of exotic pines (*Pinus* spp.) in the tropics and Southern Hemisphere. Countries such as Chile, Brazil, South Africa, New Zealand and Australia have huge, modern industries based on plantations of exotic pines. In these areas, the most widely planted species are *Pinus caribaea* Morelet, *P. elliottii* Engelm., *P. radiata* D. Don, *P. taeda* L. and *P. patula* Schiede & Deppe in Schldl. & Cham. The last three species are most commonly planted in the cooler and more temperate regions. In recent years, vegetative propagation of these trees has been used as a tool to improve productivity of these plantations. This approach has also made it possible to capitilize on opportunities linked to hybridization of species.

The success of exotic plantation forestry is commonly attributed to the separation of these trees from pests and diseases, which reduce growth and productivity where the trees are native (Bright 1998). This situation has gradually begun to change with new and damaging pathogens gradually appearing in areas where they were previously not present. Thus, the appearance of diseases such as Dothistroma needle blight caused by *Dothistroma septospora*, in Australia, New Zealand, Southern Africa and Chile led to tremendous damage and setbacks for forestry in those countries (Gibson *et al.* 1964, Gibson 1979, Gilmour 1967, Edwards and Walker 1978, Millar and Minter 1980, Roux 1984).

The arrival of new pests and diseases of exotic plantation pines in one country, has serious consequences for other countries where similar, susceptible species are grown. When a pest or disease arrives at a new location, the likelihood that it might move again, particularly to other new locations, appears to increase. New invaders might be closer geographically to unaffected areas and also increases inoculum. Furthermore, more active trade and tourism routes increases risk. The quality of quarantine regulations and inspections in one country is, therefore, linked to that in adjacent countries, and even between those separated by oceans.

While the introduction of insect pests of pines into new environments is a well recognized trend, the fact that these pests generally carry with them a large assemblage of microbes, is less often considered. Pine-infesting bark beetles (Coleoptera: Scolytidae) for example, are known to live in close association with a guild of fungi belonging to the genera *Ceratocystis*, *Ophiostoma* and their asexual states (Upadhyay 1981, Whitney 1982, Wingfield and Marasas 1980, Stone and Simpson 1987, Wingfield *et al.* 1988, Schowalter and Filip 1993). The role of many of these fungi in the life history of bark beetles is unknown, however, some are well-recognized tree pathogens (Upadhyay 1981, Whitney 1982, Owen *et al.* 1987, Harrington 1988, Wingfield *et al.* 1988). Likewise, the pine wood wasps (Siricidae) and particularly *Sirex noctilo* Fabr. exist in an obligate symbiosis with wood rotting fungi (*Amylostereum* spp.) (Cartwright 1929, Francke-Grosmann 1939, Gilmour 1965, Morgan 1968).

In this paper, we briefly consider the more obvious fungi that have been transferred to new environments through accidental introduction of pine-infesting insects. We particularly consider root and root collar infesting species of *Hylastes* and *Hylurgus* (European origin) introduced into Australia, Chile, New Zealand and Southern Africa; the stem infesting *Orthotomicus erosus* Wollaston in Southern Africa, and *Ips grandicollis* Eichoff in Australia and New Zealand. Furthermore, we briefly outline interesting aspects pertaining to the fungal associate of *Sirex noctilio* in South America, South Africa, New Zealand and Australia.

BARK BEETLES

Distribution of bark beetles in the Southern Hemisphere

The first pine bark beetle to be reported in the Southern Hemisphere was probably *Hylurgus ligniperda* Fabr. from South Africa in 1885 (Tribe 1991). This was followed by reports in 1929 and 1930 of *Hylastes ater* Payk. in New Zealand (Swan 1942) and *Hylastes angustatus* Herbst in South Africa (Serez 1987), respectively. Following these appearances, *Ips grandicollis* Eichoff was reported from Australia in 1943 (Neumann 1987), and *Orthotomicus erosus* Wollaston in South Africa in 1968 (Tribe 1990a). All the species were introduced from Europe, except for *I. grandicollis* which was from North America (Neumann 1987, Swan 1942, Tribe 1990a, 1990b, 1991).

Apart from spreading within the various countries after introduction, the pine bark beetles have subsequently been introduced to the other pine-growing countries of the Southern Hemisphere. *Hylurgus ligniperda* was reported from Australia in the 1940's (Swan 1942), from New Zealand in 1974 (Anonymous 1974), and from Chile in 1988 (Ciesla 1988). It has been suggested that this beetle was introduced into New Zealand via Australia (Anonymous 1974). *Hylastes ater* was reported from Australia in 1937 (Swan 1942) and Chile in 1988 (Ciesla 1988). *Orthotomicus erosus*, initially only known from South Africa, has also been reported from Chile (Ciesla 1988). Only *H. angustatus* (South Africa) and *Ips grandicollis* (Australia) have not been reported from other countries following their introduction in the Southern Hemisphere.

Fungi associated with bark beetles in the Southern Hemisphere

Information regarding fungi associated with the five introduced pine bark beetles in the Southern Hemisphere is fragmented. Most of the research on these beetles has focused on their life cycles and control, and it is only recently that their fungal associates were given some attention. The most comprehensive study on these fungi has been conducted on beetles occurring in Southern Africa (Zhou *et al.*, unpublished) (Table 1).

One of the more interesting fungi associated with *H. ligniperda* and *H. angustatus* is *Leptographium procerum* (Kendr.) Wingf. This fungus is of particular interest because it causes white pine root decline in the eastern United States, Europe and New Zealand (Kendrick 1962, Dochinger 1967, Shaw and Dick 1980, Wingfield *et al.* 1988). The pathogenicity of *L. procerum* has been tested in the Northern Hemisphere with contradictory results. Some reports suggest that it can cause severe symptoms (Halambek 1981, Lackner and Alexander 1982) while others indicate that it forms seemingly harmless lesions (Livingston and Wingfield 1982, Wingfield 1982, 1986, 1993). In New Zealand pathogenicity trials with *L. procerum* resulted in staining of wood, but not tree death (Shaw and Dick 1980).

The most prevalent fungus isolated from both *H. ligniperda* and *H. angustatus*, was *Leptographium lundbergii* (Lagerb. & Melin) Goid. This fungus was also isolated from *O. erosus*, but less commonly. *Leptograpium lundbergii* has been associated with bluestain of *Pinus* and *Picea* spp. in the Northern Hemisphere (Lagerberg *et al.* 1927). In South Africa, the fungus has been associated with a root disease on pines (Wingfield *et al.* 1988). Pathogenicity trials, however, have shown the fungus is only mildly pathogenic (Wingfield and Knox-Davies 1980, Zhou *et al.* unpublished) and can only infect through wounds (Wingfield and Knox-Davies 1980). Its role in the life history of its vectors has not been studied.

Another *Leptographium* species isolated from all three bark beetle species in South Africa was *Leptographium serpens* (Goid.) Siem. (Zhou *et al.* unpublished). This fungus is known as a mild pathogen causing root disease of

Another *Leptographium* species isolated from all three bark beetle species in South Africa was *Leptographium serpens* (Goid.) Siem. (Zhou *et al.* unpublished). This fungus is known as a mild pathogen causing root disease of *P. pinea* L. in Italy (Lorenzini and Gambodi 1976). It was first reported from South Africa on *P. radiata* and *P. pinaster* Ait. (Wingfield and Knox-Davies 1980). Pathogenicity trials were conducted in South Africa by inoculating side branches of *P. elliottii*, *P. patula* and a *P. ellliottii / P. caribaea* hybrid. The results have shown that the fungus causes significant lesions and a slight yellowing of needles of these pine species (Zhou *et al.* unpublished). It should, therefore, be considered as mildly pathogenic and possibly contributes to tree disease.

The only *Ophiostoma* species recorded from *H. ligniperda* and *O. erosus* in South Africa that can be considered a pathogen, is *O. ips* (Rumb.) Nannf. This fungus is well-known as a causal agent of blue stain on pine (Seifert 1993). Pathogenicity trials in the Northern Hemisphere, however, led to contradictory results (Basham 1970, Mathre 1964, Parmeter *et al.* 1989, Raffa and Smalley 1988, Rane and Tattar 1987). Pathogenicity trials conducted in South Africa, as described above, have shown that although not severe, *O. ips* is more pathogenic than either *L. lundbergii* or *L. serpens* (Zhou *et al.* unpublished).

There are few reports of fungi associated with bark beetles occurring in other countries of the Southern Hemisphere (Table 1). From Australia, *Ophiostoma ips* has been reported from *Ips grandicollis* (Vaartaja 1966, Lawson 1993) and *O. pluriannulatum* (Hedgc.) H. & D.Syd. from *H. ater* (De Beer, personal communication). According to Jacobs *et al.* (1998), *O. huntii* (Robinson-Jeffrey) de Hoog & Scheffer has been isolated from *H. ater* in both Australia and New Zealand.

It is clear that bark beetles are moving between pine growing countries of the Southern Hemisphere. It is also likely that more species, including some of the more aggressive insects, will be introduced to this area in years to come. This implies that more serious fungal pathogens might also be introduced. The prospect of diseases such as pitch canker (caused by *Fusarium circinatum*) being introduced by bark beetles (Dick 1998) into clonal pine plantations, should not be underestimated.

Sirex wood wasp

Sirex noctilio is found throughout the temperate regions of the Northern Hemisphere and is thought to be native to Eurasia (Benson 1943, Morgan 1968, Spradbery and Kirk 1978). In its native range, *S. noctilio* is considered a secondary pest that mainly affects felled or severely stressed and damaged trees (Chrystal 1928, Hanson 1939, Hall 1978). Levels of infestation by *Sirex* are in general kept low by natural parasites, except in cases were other factors severely damage and stress the trees (Hall 1978). These wasps are thus viewed as natural thinning agents and as indicators of pathological conditions, rather than being a primary factor causing them (Chrystal 1928, Cartwright 1929).

In contrast to the Northern Hemisphere, *Sirex noctilio* has caused extensive damage in the exotic pine plantations in the Southern Hemisphere (Neumann and Marks 1990, Chou 1991). Different species of wood wasps have occasionally been recorded from the Southern Hemisphere on imported timber or timber products (Chrystal 1928, Taylor 1962, Morgan 1968). Of these, only *Sirex noctilio* has successfully established itself in Australasia, where it has become an economically serious pest (Neumann and Marks 1990, Chou 1991).

Sirex noctilio was first reported from standing trees in New Zealand around 1900. It was found in Tasmania in the early 1950's and on the mainland of Australia in 1961 (Neumann *et al.* 1987, Madden 1988). More recently, the softwood plantations in South America and South Africa have also been attacked by *S. noctilio* (Tribe 1995, Reardon *et al.* 1995). Despite attempts to control the pest, *S. noctilio* spread steadily through South America from the initial point of introduction in Uruguay in 1980 (Maderni 1998) to Argentina in 1985 (Klasmer *et al.* 1998) and Brazil in the late 1980's (Iede *et al.* 1998, Reardon *et al.* 1995). In 1994, *S. noctilio* was reported from *P. radiata* trees in Cape Province in South Africa (Tribe 1995).

Sirex noctilio co-exists in a specialised association with the Basidiomycete fungus, *Amylostereum areolatum* Boid. (Cartwright 1929, Francke-Grosmann 1939, Gilmour 1965, Morgan 1968, Talbot 1977). Fungal spores (conidia or oidia) or bundles of fungal mycelium are carried in a pair of intersegmental pouches (mycangia) of the wasp. These structures are located near the base of the ovipositor of the adult female wasp and in external hypopleural organs of female larvae (Buchner 1928, Francke-Grosmann 1939, Parkin 1941). During oviposition, the fungal cells and a mucus droplet are introduced into suitable hosts together with the eggs (Madden 1974, Madden and Coutts 1979). The fungus rots and dries the wood, and thus provides a suitable environment, nutrients and enzymes that are important for the survival and development of the wasp larvae (Francke-Grosmann

1939, Morgan 1968, Madden and Coutts 1979, Kukor and Martin 1983, Martin 1987). In combination, the phytotoxic mucus of the wasp and the wood rotting fungus have the ability to kill living trees (Coutts 1969a, 1969b).

In its association with *S. noctilio*, *A. areolatum* mainly reproduces by asexually formed arthrospores, which are spread by the woodwasp vector. As a result, clonal lines (Vegetative Compatibility Groups - VCG's) of these fungi are preserved over time and are spread over large areas (Vasiliauskas *et al.* 1998, Thomsen and Koch 1999, Vasiliauskas and Stenlid 1999). Large vegetative compatibility groups (VCG's) have been shown to occur in isolates of *A. areolatum* associated with *S. noctilio* in the Southern Hemisphere (Slippers *et al.* 2000a). From these data, it was clear that South Africa and Brazil share a common origin of *S. noctilio* and *A. areolatum*. Subsequently, RFLP and sequence data have shown that isolates of *A. areolatum* from all countries in the Southern Hemisphere are more closely related to each other than to isolates from other parts of the world (Slippers 1999, Slippers *et al.* 2000a). It is therefore likely that the wasp and fungus spread between countries of the Southern Hemisphere after its initial introduction into New Zealand.

Recent studies using sequence data of the mt-SSU-rDNA and nuc-IGS-rDNA regions successfully defined the taxonomic status and phylogenetic relationships of *Amylostereum* species (Slippers *et al.* 2000b). Using these data, PCR RFLP fingerprints were developed which provide a quick, yet precise, identification tool to distinguish these morphologically similar fungal species in culture (Slippers 1999). Gaut (1970) showed conclusively that the symbiosis between certain siricid and fungal species are always species specific, but that certain fungal species are carried by more than one siricid species. Using PCR RFLP fingerprints of the associated fungi, the specificity of the symbiosis can thus be used to clarify questions regarding the taxonomy of the Siricidae, as proposed by Talbot (1977).

Neither chemical control nor breeding for resistance has been successfully used to manage the *Sirex-Amylostereum* pest complex in the Southern Hemisphere. Much research has concentrated on natural enemies of siricids in an attempt to control *Sirex* in areas where it has become established without them. Of the different parasites used, the nematode, *Deladenus siricidicola* Bedding, is the most effective (Bedding 1995) and is used extensively in biological control programmes throughout the Southern Hemisphere (Tribe 1995). Apart from infecting the wasp, the nematode also feeds on *A. areolatum*, on which it is mass reared for large scale distribution (Bedding 1967, 1972). The nematode, and unavoidably also the isolates of the fungus on which it was reared, has been imported from Australia and released in both South Africa and Brazil as part of a biological control initiative against *S. noctilio*. Isolates of *A. areolatum* introduced this way, have been shown to be genetically distinct from other field isolates from South Africa, Brazil, New Zealand and Tasmania (Slippers *et al.* 2000a). This has the potential to influence the population structure of *A. areolatum* in these countries. Furthermore, the feeding and reproduction of *D. siricidicola* might be influenced by a wild strain of the fungus that is different from the one on which it was reared. This might explain initial low parasitism rates by *D. siricidicola* on *Sirex* in South Africa and Brazil.

Molecular techniques, particularly those focussed on DNA characters, have only recently been applied to answer questions regarding *Amylostereum* spp. These studies have not only clarified previous hypotheses and raised new and challenging questions about the fungi, but also about their associated wasp species. The tools they provide are useful to overcome difficulties in identifying and studying the morphologically similar *Amylostereum* spp. and their symbiotic wasp species. The study of the population structure of these fungi from many parts of the world gives valuable insight into the evolutionary relationships, geographical origin and spread of the *Sirex-Amylostereum* complex as a whole. These techniques and information emerging from their application will be very valuable for future study of these organisms, especially in planning of control strategies for this destructive pest complex.

CONCLUSIONS

The magnitude of plantations of exotic *Pinus* spp. in the tropics and Southern Hemisphere has increased dramatically in recent years and is a trend that seems likely to continue. In the past, these countries were relatively isolated but travel and trade amongst them, and between countries elsewhere in the world, has increased greatly. This has led to increasing numbers of pests appearing in new locations. These include bark beetles and wood wasps that are known to carry fungi.

Although this has not been commonly recognized, the accidental introduction of bark beetles and wood wasps into new environments has also meant an introduction of a large number of exotic fungi. These range from symbionts that contribute to the survival of these insects, primary tree pathogens and agents of sap stain. The identity of most of these fungi is only now being considered in detail.

Very little is known concerning the population structures of fungi introduced together with bark beetles and wood wasps. Some investigations pertaining to this topic have begun, particularly with wood wasps. Early findings are showing that information from these investigations improve our understanding of the origin of the pests. Data will also contribute to improving quarantine measures that might ideally reduce occurrence of new introductions.

The role of fungi associated with introduced pine infesting bark beetles is poorly understood. There is a great need for studies of their biology, which will inevitably improve the biological knowledge of their vectors and of host pathogen relationships.

All indications are that introductions of exotic pests and pathogens into Southern Hemisphere pine growing areas will continue. Many pests are likely to be introduced carrying microbes, including fungi. The importance of these organisms should not be underestimated. Comprehensive studies, leading to an understanding of the entire insect/ microbe niche are, therefore, recommended.

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Table 1. Northern Hemisphere, pine infesting bark beetles and their associated fungi that have been introduced into pine plantations of the Southern Hemisphere.

Country	Bark beetle	Associated fungi
South Africa	*Hylurgus ligniperda*	*Leptographium lundbergii, L. serpens, L. procerum, Ophiostoma piceae, O. ips, O. pluriannulatum, O. stenoceras*
	Hylastes angustatus	*L. lundbergii, L. serpens, L. procerum, O. stenoceras, O. galeiformis, O. pluriannulatum, Ceratocystiopsis minuta*
	Orthotomicus erosus	*O. ips, O. pluriannulatum, L. lundbergii, L. serpens, Cop. minuta*
New Zealand	*H. ater* *H. ligniperda*	*O. huntii*
Australia	*Ips grandicollis*	*O. ips*
	H. ater	*O. pluriannulatum, O. huntii*
	O. erosus	
Chile	*H. ligniperda* *Hylastes angustatus* *O. erosus*	