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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, 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

49 native specialised insect herbivores. Occasionally, some native insects attack pines, although
 50 their direct impact is mostly benign. However, several insect pests of pines have become
 51 introduced over the years. Preliminary reviews of the role of insects associated with pines in New
 52 Zealand as potential vectors of *F. circinatum* have been provided by Gadgil et al. (2003) and
 53 Storer et al. (2004b). Currently, there appear to be few insects in New Zealand that are likely to
 54 act as vectors of the fungus, and this may limit the spread of the fungus and its impact on pine
 55 plantations, if it ever became established there. However, a formal analysis of the potential
 56 vectors of *F. circinatum* in New Zealand is not available.

57
 58 Knowledge about any potential disease vectors and other insect associates is necessary to enable
 59 an informed response in the event of an incursion of *F. circinatum* and to evaluate the risk of
 60 spread (Gadgil et al. 2003; Ganley 2007; Fourrier et al. 2015). The vector issue is also important
 61 for an assessment of the risk of the potential intentional introduction of seed-feeding insects for
 62 biological control of wilding (invasive) *Pinus contorta* Loudon. Several pine species are now
 63 considered environmental weeds in New Zealand and other southern hemisphere countries
 64 (Richardson and Higgins 1998; Rundel et al. 2014). In some regions of New Zealand, pines have
 65 invaded natural or semi-natural grassland and scrub communities (Ledgard 1998). Although
 66 plantings of *Pinus contorta* were of limited extent, this species is now considered the most
 67 serious invader among the pines (Ledgard 1998). Options for biological control have been
 68 assessed (Brockhoff and Kay 1998; Brockhoff et al. 2004). Because several pine species are
 69 highly valued in plantation forestry and also in urban amenity plantings, the potential use of cone
 70 and seed insects is a favoured approach as such insects may reduce the spread of pines without
 71 affecting growth or causing damage to other parts of trees. In addition, most cone and seed
 72 insects are specialised, adapted species that exhibit a high degree of host plant specificity
 73 (Turgeon et al. 1994), therefore limiting risks to non-target plants. On the other hand, seed-eating

74 insects may not be as effective as other types of biocontrol agents, and it remains to be
 75 determined whether their effect actually reduces plant spread rates (e.g., Rees and Paynter 1997).
 76 Based on a review of cone and seed insects that attack *Pinus contorta*, considering host
 77 specificity, potential impact on seed production and other criteria, some insects are thought to
 78 show promise as potential biocontrol agents, both in New Zealand and South Africa (Brockhoff
 79 and Kay 1998; Brockhoff et al. 2004; Roques et al. 2004). However, it is feared that the
 80 introduction of such insects to New Zealand would greatly increase the risks associated with *F.*
 81 *circinatum* because the biocontrol agent may act as an additional, and potentially important,
 82 vector of the pitch canker pathogen. In South Africa, such concerns have halted plans to
 83 introduce a cone insect for biocontrol of invasive pines (Lennox et al. 2009), although there is
 84 renewed interest in the approach.

85
 86 Here we review the role of insects in the epidemiology of pitch canker world-wide and assess
 87 which insects present in New Zealand may act as vectors. We also review the preliminary
 88 selection of biocontrol agents against invasive pines and explore the risks of introducing such
 89 biocontrol agents to New Zealand, particularly with regard to our current knowledge about
 90 implications for vectoring *F. circinatum*. Our specific objectives are:

- 91 i. to provide an overview of the insects associated with pitch canker and their role in
- 92 disease epidemiology in the countries where the disease occurs to date;
- 93 ii. to review the native and introduced insects found on pines in New Zealand, to determine
- 94 the likelihood of these species acting as vectors of *F. circinatum*;
- 95 iii. to evaluate the insects potentially suitable for biocontrol of *Pinus contorta* in New
- 96 Zealand and to assess the risk of their introduction in relation to the potential
- 97 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).

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

135
 136 To assess the role of insects in the infection of trees by *F. circinatum* and the epidemiology of the
 137 disease, it is important to consider the life cycles of both the pathogen and potential vectors and
 138 the nature of potential interactions between these organisms. Fruit bodies of *F. circinatum*
 139 (known as sporodochia) containing thousands of asexual spores (conidia) may be produced on
 140 the surface of infected tissues when conditions are moist. These are dispersed by water-splash
 141 and can be carried in air currents throughout the year (Blakeslee et al. 1978; Correll et al. 1991).
 142 Spores can also be recovered from the surface bark of trees even when fruit bodies are not readily
 143 apparent (Adams et al. 1999). Two rounds of studies have been conducted where spore
 144 suspensions were sprayed on small trees in the field and the branches were then baited with twig
 145 beetle pheromones (Sakamoto et al. 2007). The results showed no difference in disease between
 146 treated and untreated trees. It is likely that spore loads were very high in these studies compared

147 with what occurs naturally. It seems likely that the insects pick up spores in the tree, perhaps
 148 while chewing their way out through diseased tissue. Insects coming into contact with the
 149 sporodochia may readily pick up many of the sticky spores that are likely to adhere to the surface
 150 of the body and be trapped amongst hairs and other surface structures (e.g., Yamoah et al. 2011).
 151 Fox et al. (1990) reported the isolation of the pathogen from galleries of *Ips* spp. in *Pinus radiata*
 152 trees. The beetles carry propagules that presumably can include hyphal fragments as well as
 153 spores. By contrast, it is likely that the importance of casually acquiring spores from the tree
 154 surface is low. The risk of transmission appears to vary at different times of the year according to
 155 propagule loads on two *Ips* species (Erbilgin et al. 2008). Spore loads of twig beetles were
 156 considered an important factor in studies of the vector efficiency (Erbilgin et al. 2009).
 157
 158 Once infection has occurred the fungus colonises the sapwood and can be readily isolated from
 159 discoloured or resinous tissues (McCain et al. 1987; Correll et al. 1991). However, the fungus
 160 does not spread great distances within the wood. Infection of a cone, or a cone whorl, vectored by
 161 cone insects or other borers leads to death of the branch beyond the cone, with each dead branch
 162 being the result of a separate infection. Although unsightly, the branch and twig death that would
 163 result from infections transmitted by cone and seed insects would probably have relatively little
 164 impact on tree growth. Lesions on branches girdle the branch so the distal portion dies; spread
 165 down the branch or shoot is usually arrested at the node (Dwinell et al 1985; Gordon et al. 2001).
 166 Individual trees may thus sustain crown infections for many years. However, crown dieback can
 167 be extensive due to the multiple infections. Trunk infections are often initiated by bark beetles,
 168 and tree death will follow girdling of the stem from a number of separate infections and/or
 169 attacks by bark beetles. Multiple trunk attacks are required in order to kill the cambium around
 170 the circumference and for tree death to result (Gordon et al. 2001; Storer et al. 2002). Bark

171 beetles (especially *Ips* spp. and *Dendroctonus* spp.) can cause considerable mortality of pines
 172 also in the absence of any other disease agents (e.g., Six and Wingfield 2011).
 173
 174 In the absence of insects vectoring *F. circinatum* to the trunk of the trees, any stem infections
 175 would be initiated through infection of wounds created by other causes including weather events
 176 (such as wind and hail), pruning or cone collection (Dwinell et al. 1985; Gordon et al. 2001). In
 177 New Zealand, wounds could also occur from bark stripping by native parrots (Dick 1998),
 178 although this is rare.
 179
 180 Spread of the pitch canker disease in nurseries is different from what occurs in forests. The
 181 fungus has been reported to be capable of spreading through nurseries very rapidly, with
 182 devastating losses recorded (Viljoen et al. 1994). Unlike in older trees, wounds are not required
 183 for infection of young seedlings. Insect-vectored transmission is apparently not important (Hurley
 184 et al. 2007). Unfortunately, in contrast to the majority of pine nursery diseases where diligent
 185 application of fungicides will generally reduce the impacts of pathogens, chemical control of
 186 pitch canker disease has been found to be relatively ineffective (M.J. Wingfield pers. com.).
 187 However, rigorous sanitation procedures can reduce disease incidence to insignificant levels in a
 188 nursery where all plants are containerised (Van Wyk et al. 2012). Based on this knowledge, we
 189 can predict with reasonable confidence the outcome of an introduction of *F. circinatum* to a
 190 nursery in New Zealand where plants are reared both as bare root in nursery beds and in
 191 containers (Gadgil et al. 2003). Eradication attempts are likely to result in nursery closure while
 192 soil fumigation is undertaken followed by a high level of sanitation. Although insects are not
 193 thought to be important in the disease epidemiology within nurseries, certain insects may be
 194 involved in spreading the disease from nurseries to surrounding forests. It is more likely that

195 transmission of the fungus to a plantation would occur via out planting of asymptomatic infected
 196 seedlings from a nursery than by insects.

197

198

199 **Potential vectors present in New Zealand**

200

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

206

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

213

214 To obtain an indication of the relative abundance of insects associated with pines in New
 215 Zealand we queried the *Forest Health Database* (maintained by Scion/New Zealand Forest
 216 Research Institute) (Bulman 1990). The database of forest health surveillance reports contains
 217 over 3000 records of formally identified insects. This provided a list of over 500 insect species
 218 although most of these represent incidental observations of species that do not feed on pines.
 219 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 *Sequoiadendron 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

245 in New Zealand (Table 2). Of the other species, *Hylastes ater* is a representative of a genus that
 246 is known to carry the pathogen in the United States (Storer et al 2004b). In Spain, *F. circinatum*
 247 has not been isolated from *H. ater*, however, another species in the same genus, *Hylastes*
 248 *attenuatus*, can be a carrier of the pathogen (Romón et al. 2007, 2008). Nevertheless, *Hylastes*
 249 *ater* is known to attack seedlings (for maturation feeding) and this could raise its risk status but
 250 based on current information, it is not thought to be a potential vector. *Sirex noctilio* is known to
 251 attack live pine trees but for several decades the species has been generally uncommon in New
 252 Zealand (Bain et al. 2011). Furthermore, it is not known to be a carrier of *F. circinatum* in any
 253 country where pitch canker occurs. Therefore, it is unlikely to become an important vector if *F.*
 254 *circinatum* became established in New Zealand.

255
 256 Gadgil et al. (2003) list 14 sap-feeding species as potential vectors of the pitch canker pathogen
 257 in New Zealand, although most of these are not associated with pines. Among sap feeding
 258 species in California, only spittlebugs have been shown to be associated with pitch canker (Storer
 259 et al. 1998), even though other sap feeding species such as the Monterey pine scale, *Physokermes*
 260 *insignicola* (Homoptera: Coccidae), commonly occur in native and planted *Pinus radiata* forests
 261 in California. The absence of a spittlebug feeding on *Pinus radiata* in New Zealand and the
 262 apparent lack of association of the pathogen with other sap feeders suggests that these species
 263 should not be considered to be significant associates of *F. circinatum* in New Zealand.

264

265

266 **Potential biological control agents for invasive pines**

267

268 A preliminary evaluation of potential biological control agents against wilding pines in New
 269 Zealand was conducted by Brouckhoff and Kay (1998). The main target species was *Pinus*

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

285
 286 The North American cone moth *Eucosma rescissoriana* can significantly reduce seed production,
 287 but this species was disregarded on the basis of its wider host range that covers firs (*Abies*
 288 *grandis*, *A. lasiocarpa*) and pines (*Pinus contorta*, *Pinus monticola* and possibly *Pinus*
 289 *albicaulis*; Hedlin et al., 1980). However, the host range of this species should be reviewed as all
 290 other species of *Eucosma* are genus-specific, and it is unusual that *Eucosma rescissoriana* attacks
 291 both firs and pines. Three other species, the anobiid *Ernobius nigrans*, the cerambycid *Paratimia*
 292 *conicola*, and the tortricid *Cydia toreuta*, may be sufficiently host specific but they usually have a
 293 more limited effect on seed production, at least in their natural geographic range. Most promising
 294 were the pine cone beetle *Conophthorus ponderosae*, a North American species, and *Pissodes*

295 *validirostris*, the European pine cone weevil. Both these species have a narrow host range and
 296 the ability to reduce seed production considerably (Brockerhoff and Kay 1998; Brockerhoff et al.
 297 2004). However, *Pissodes validirostris* appeared to be the most effective in terms of its effects
 298 on seed production, possibly because the two species did not co-evolve, and *Pinus contorta* may
 299 not have developed adaptations against this particular cone insect. Based on these findings, we
 300 prioritised *Pissodes validirostris* as the agent of first choice for more detailed consideration and
 301 for potential introduction to New Zealand.

302
 303 Out of a total of 21 insect species known to develop in the cones of *Pinus* spp. in Europe and in
 304 the Mediterranean basin, *Pissodes validirostris* is the most damaging cone insect (Roques 1983;
 305 Roques & El Alaoui El Fels 2002). Most other species cause only minor damage. *Pissodes*
 306 *validirostris* is present all over the Palaearctic region from Portugal and Scandinavia to northern
 307 China (Roques 1983). Larvae of *Pissodes validirostris* develop exclusively in pine cones,
 308 tunneling through the tissues and destroying the seeds. They attack native pines of the subgenus
 309 *Pinus* such as *Pinus sylvestris*, *P. mugo*, *P. uncinata*, *P. nigra* and subspecies, and *P.*
 310 *leucodermis* which all belong to the subsection *Pinus* (Gernandt et al. 2005), as well as
 311 Mediterranean pines of the subsection *Pinaster*, such as *P. pinaster*, *P. halepensis*, and *P. pinea*)
 312 (Roques, 1983). Weevil attacks are also recorded on some North American pines widely planted
 313 in Europe such as lodgepole pine, *Pinus contorta* (Annala 1975; Delplanque et al. 1988), a
 314 species of the subgenus *Pinus* but from the section *Trifoliae*. Cone damage from *P. validirostris*
 315 was recently noticed in French arboreta on *Pinus hartwegii* (= *P. rudis*), a member of the
 316 subsection *Ponderosae* (Alain Roques, unpublished data). By contrast, the North American
 317 pines *Pinus radiata* and *P. taeda*, belonging to the subsection *Austerales* of the subgenus *Pinus*,
 318 are not known to be attacked or damaged, despite the presence of large areas of planted forest of
 319 these species in parts of south-western Europe where *Pissodes validirostris* is generally very

320 common on its normal hosts (Roques et al. 2004). In addition, native pine species in the
 321 subgenus *Strobos* such as Swiss stone pine (*Pinus cembra*), are avoided (Dormont and Roques
 322 1999) as are exotic pines of the same subgenus, probably due to specific host volatiles (Dormont
 323 and Roques 2001). However, host-specificity tests revealed that there are different biotypes of *P.*
 324 *validirostris* which specialize on pines either of the subsection *Pinus* or of the subsection
 325 *Pinaster* (Roques et al. 2004). Recent molecular and morphometric studies confirmed that the
 326 species *Pissodes validirostris* probably incorporates discrete taxa, or at least independent
 327 evolutionary lineages. At least three phylogeographic lineages were identified corresponding to
 328 the populations of the Iberian Peninsula, Central Europe and Northern/ Eastern Europe,
 329 respectively, which correspond to the differences in host plant preferences (Géraldine Roux, pers.
 330 comm.). Populations that colonized *Pinus contorta* are more closely associated with Central and
 331 Northern European populations on *Pinus sylvestris* than with those developing on Mediterranean
 332 pines (Roques et al. 2004; Géraldine Roux, pers. comm.). This suggests that *Pinus sylvestris* was
 333 the original host for these populations. In no-choice host selection experiments, both biotypes of
 334 *Pissodes* were capable of laying eggs on cones of *Pinus radiata*, but only the larvae originating
 335 from populations of the *Pinus sylvestris* biotype were capable of completing their development in
 336 these cones (Roques et al. 2004).

337
 338 Cone damage by *Pissodes validirostris* greater than 80% has been reported from natural stands of
 339 *Pinus pinea* in Spain (Bachiller 1966) and of *Pinus sylvestris* and *Pinus uncinata* in France
 340 (Roques 1977; Roques et al. 1983). However, *Pinus contorta* appears to be significantly more
 341 attacked than *Pinus sylvestris* when these two species are planted in proximity. In Finland, 42% -
 342 94% of *Pinus contorta* cones were damaged by *Pissodes validirostris* compared with 1% - 55%
 343 of *Pinus sylvestris* (Annala and Hiltunen 1977). In central France, cone damage in *Pinus contorta*
 344 was nearly twice the damage in *P. sylvestris* (82.0% vs. 46.3%) (Delplanque et al. 1988). Larvae

345 of *Pissodes validirostris* affect seed yield by direct feeding and by inducing resin bleeding
 346 (Roques 1976). Resin bleeding reduces seed dispersal by preventing the cone scales from
 347 opening (Roques 1976). In *Pinus sylvestris*, 3-4 larvae of *P. validirostris* are enough to destroy a
 348 cone completely (Roques 1976), but in pine species with larger cones (e.g., *Pinus pinaster*) the
 349 number of larvae must be greater than four to get the same result. In the small-sized cones of
 350 *Pinus contorta*, each weevil larva is responsible for a loss of 40 to 60% of the seed content
 351 (Delplanque et al. 1988) whilst the presence of 2 larvae per cone increases seed loss to ca. 80%
 352 (Annala 1975).

353

354

355 **Risks associated with introducing biocontrol agents against invasive pines**

356

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

368

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

372

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

377

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

390

391 Based on these findings, it cannot be ruled out that *Pissodes validirostris*, if it were introduced to
 392 New Zealand, could act as a vector of *F. circinatum* should the pathogen become established
 393 there. The behavior of this species would allow several types of association with the pitch canker

394 pathogen including spreading the pathogen by dissemination through adults emerging with the
 395 pathogen, inoculation of the pathogen during egg laying and adult feeding, ingress through
 396 egg laying, adult and larval feeding, and invasion during larval feeding. The most likely
 397 responsible mechanism is the maturation feeding behaviour of this weevil. Furthermore, *Pissodes*
 398 *validirostris* has a demonstrated ability to colonise new hosts, such as *Pinus contorta*, and this
 399 represents a new insect-host plant association. The potential for additional changes in host use in
 400 new environments cannot be ruled out. If *Pissodes validirostris* were to colonise and damage
 401 cones of *Pinus radiata*, then it could also affect breeding programmes and the production of seed
 402 for nurseries.

403

404

405 **Conclusions**

406

407 The pitch canker disease caused by the pathogen *F. circinatum* represents a major threat to pine
 408 forests worldwide. *Pinus radiata* is one of the most susceptible pines, and it is an important tree
 409 in planted forests in New Zealand and several other countries where *F. circinatum* does not yet
 410 occur. In New Zealand, this risk is moderated by the fact that no known vectors of *F. circinatum*
 411 are present. Our review identified several species that could play a role in the epidemiology of
 412 the disease in New Zealand, as wounding agents or carriers of the pathogen, but no insects appear
 413 to be present that could act as effective vectors. Against this background, the proposed
 414 introduction of biocontrol agents against invasive *Pinus contorta* or other pines has been deemed
 415 too risky, mainly because of the pitch canker pathogen vectoring issue (Dick and Bain 2004).
 416 Furthermore, it is not certain how effective a biocontrol agent would be in terms of reducing the
 417 spread of wilding pines. While the success of past biocontrol introductions has been high, with
 418 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					
<i>Pissodes nemorensis</i>	Col., Curculionidae, Molytinae	+	+		Blakeslee et al. 1978, Blakeslee and Foltz 1981
Shoot and foliage-feeders					
<i>Rhyacionia</i> spp.	Lepidoptera, Tortricidae	+			Matthews 1962
<i>Contarinia</i> spp.	Diptera, Cecidomyiidae	+			Dwinell et al. 1985
Cone insects					
<i>Cydia</i> spp.	Lepidoptera, Tortricidae	+			Dwinell et al. 1985
<i>Leptoglossus corculus</i>	Heteroptera, Coreidae	+			Dwinell et al. 1985
USA (CALIFORNIA)					
Bark beetles and wood borers					
<i>Ips paraconfusus</i>	Col., Curculionidae, Scolytinae	+	+	+	Fox et al. 1991
<i>Ips mexicanus</i> ,	Col., Curculionidae, Scolytinae	(+)	+	(+)	Fox et al. 1991, Erbilgin et al. 2008
<i>Ips plastographus maritimus</i>	Col., Curculionidae, Scolytinae	(+)	+	(+)	Fox et al. 1991, Erbilgin et al. 2008
<i>Pityophthorus setosus</i>	Col., Curculionidae, Scolytinae	+	+	+	Hoover et al. 1995, Storer et al. 2004a, Erbilgin et al. 2005
<i>Pityophthorus carmeli</i>	Col., Curculionidae, Scolytinae	+	+	(+)	Hoover et al. 1995, Storer et al. 2004a, Erbilgin et al. 2005
<i>Hylastes</i> spp.	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
<i>Hylurgops</i> spp.	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
<i>Dendroctonus valens</i>	Col., Curculionidae, Scolytinae	(+)	+		Storer et al. 2004b
<i>Pissodes radiatae</i>	Col., Curculionidae, Molytinae?	(+)	+		Storer et al. 2004b
Sapsuckers					
<i>Aphrophora canadensis</i>	Homoptera, Cercopidae	+			Storer et al. 1998
Shoot and foliage-feeders (none)					
Cone insects					
<i>Conophthorus radiatae</i>	Col., Curculionidae, Scolytinae	+	+	+	Hoover et al. 1995, 1996
<i>Ernobius punctulatus</i>	Col., Anobiidae		+	+	Hoover et al. 1995, 1996
Predatory insects					
<i>Enoclerus sphegeus</i>	Col., Cleridae		+		Dallara 1997, Storer et al. 2004b
<i>Lasconotus</i> spp.	Col., Colydiidae		+		Dallara 1997, Storer et al. 2004b
<i>Medetera</i> spp.	Dipt: Dolychopodidae		+		Storer et al., 2004b
Non-insect taxa					
Snails and Pillbugs/Sowbugs	Mollusca and Crustacea (Isopoda)		+		Storer et al., 2004b

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SOUTH AFRICA**Shoot and foliage-feeders**

<i>Pissodes nemorensis</i> *	Col., Curculionidae, Molytinae	(+)	(?)	(?)	Coutinho et al. 2007
<i>Bradysia difformis</i>	Diptera, Sciaridae	(?)			Hurley et al. 2007

CHILE**Bark beetles and wood borers**

<i>Hylastes ater</i> *	Col., Curculionidae, Scolytinae	(+)			Wingfield et al. 2008
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JAPAN

None (?, see text)					Viljoen et al. 1997
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SPAIN**Bark beetles and wood borers**

<i>Hylastes attenuatus</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
<i>Hylurgops palliatus</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
<i>Hypothenemus eruditus</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
<i>Ips sexdentatus</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
<i>Orthotomicus erosus</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007
<i>Pissodes castaneus</i>	Col., Curculionidae, Molytinae	(+)	+		Iturrutxa et al. 2011
<i>Pityophthorus pubescens</i>	Col., Curculionidae, Scolytinae	(+)	+		Romón et al. 2007, Iturrutxa et al. 2011
<i>Tomicus piniperda</i>	Col., Curculionidae, Scolytinae	(+)	+		Iturrutxa et al. 2011

Cone insects

<i>Pissodes validirostris</i>	Col., Curculionidae, Molytinae	+	(?)		Roques et al. 2004, Lennox et al. 2009
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Root borers

<i>Brachyderes incanus</i>	Col., Curculionidae, Entiminae	(+)	+		Romón et al. 2007
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^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				
<i>Hylastes ater</i> *	Curculionidae, Scolytinae	Europe	(L) ^a D	W, C
<i>Hylurgus ligniperda</i> *	Curculionidae, Scolytinae	Europe	D	C
<i>Pachycotes peregrinus</i>	Curculionidae, Scolytinae	NZ	D	C
<i>Platypus apicalis</i>	Curculionidae, Platypodinae	NZ	D	C
<i>Arhopalus ferus</i> *	Cerambycidae	Europe	(L) ^a D	(W), C
<i>Calliprason pallidus</i>	Cerambycidae	NZ	D	C
<i>Hexatricha pulverulenta</i>	Cerambycidae	NZ	(L) ^a D	C
<i>Oemona hirta</i>	Cerambycidae	NZ	(L) ^a D	(W), (C)
<i>Prionoplus reticularis</i>	Cerambycidae	NZ	D	C
<i>Ernobius mollis</i> *	Anobiidae	Cosmopolitan	D	C
<i>Sirex noctilio</i> *	Siricidae	Europe	L	C
<i>Mitrastethus baridioides</i>	Curculionidae, Cryptorhynchinae	NZ	D	(C)
<i>Pycnomerus sophorae</i>	Colydiidae	NZ	D	(C)
Shoot and foliage-feeders				
<i>Pseudocoremia suavis</i>	Geometridae	NZ	L	W, (C)
<i>Hierodoris atychioides</i>	Oecophoridae	NZ	L	W, (C)
<i>Ctenopseustis obliquana</i>	Tortricidae	NZ	L	W, (C)
<i>Epiphyas postvittana</i> *	Tortricidae	Australia	L	W, (C)
<i>Planotortrix notophaea</i>	Tortricidae	NZ	L	W, (C)
Sapsuckers				
<i>Pineus boemeri</i> *	Adelgidae	USA	L	(W), (C)
<i>P. pini</i> *	Adelgidae	Europe	L	(W), (C)
<i>Essigella californica</i> *	Aphididae	USA	L	(W), (C)
<i>Eulachnus brevipilosus</i> *	Aphididae	Europe	L	(W), (C)
<i>Heliothrips haemorrhoidalis</i> *	Thripidae	Cosmopolitan?	L	(W), (C)
Cone insects				
<i>Erechthias fulguritella</i>	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 ^c
Coleoptera				
<i>Conophthorus ponderosae</i>	Curculionidae	<i>Pinus</i> spp., not <i>P. radiata</i>	Only seed cones	W, C, (V)
<i>Ernobius nigrans</i>	Anobiidae	<i>Pinus</i> spp., not <i>P. radiata</i>	Only seed cones	W, C, (V)
<i>Paratimia conicola</i>	Cerambycidae	<i>Pinus</i> spp., not <i>P. radiata</i>	Only seed cones	W, C, (V)
<i>Pissodes validirostris</i>	Curculionidae	<i>Pinus</i> spp., not <i>P. radiata</i> ^c	Mainly seed cones ^d	W, C, (V)
Lepidoptera				
<i>Cydia toreuta</i>	Tortricidae	<i>Pinus</i> spp., not <i>P. radiata</i>	Only seed cones	W, C, (V?)
<i>Eucosma rescissoriana</i>	Tortricidae	<i>Pinus</i> and <i>Abies</i> spp., not <i>P. radiata</i>	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)