Role of insect vectors in epidemiology and invasion risk of Fusarium circinatum, and risk assessment of biological control of invasive Pinus contorta

Eckehard G. Brockerhoff, Margaret Dick, Rebecca Ganley, Alain Roques, Andrew J. Storer

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Eckehard G. Brockerhoff, Scion (New Zealand Forest Research Institute), Christchurch, New Zealand, e-mail: eckehard.brockerhoff@scionresearch.com

Margaret Dick, Scion (New Zealand Forest Research Institute), Rotorua, New Zealand, e-mail: margaret.dick@scionresearch.com

Rebecca Ganley, Scion (New Zealand Forest Research Institute), Rotorua, New Zealand, e-mail: rebecca.ganley@scionresearch.com

Alain Roques, INRA – UR0633, Zoologie Forestière, 2163 Av. Pomme de pin, CS 40001, 45075 Orléans, France, e-mail: alain.roques@orleans.inra.fr

Andrew J. Storer, School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA, e-mail: storer@mtu.edu

Correspondence:

Eckehard G. Brockerhoff, Scion (New Zealand Forest Research Institute), Christchurch, New Zealand, e-mail: eckehard.brockerhoff@scionresearch.com, Tel +64 364 2949, Fax +64 364 2812

Abstract

Pitch canker, caused by the pathogen *Fusarium circinatum*, is a serious disease of pines, *Pinus* species. It is a threat to natural and planted pine forests, and to date it has invaded countries across five continents. Pine-feeding insects can play a key role in the epidemiology of the disease, as wounding agents allowing pathogen access or as vectors transmitting the pathogen from infected to healthy trees. We reviewed the role of insects in the epidemiology of pitch canker worldwide and assessed which insects are present in New Zealand that may act as wounding agents or vectors to determine whether pathogen invasion could adversely affect *Pinus radiata* plantation forests and urban trees. We also evaluated whether cone or seed insects of pines could be introduced as biological control agents of invasive *Pinus contorta* and how this may affect the impact of a potential *F. circinatum* invasion. As there are no native pines or other Pinaceae in New Zealand, there are only few pine insects, mainly accidental introductions. None of the insects recorded on pines in New Zealand is likely to be a vector, suggesting low disease risk. Of six potentially suitable biocontrol candidates, the European pine cone weevil *Pissodes validirostris* is the most promising regarding host specificity and impact on seed production, but there is uncertainty about its ability to act as vector of *F. circinatum*. Our methodology to review and evaluate the vector potential of pine associates can be used as a generic framework to assess the potential impacts of *F. circinatum* invasion.

Keywords: Cone and seed insects; invasive alien species; pathogen vectors; pitch canker

Introduction

Pitch canker, caused by the pathogen *Fusarium circinatum* (Nirenberg and O'Donnell), is a serious disease of some pines (*Pinus* spp.) (Dick 1998; Gordon et al. 2001; Wingfield et al. 2008). Since the 1980's it has emerged as a particularly damaging disease of *Pinus radiata* D. Don in the native range of this pine in various parts of California (Storer et al. 1997; Gordon et al. 2001). The pathogen is assumed to originate from Mexico/Central America (Wingfield et al. 2008) from where it has invaded the United States, Haiti, Japan, South Africa, Chile, Spain, Brazil and Italy, affecting a range of pine species (Dwinell 1999; Wingfield et al. 2002; Carlucci et al. 2007; Wingfield et al. 2008; Pfenning et al. 2014). The extent of disease problems varies among regions and host species, and symptoms can be common in forests and plantations (as in Spain, for example), restricted to nurseries (as reported from Chile), or parks and gardens (as in Italy). In South Africa, where pitch canker was first detected in 1990 (Viljoen et al. 1994), the disease remained confined to nurseries until 2005 when an outbreak was reported in young plantations in the Western Cape Province (Coutinho et al. 2007). Several countries where the disease has not yet been recorded, including New Zealand, China, and Australia, are thought to have a climate that is suitable for establishment of the fungus and development of pitch canker disease (Ganley et al. 2009).

Studies in California have shown that bark-feeding insects as well as cone and seed insects play an important role in the infection process, as wounding agents of trees that may allow pathogen access or as vectors of the pathogen from infected to healthy trees (Fox et al. 1991; Hoover et al. 1996; Storer et al. 1998; Storer et al. 2004a). In New Zealand and other countries in the southern hemisphere where *Pinus radiata* is widely planted as an exotic tree, there are relatively few associated insects, mainly because no native Pinaceae are present, and consequently there are no native specialised insect herbivores. Occasionally, some native insects attack pines, although their direct impact is mostly benign. However, several insect pests of pines have become introduced over the years. Preliminary reviews of the role of insects associated with pines in New Zealand as potential vectors of *F. circinatum* have been provided by Gadgil et al. (2003) and Storer et al. (2004b). Currently, there appear to be few insects in New Zealand that are likely to act as vectors of the fungus, and this may limit the spread of the fungus and its impact on pine plantations, if it ever became established there. However, a formal analysis of the potential vectors of *F. circinatum* in New Zealand is not available.

Knowledge about any potential disease vectors and other insect associates is necessary to enable an informed response in the event of an incursion of *F. circinatum* and to evaluate the risk of spread (Gadgil et al. 2003; Ganley 2007; Fourrier et al. 2015). The vector issue is also important for an assessment of the risk of the potential intentional introduction of seed-feeding insects for biological control of wilding (invasive) *Pinus contorta* Loudon. Several pine species are now considered environmental weeds in New Zealand and other southern hemisphere countries (Richardson and Higgins 1998; Rundel et al. 2014). In some regions of New Zealand, pines have invaded natural or semi-natural grassland and scrub communities (Ledgard 1998). Although plantings of *Pinus contorta* were of limited extent, this species is now considered the most serious invader among the pines (Ledgard 1998). Options for biological control have been assessed (Brockerhoff and Kay 1998; Brockerhoff et al. 2004). Because several pine species are highly valued in plantation forestry and also in urban amenity plantings, the potential use of cone and seed insects is a favoured approach as such insects may reduce the spread of pines without affecting growth or causing damage to other parts of trees. In addition, most cone and seed insects are specialised, adapted species that exhibit a high degree of host plant specificity (Turgeon et al. 1994), therefore limiting risks to non-target plants. On the other hand, seed-eating insects may not be as effective as other types of biocontrol agents, and it remains to be determined whether their effect actually reduces plant spread rates (e.g., Rees and Paynter 1997). Based on a review of cone and seed insects that attack *Pinus contorta*, considering host specificity, potential impact on seed production and other criteria, some insects are thought to show promise as potential biocontrol agents, both in New Zealand and South Africa (Brockerhoff and Kay 1998; Brockerhoff et al. 2004; Roques et al. 2004). However, it is feared that the introduction of such insects to New Zealand would greatly increase the risks associated with *F. circinatum* because the biocontrol agent may act as an additional, and potentially important, vector of the pitch canker pathogen. In South Africa, such concerns have halted plans to introduce a cone insect for biocontrol of invasive pines (Lennox et al. 2009), although there is renewed interest in the approach.

Here we review the role of insects in the epidemiology of pitch canker world-wide and assess which insects present in New Zealand may act as vectors. We also review the preliminary selection of biocontrol agents against invasive pines and explore the risks of introducing such biocontrol agents to New Zealand, particularly with regard to our current knowledge about implications for vectoring *F. circinatum*. Our specific objectives are:

i. to provide an overview of the insects associated with pitch canker and their role in disease epidemiology in the countries where the disease occurs to date;
ii. to review the native and introduced insects found on pines in New Zealand, to determine the likelihood of these species acting as vectors of *F. circinatum*;
iii. to evaluate the insects potentially suitable for biocontrol of *Pinus contorta* in New Zealand and to assess the risk of their introduction in relation to the potential establishment of *F. circinatum*; and

iv. to develop a general framework for the assessment of risks associated with vectors of *F. circinatum* or similar pathogens that can also be used for other countries.

Wounding agents, vectors and carriers of *Fusarium circinatum* and their interactions with the pathogen

In some regions insects have been shown to play an important role in the infection process while in other regions insects appear to play a minor role. Associations with insects have been best studied in California where pitch canker has become a major disease of the native *Pinus radiata*, which is among the most susceptible species of pine (Correll et al. 1991; Adams et al. 1999; Storer et al. 2002). Insects can act as 'wounding agents' that allow the pathogen to enter the plant via the damaged cuticle or via tunnels such as those made by bark beetles. Some insects are 'carriers' because they carry inoculum from diseased plants they either visited or on which they have developed. However, in order to be classified as a 'vector', Leach's postulates need to be met (Leach 1940). These state that in addition to being associated with diseased plants, carrying the pathogen, and visiting susceptible plant hosts, an organism must be capable of successfully transmitting the pathogen to plants that were not yet infected under controlled conditions. Some wounding agents act concurrently as vectors but a vector can also cause an infection via a wound caused by another species. Not all carriers of inoculum are necessarily successful vectors, for example, if they are not causing any wounding that would be sufficient for transmission. It is therefore important to consider the differences in involvement of the various insects associated with diseased or healthy host plants and to classify each species accordingly (Table 1).

Insects that feed subcortically on live trees or that wound live trees during exploratory host feeding have been shown to vector the pitch canker pathogen in California, especially bark beetles such as *Ips paraconfusus* (Fox et al. 1991) and twig beetles, *Pityophthorus* spp. (Storer et al. 2004a; Erbilgin et al 2008; Table 1; see Supplementary Table S1 for an alphabetical listing of insect species). Twig beetles are thought to vector the pitch canker pathogen into pines also during exploratory feeding to find suitable host material. Baiting trees with pheromones of *Pityophthorus setosus* resulted in pitch canker infections on those trees despite the lack of colonization by the insect (Storer et al 2004a). Other habits that may result in wounding include shoot feeding and the creation of wounds during oviposition. The cone beetles, *Conophthorus radiatae* and *Ernobius punctulatus* are also confirmed vectors (Hoover et al. 1995, 1996; Table 1). Several other species, including shoot and foliage feeders, sap suckers and predatory insects are known wounding agents or carriers but none of these are known vectors (Table 1, Supplementary Table S1).

To assess the role of insects in the infection of trees by *F. circinatum* and the epidemiology of the disease, it is important to consider the life cycles of both the pathogen and potential vectors and the nature of potential interactions between these organisms. Fruit bodies of *F. circinatum* (known as sporodochia) containing thousands of asexual spores (conidia) may be produced on the surface of infected tissues when conditions are moist. These are dispersed by water-splash and can be carried in air currents throughout the year (Blakeslee et al. 1978; Correll et al. 1991). Spores can also be recovered from the surface bark of trees even when fruit bodies are not readily apparent (Adams et al. 1999). Two rounds of studies have been conducted where spore suspensions were sprayed on small trees in the field and the branches were then baited with twig beetle pheromones (Sakamoto et al. 2007). The results showed no difference in disease between treated and untreated trees. It is likely that spore loads were very high in these studies compared with what occurs naturally. It seems likely that the insects pick up spores in the tree, perhaps while chewing their way out though diseased tissue. Insects coming into contact with the sporodochia may readily pick up many of the sticky spores that are likely to adhere to the surface of the body and be trapped amongst hairs and other surface structures (e.g., Yamoah et al. 2011). Fox et al. (1990) reported the isolation of the pathogen from galleries of *Ips* spp. in *Pinus radiata* trees. The beetles carry propagules that presumably can include hyphal fragments as well as spores. By contrast, it is likely that the importance of casually acquiring spores from the tree surface is low. The risk of transmission appears to vary at different times of the year according to propagule loads on two *Ips* species (Erbilgin et al. 2008). Spore loads of twig beetles were considered an important factor in studies of the vector efficiency (Erbilgin et al. 2009).

Once infection has occurred the fungus colonises the sapwood and can be readily isolated from discoloured or resinous tissues (McCain et al. 1987; Correll et al. 1991). However, the fungus does not spread great distances within the wood. Infection of a cone, or a cone whorl, vectored by cone insects or other borers leads to death of the branch beyond the cone, with each dead branch being the result of a separate infection. Although unsightly, the branch and twig death that would result from infections transmitted by cone and seed insects would probably have relatively little impact on tree growth. Lesions on branches girdle the branch so the distal portion dies; spread down the branch or shoot is usually arrested at the node (Dwinell et al 1985; Gordon et al. 2001). Individual trees may thus sustain crown infections for many years. However, crown dieback can be extensive due to the multiple infections. Trunk infections are often initiated by bark beetles, and tree death will follow girdling of the stem from a number of separate infections and/or attacks by bark beetles. Multiple trunk attacks are required in order to kill the cambium around the circumference and for tree death to result (Gordon et al. 2001; Storer et al. 2002). Bark beetles (especially *Ips* spp. and *Dendroctonus* spp.) can cause considerable mortality of pines also in the absence of any other disease agents (e.g., Six and Wingfield 2011).

In the absence of insects vectoring *F. circinatum* to the trunk of the trees, any stem infections would be initiated through infection of wounds created by other causes including weather events (such as wind and hail), pruning or cone collection (Dwinell et al. 1985; Gordon et al. 2001). In New Zealand, wounds could also occur from bark stripping by native parrots (Dick 1998), although this is rare.

Spread of the pitch canker disease in nurseries is different from what occurs in forests. The fungus has been reported to be capable of spreading through nurseries very rapidly, with devastating losses recorded (Viljoen et al. 1994). Unlike in older trees, wounds are not required for infection of young seedlings. Insect-vectored transmission is apparently not important (Hurley et al. 2007). Unfortunately, in contrast to the majority of pine nursery diseases where diligent application of fungicides will generally reduce the impacts of pathogens, chemical control of pitch canker disease has been found to be relatively ineffective (M.J. Wingfield pers. com.). However, rigorous sanitation procedures can reduce disease incidence to insignificant levels in a nursery where all plants are containerised (Van Wyk et al. 2012). Based on this knowledge, we can predict with reasonable confidence the outcome of an introduction of *F. circinatum* to a nursery in New Zealand where plants are reared both as bare root in nursery beds and in containers (Gadgil et al. 2003). Eradication attempts are likely to result in nursery closure while soil fumigation is undertaken followed by a high level of sanitation. Although insects are not thought to be important in the disease epidemiology within nurseries, certain insects may be involved in spreading the disease from nurseries to surrounding forests. It is more likely that transmission of the fungus to a plantation would occur via out planting of asymptomatic infected seedlings from a nursery than by insects.

Potential vectors present in New Zealand

Where pines occur naturally there is a substantial fauna of associated insects. For example, in North America (north of Mexico) over 1100 insect species have been recorded as feeding on pines, including about 30 introduced insect species (de Groot and Turgeon 1998). The majority of these species were classed as either monophagous (ca. 50%) or oligophagous (ca. 30%) (i.e., more or less specific to pines).

The New Zealand flora includes no native pines or any other native Pinaceae, and as a result there are no native insects that are closely associated with pines. However, several native insects, primarily polyphagous species, have colonised pines growing in New Zealand, usually occurring at low densities (e.g., Berndt et al. 2004). The most common insects found on pines in New Zealand are introduced species from the native range of pines, mainly from Europe and North America, such as a number of bark beetles and longhorned beetles (Brockerhoff et al. 2006).

To obtain an indication of the relative abundance of insects associated with pines in New Zealand we queried the *Forest Health Database* (maintained by Scion/New Zealand Forest Research Institute) (Bulman 1990). The database of forest health surveillance reports contains over 3000 records of formally identified insects. This provided a list of over 500 insect species although most of these represent incidental observations of species that do not feed on pines. Nevertheless, the results of this database query do reflect which pine-feeding insects are most commonly found on pines growing in New Zealand's plantation forests and as amenity trees. These common associates are most likely to play a role in the epidemiology of the pitch canker disease, should it become established in New Zealand. By contrast, insects that are only rarely found on pines are probably irrelevant, especially if they have no feeding or other close relationship. The 25 most commonly recorded insect species on pines in New Zealand (Table 2) represent all the feeding guilds of insects that have been considered overseas with regard to their association with pitch canker, except for pine cone insects (of which there are none in New Zealand), and predators or parasitoids (of which several were recorded but at low frequencies). These common associates were categorised with regard to the host status during attack (i.e., live or dead trees) using information from Scion's *Forest Health Database* and from the *Forest and Timber Insects* series (e.g., Brockerhoff and Hosking 2001). All species were then assessed for their potential to act as a wounding agent, carrier of *F. circinatum* inoculum, or vector (Table 2).

Currently there are no high-risk species in New Zealand that could act as vector of the pitch canker pathogen. Of the insect species that have been demonstrated to vector *F. circinatum* elsewhere, none are currently known to exist in New Zealand. *Ernobius mollis*, an alien anobiid, is the only species that occurs in New Zealand that has a congeneric species known to vector the pathogen in the United States. *Ernobius mollis* colonises and breeds mostly in dead trees and it is therefore unlikely to be able to vector the pathogen to live trees although it has occasionally been observed in Europe to colonize cones of *Pinus brutia, Pseudotsuga menziesii* and *Sequaiodendron gigantea* attacked by cone pyralids (Roques, 1983). Of the insects that have been recorded from *Pinus radiata* in New Zealand, it is those that feed subcortically on live trees or that wound live trees during exploratory host feeding (such as *Ips paraconfusus* and *Pityophthorus setosus* in California) that would represent the greatest concern regarding association with the pitch canker pathogen. No such species that is a confirmed vector is present in New Zealand (Table 2). Of the other species, *Hylastes ater* is a representative of a genus that is known to carry the pathogen in the United States (Storer et al 2004b). In Spain, *F. circinatum* has not been isolated from *H. ater*, however, another species in the same genus, *Hylastes attenuatus*, can be a carrier of the pathogen (Romón et al. 2007, 2008). Nevertheless, *Hylastes ater* is known to attack seedlings (for maturation feeding) and this could raise its risk status but based on current information, it is not thought to be a potential vector. *Sirex noctilio* is known to attack live pine trees but for several decades the species has been generally uncommon in New Zealand (Bain et al. 2011). Furthermore, it is not known to be a carrier of *F. circinatum* in any country where pitch canker occurs. Therefore, it is unlikely to become an important vector if *F. circinatum* became established in New Zealand.

Gadgil et al. (2003) list 14 sap-feeding species as potential vectors of the pitch canker pathogen in New Zealand, although most of these are not associated with pines. Among sap feeding species in California, only spittlebugs have been shown to be associated with pitch canker (Storer et al. 1998), even though other sap feeding species such as the Monterey pine scale, *Physokermes insignicola* (Homoptera: Coccidae), commonly occur in native and planted *Pinus radiata* forests in California. The absence of a spittlebug feeding on *Pinus radiata* in New Zealand and the apparent lack of association of the pathogen with other sap feeders suggests that these species should not be considered to be significant associates of *F. circinatum* in New Zealand.

Potential biological control agents for invasive pines

A preliminary evaluation of potential biological control agents against wilding pines in New Zealand was conducted by Brockerhoff and Kay (1998). The main target species was *Pinus* *contorta* because it is considered the most important invader. Also, this pine has not been planted in commercial plantations for several decades, and biocontrol using seed-feeding insects is therefore less controversial than against a target species that is economically important (Brockerhoff and Kay 1998). A number of criteria were applied in the selection of potential agents including: the candidate agent should have a host range that includes the target species and subspecies, be sufficiently host specific such that it would not attack non-target tree species, be compatible with the climate in the target region(s) in New Zealand, reduce seed production of the target species substantially, and be able to disperse to isolated tree populations. In addition, the agent should not have any other unwanted effects such as a potential contribution to tree disease dynamics (see below). The survey focussed on cone insects within the natural range of *Pinus contorta* and also on cone insects that have colonised the species in areas where the tree was introduced, especially in parts of Europe. Based on this, 16 species were assessed (Brockerhoff and Kay 1998) of which six species were considered to be potentially suitable and worthy of further consideration and research (Table 3). The other species were insufficiently host specific or attacked other parts of trees, which could affect tree growth.

The North American cone moth *Eucosma rescissoriana* can significantly reduce seed production, but this species was disregarded on the basis of its wider host range that covers firs (*Abies grandis*, *A. lasiocarpa*) and pines (*Pinus contorta*, *Pinus monticola* and possibly *Pinus albicaulis*; Hedlin et al., 1980). However, the host range of this species should be reviewed as all other species of *Eucosma* are genus-specific, and it is unusual that *Eucosma rescissoriana* attacks both firs and pines. Three other species, the anobiid *Ernobius nigrans*, the cerambycid *Paratimia conicola*, and the tortricid *Cydia toreuta*, may be sufficiently host specific but they usually have a more limited effect on seed production, at least in their natural geographic range. Most promising were the pine cone beetle *Conophthorus ponderosae*, a North American species, and *Pissodes* *validirostris*, the European pine cone weevil. Both these species have a narrow host range and the ability to reduce seed production considerably (Brockerhoff and Kay 1998; Brockerhoff et al. 2004). However, *Pissodes validirostris* appeared to be the most effective in terms of its effects on seed production, possibly because the two species did not co-evolve, and *Pinus contorta* may not have developed adaptations against this particular cone insect. Based on these findings, we prioritised *Pissodes validirostris* as the agent of first choice for more detailed consideration and for potential introduction to New Zealand.

Out of a total of 21 insect species known to develop in the cones of *Pinus* spp. in Europe and in the Mediterranean basin, *Pissodes validirostris* is the most damaging cone insect (Roques 1983; Roques & El Alaoui El Fels 2002). Most other species cause only minor damage. *Pissodes validirostris* is present all over the Palaearctic region from Portugal and Scandinavia to northern China (Roques 1983). Larvae of *Pissodes validirostris* develop exclusively in pine cones, tunneling through the tissues and destroying the seeds. They attack native pines of the subgenus *Pinus* such as *Pinus sylvestris*, *P. mugo*, *P. uncinata*, *P. nigra* and subspecies, and *P. leucodermis* which all belong to the subsection *Pinus* (Gernandt et al. 2005), as well as Mediterranean pines of the subsection *Pinaster*, such as *P. pinaster*, *P. halepensis*, and *P. pinea*) (Roques, 1983). Weevil attacks are also recorded on some North American pines widely planted in Europe such as lodgepole pine, *Pinus contorta* (Annila 1975; Delplanque et al. 1988), a species of the subgenus *Pinus* but from the section Trifoliae. Cone damage from *P. validirostris* was recently noticed in French arboreta on *Pinus hartwegii* (= *P. rudis*), a member of the subsection *Ponderosae* (Alain Roques, unpublished data). By contrast, the North American pines *Pinus radiata* and *P. taeda*, belonging to the subsection *Australes* of the subgenus *Pinus*, are not known to be attacked or damaged, despite the presence of large areas of planted forest of these species in parts of south-western Europe where *Pissodes validirostris* is generally very common on its normal hosts (Roques et al. 2004). In addition, native pine species in the subgenus *Strobus* such as Swiss stone pine (*Pinus cembra*), are avoided (Dormont and Roques 1999) as are exotic pines of the same subgenus, probably due to specific host volatiles (Dormont and Roques 2001). However, host-specificity tests revealed that there are different biotypes of *P. validirostris* which specialize on pines either of the subsection *Pinus* or of the subsection *Pinaster* (Roques et al. 2004). Recent molecular and morphometric studies confirmed that the species *Pissodes validirostris* probably incorporates discrete taxa, or at least independent evolutionary lineages. At least three phylogeographic lineages were identified corresponding to the populations of the Iberian Peninsula, Central Europe and Northern/ Eastern Europe, respectively, which correspond to the differences in host plant preferences (Géraldine Roux, pers. comm.). Populations that colonized *Pinus contorta* are more closely associated with Central and Northern European populations on *Pinus sylvestris* than with those developing on Mediterranean pines (Roques et al. 2004; Géraldine Roux, pers. comm.). This suggests that *Pinus sylvestris* was the original host for these populations. In no-choice host selection experiments, both biotypes of *Pissodes* were capable of laying eggs on cones of *Pinus radiata*, but only the larvae originating from populations of the *Pinus sylvestris* biotype were capable of completing their development in these cones (Roques et al. 2004).

Cone damage by *Pissodes validirostris* greater than 80% has been reported from natural stands of *Pinus pinea* in Spain (Bachiller 1966) and of *Pinus sylvestris* and *Pinus uncinata* in France (Roques 1977; Roques et al. 1983). However, *Pinus contorta* appears to be significantly more attacked than *Pinus sylvestris* when these two species are planted in proximity. In Finland, 42% - 94% of *Pinus contorta* cones were damaged by *Pissodes validirostris* compared with 1% - 55% of *Pinus sylvestris* (Annila and Hiltunen 1977). In central France, cone damage in *Pinus contorta* was nearly twice the damage in *P. sylvestris* (82.0% vs. 46.3%) (Delplanque et al. 1988). Larvae of *Pissodes validirostris* affect seed yield by direct feeding and by inducing resin bleeding (Roques 1976). Resin bleeding reduces seed dispersal by preventing the cone scales from opening (Roques 1976). In *Pinus sylvestris*, 3-4 larvae of *P. validirostris* are enough to destroy a cone completely (Roques 1976), but in pine species with larger cones (e.g., *Pinus pinaster*) the number of larvae must be greater than four to get the same result. In the small-sized cones of *Pinus contorta*, each weevil larva is responsible for a loss of 40 to 60% of the seed content (Delplanque et al. 1988) whilst the presence of 2 larvae per cone increases seed loss to ca. 80% (Annila 1975).

Risks associated with introducing biocontrol agents against invasive pines

Based on the available information about potential effectiveness and non-target impacts, the most promising potential biocontrol agents against wilding pines in New Zealand are the ponderosa pine cone beetle, *Conophthorus ponderosae*, and the pine cone weevil, *Pissodes validirostris* (Brockerhoff and Kay 1998, above). In addition, the lodgepole pine cone moth, *Eucosma rescissoriana*, could be considered if it can be determined that it is sufficiently host specific. There are important issues that need to be addressed concerning the risk of these insects becoming vectors of the pitch canker pathogen and thereby causing unwanted damage of pines in planted forests. Biocontrol agents that enter the host tissues (as opposed to feeding externally) have a high potential to act as vectors of the pitch canker pathogen. In addition, those that cause wounds to branches and stems may also act as vectors as has been shown for twig beetles in the Western United States (e.g. Storer et al. 2004a).

Conophthorus ponderosae has a congeneric species that is a confirmed vector of the pathogen in California and therefore it may be a vector in New Zealand. Although *Pinus radiata* is not a known host species (Storer et al. 2004b), a host switch could occur.

The lodgepole pine cone moth, *Eucosma rescissoriana*, may become associated with the pitch canker pathogen as a vector or as a wounding agent. A shift in habit by this species to include the shoot feeding habit exhibited by other members of the genus could also increase the significance of any association with the pathogen.

Although larval and pupal development of *Pissodes validirostris* occurs entirely in seed cones, adult weevils require maturation feeding, typically on the pine leader shoots, in spring in order to become sexually mature and capable of laying eggs on cones (Roques 1976). Another period of feeding on leader shoots is observed in autumn before the adults settle to overwinter in the bark of the trees (Roques et al. 2004). In contrast to egg-laying, behavioral tests showed that the different biotypes of *Pissodes validirostris* can feed on the shoots of a large number of pine species. Such damage did not appear to affect plant health (Roques et al. 2004), but it may help fungal transmission. Fresh adults washed immediately after emergence from the cones did not carry any *F. circinatum* conidia (Lennox et al. 2009). In an experiment, feeding on *Pinus radiata* seedlings by adult *P. validirostria* that had been artificially infected with *F. circinatum* did not show any transmission of conidia. However, its feeding damage appeared to facilitate the ingress of the fungus into the host plant (Lennox et al. 2009).

Based on these findings, it cannot be ruled out that *Pissodes validirostris*, if it were introduced to New Zealand, could act as a vector of *F. circinatum* should the pathogen become established there. The behavior of this species would allow several types of association with the pitch canker pathogen including spreading the pathogen by dissemination through adults emerging with the pathogen, inoculation of the pathogen during egg laying and adult feeding, ingression through egg laying, adult and larval feeding, and invasion during larval feeding. The most likely responsible mechanism is the maturation feeding behaviour of this weevil. Furthermore, *Pissodes validirostris* has a demonstrated ability to colonise new hosts, such as *Pinus contorta*, and this represents a new insect-host plant association. The potential for additional changes in host use in new environments cannot be ruled out. If *Pissodes validirostris* were to colonise and damage cones of *Pinus radiata*, then it could also affect breeding programmes and the production of seed for nurseries.

Conclusions

The pitch canker disease caused by the pathogen *F. circinatum* represents a major threat to pine forests worldwide. *Pinus radiata* is one of the most susceptible pines, and it is an important tree in planted forests in New Zealand and several other countries where *F. circinatum* does not yet occur. In New Zealand, this risk is moderated by the fact that no known vectors of *F. circinatum* are present. Our review identified several species that could play a role in the epidemiology of the disease in New Zealand, as wounding agents or carriers of the pathogen, but no insects appear to be present that could act as effective vectors. Against this background, the proposed introduction of biocontrol agents against invasive *Pinus contorta* or other pines has been deemed too risky, mainly because of the pitch canker pathogen vectoring issue (Dick and Bain 2004). Furthermore, it is not certain how effective a biocontrol agent would be in terms of reducing the spread of wilding pines. While the success of past biocontrol introductions has been high, with 83% providing partial or complete control of target plants, seed eating agents have perhaps been less effective (Fowler et al. 2000; Suckling 2013). A similar proposal to introduce seed eating insects for the control of invasive pines has been considered in South Africa (Hoffmann et al. 2011). Recently it has been decided not to pursue this further due to risks associated with pitch canker in South Africa where the disease is already present, and because of questions about the effectiveness of biocontrol relying solely on cone and seed insects (Lennox et al. 2009). Further research on insects present in New Zealand and on potential biocontrol agents could be conducted in regions where these species occur and where *F. circinatum* is also present (e.g., Spain and South Africa for some of the European insects). This would assist with further risk assessments and possible future incursion responses.

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Table 1. Insects associated with *Fusarium circinatum* in regions where pitch canker occurs and the nature of their association. See Supplementary Table S1 for an alphabetical listing of insect species.

Species (* non-indigenous sp.)	Order, family (subfamily)	Wounding agent[a]	Carrier[a]	Confirmed vector[a]	References
USA (SOUTH-EAST)					
Bark beetles and wood borers					
Pissodes nemorensis	Col., Curculionidae, Molytinae	+	+		Blakeslee et al. 1978, Blakeslee and Foltz 1981
Shoot and foliage-feeders					
Rhyacionia spp.	Lepidoptera, Tortricidae	+			Matthews 1962
Contarinia spp.	Diptera, Cecidomyiidae	+			Dwinell et al. 1985
Cone insects					
Cydia spp.	Lepidoptera, Tortricidae	+			Dwinell et al. 1985
Leptoglossus corculus	Heteroptera, Coreidae	+			Dwinell et al. 1985
USA (CALIFORNIA)					
Bark beetles and wood borers					
Ips paraconfusus	Col., Curculionidae, Scolytinae	+	+	+	Fox et al. 1991
Ips mexicanus,	Col., Curculionidae, Scolytinae	(+)	+	(+)	Fox et al. 1991, Erbilgin et al. 2008
Ips plastographus maritimus	Col., Curculionidae, Scolytinae	(+)	+	(+)	Fox et al. 1991, Erbilgin et al. 2008
Pityophthorus setosus	Col., Curculionidae, Scolytinae	+	+	+	Hoover et al. 1995, Storer et al. 2004a, Erbilgin et al. 2005
Pityophthorus carmeli	Col., Curculionidae, Scolytinae	+	+	(+)	Hoover et al. 1995, Storer et al. 2004a, Erbilgin et al. 2005
Hylastes spp.	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
Hylurgops spp.	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
Dendroctonus valens	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
Pissodes radiatae	Col., Curculionidae, Molytinae?	(+)	+		Storer et al. 2004b
Sapsuckers					
Aphrophora canadensis	Homoptera, Cercopidae	+			Storer et al. 1998
Shoot and foliage-feeders					
(none)					
Cone insects					
Conophthorus radiatae	Col., Curculionidae, Scolytinae	+	+	+	Hoover et al. 1995, 1996
Ernobius punctulatus	Col., Anobiidae		+	+	Hoover et al. 1995, 1996
Predatory insects					
Enoclerus sphegeus	Col., Cleridae		+		Dallara 1997, Storer et al. 2004b
Lasconotus spp.	Col., Colydiidae		+		Dallara 1997, Storer et al. 2004b
Medetera spp.	Dipt: Dolychopodidae		+		Storer et al., 2004b
Non-insect taxa					
Snails and Pillbugs/Sowbugs	Mollusca and Crustacea (Isopoda)		+		Storer et al., 2004b

SOUTH AFRICA					
Shoot and foliage-feeders					
*Pissodes nemorensis**	Col., Curculionidae, Molytinae	(+)	(?)	(?)	Coutinho et al. 2007
Bradysia difformis	Diptera, Sciaridae	(?)			Hurley et al. 2007
CHILE					
Bark beetles and wood borers					
*Hylastes ater**	Col., Curculionidae, Scolytinae	(+)			Wingfield et al. 2008
JAPAN					
None (?, see text)					Viljoen et al. 1997
SPAIN					
Bark beetles and wood borers					
Hylastes attenuatus	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
Hylurgops palliatus	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
Hypothenemus eruditus	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
Ips sexdentatus	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
Orthotomicus erosus	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
Pissodes castaneus	Col., Curculionidae, Molytinae	(+)	+		Iturritxa et al. 2011
Pityophthorus pubescens	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007, Iturritxa et al. 2011
Tomicus piniperda	Col., Curculionidae, Scolytinae	(+)	+		Iturritxa et al. 2011
Cone insects					
Pissodes validirostris	Col., Curculionidae, Molytinae	+	(?)		Roques et al. 2004, Lennox et al. 2009
Root borers					
Brachyderes incanus	Col., Curculionidae, Entiminae	(+)	+		Romón et al. 2007

[a] Nature of association: +, confirmed association; (+), presumed association not yet verified; (?), suspected but less likely or unknown association (for details see text)

Table 2. Insects present in New Zealand that may act as associates with *Fusarium circinatum*.

Species (* non-indigenous sp.)	Family (subfamily)	Origin (native region)	Attacks live (L) or dead plants (D)[a]	Potential pitch canker association[b]
Bark beetles and wood borers				
*Hylastes ater**	Curculionidae, Scolytinae	Europe	(L)[a] D	W, C
*Hylurgus ligniperda**	Curculionidae, Scolytinae	Europe	D	C
Pachycotes peregrinus	Curculionidae, Scolytinae	NZ	D	C
Platypus apicalis	Curculionidae, Platypodinae	NZ	D	C
*Arhopalus ferus**	Cerambycidae	Europe	(L)[a] D	(W), C
Calliprason pallidus	Cerambycidae	NZ	D	C
Hexatricha pulverulenta	Cerambycidae	NZ	(L)[a] D	C
Oemona hirta	Cerambycidae	NZ	(L)[a] D	(W), (C)
Prionoplus reticularis	Cerambycidae	NZ	D	C
*Ernobius mollis**	Anobiidae	Cosmopolitan	D	C
*Sirex noctilio**	Siricidae	Europe	L	C
Mitrastethus baridioides	Curculionidae, Cryptorhynchinae	NZ	D	(C)
Pycnomerus sophorae	Colydiidae	NZ	D	(C)
Shoot and foliage-feeders				
Pseudocoremia suavis	Geometridae	NZ	L	W, (C)
Hierodoris atychioides	Oecophoridae	NZ	L	W, (C)
Ctenopseustis obliquana	Tortricidae	NZ	L	W, (C)
*Epiphyas postvittana**	Tortricidae	Australia	L	W, (C)
Planotortrix notophaea	Tortricidae	NZ	L	W, (C)
Sapsuckers				
*Pineus boerneri**	Adelgidae	USA	L	(W), (C)
*P. pini**	Adelgidae	Europe	L	(W), (C)
*Essigella californica**	Aphididae	USA	L	(W), (C)
*Eulachnus brevipilosus**	Aphididae	Europe	L	(W), (C)
*Heliothrips haemorrhoidalis**	Thripidae	Cosmopolitan?	L	(W), (C)
Cone insects				
Erechthias fulguritella	Tineidae	NZ	(?)	(?)

[a] *Hylates ater* sometimes attacks pine seedlings for maturation feeding; *Arhopalus ferus* has been recorded as attacking live trees but this is rare and probably limited to fire-damaged trees; *Hexatricha pulverulenta* sometimes breeds in pines, always dead trees, but occasionally it feeds on green twigs of pine (Bain and Hosking 1988); *Oemona hirta* is normally associated with hardwood trees and attacks of softwoods are very rare (Hosking 1978).

[b] Possible association in case of establishment of *F. circinatum* in New Zealand: W, wounding agent of live trees; C, carrier; V, vector; values in brackets indicate uncertainty of association; (see text for details).

Table 3. Most promising candidate agents for biocontrol of *Pinus contorta* in New Zealand[a], their characteristics, and potential for involvement with the pitch canker disease.

Species	Family (subfamily)	Host range[b]	Host structures attacked	Potential pitch canker association[e]
Coleoptera				
Conophthorus ponderosae	Curculionidae	*Pinus* spp., not *P. radiata*	Only seed cones	W, C, (V)
Ernobius nigrans	Anobiidae	*Pinus* spp., not *P. radiata*	Only seed cones	W, C, (V)
Paratimia conicola	Cerambycidae	*Pinus* spp., not *P. radiata*	Only seed cones	W, C, (V)
Pissodes validirostris	Curculionidae	*Pinus* spp., not *P. radiata*[c]	Mainly seed cones[d]	W, C, (V)
Lepidoptera				
Cydia toreuta	*Tortricidae*	*Pinus* spp., not *P. radiata*	Only seed cones	W, C, (V?)
Eucosma rescissoriana	*Tortricidae*	*Pinus* and *Abies* spp., not *P. radiata*	Only seed cones	W, C, (V?)

[a] Preliminary selection of potential agents according to Brockerhoff and Kay (1998) and Brockerhoff et al. (2004)

[b] Host range information based on Keen (1958), Hedlin et al. (1980) and other publications listed in Brockerhoff and Kay (1998).

[c] Depending on the subspecies / host race of *P. validirostris* (see text).

[d] Maturation feeding, apparently causing little damage, may occur on shoots (see text).

[e] Possible association in case of establishment of *Fusarium circinatum* in New Zealand: W, wounding agent of live trees; C, carrier; V, vector; values in brackets indicate uncertainty of association; (for details see text)