

Review

Options for control of scolytid beetles that attack pines

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Abstract

Scolytid beetles (Coleoptera: Curculionidae: Scolytinae) are a large group of beetles associated with many tree species. Some species consume dead wood and vector an array of fungi which contribute to recycling of organic material, so are often an important component of forest ecology. However, populations can increase to pest levels. In this review, we look at options for control of scolytid pests of *Pinus* spp. Pines, valued for their softwood and pulp, are grown commercially in many countries. Both indigenous and exotic species of bark beetle are pests of pines. There have been numerous approaches to reducing the impact of bark beetle attack on pines. Management strategies have included thinning stands and timing of harvesting and planting, through to efforts to predict outbreaks. Bark beetles use semiochemicals to locate hosts and attract conspecifics and these have been used to trap or repel beetles, or disrupt their behaviour. Chemical pesticides have been used, especially for protection of high-value trees. Pesticides can be effective in some situations, but the commonly used actives such as organophosphates and pyrethroids have non-target and other health and safety concerns. There have been few successful introductions or applications of natural enemies (predators, parasitoids and microbial pathogens) reported for scolytid pests of pines. The cryptic, within-tree, habitats used for much of the bark beetle life cycle provide significant protection against most forms of control. Successful control will require novel approaches and will likely involve multiple agents and strategies.

Keywords: Scolytinae, Bark beetles, *Pinus* spp., Control, Management

Review Methodology: We used standard databases including CAB Abstracts and ISI Web of Knowledge using bark beetle(s), Scolytidae, scolytid(s), control, *Pinus* and pines as search words. Key references were also found in recent papers. Colleagues were consulted and some of our own research findings included.

Scolytid Pests of pines

The scolytids (Coleoptera: Curculionidae: Scolytinae) are a subfamily of bark beetles and wood borers, which affect many plant species. They include over 6000 species worldwide, with some 1430 species in North and Central America [1, 2]. They are a very diverse group in terms of biology and ecology, and are often integral species in ecosystem health, aiding forest regeneration by killing unhealthy trees. Although most species will only colonize dead, dying and stressed trees, some can attack and kill healthy trees [1, 3, 4]. Through disruption events such as

storms or fire, through human-induced events, and promoted by the use of monoculture plantings, beetles can reach epidemic populations, causing major damage to healthy trees [5, 6].

Scolytids attack a wide range of plant species, but this review will be limited to those that attack the trees of *Pinus* spp. There are over 100 species of pine, many of which are commercially exploited for their wood [7]. Pines are native to most of the northern hemisphere and have been extensively planted as exotic production trees elsewhere in the world. These evergreen, resinous softwood trees are considered the most ecologically and

Table 1 Some common scolytids associated with *Pinus* spp.

Species	Common names	Main <i>Pinus</i> host(s)	Regions affected	References
<i>Dendroctonus adjunctus</i>	Roundheaded pine beetle	<i>Pinus</i> spp., especially <i>P. montezumae</i> , <i>P. ponderosa</i>	Mexico, USA, Central America, Caribbean, Guatemala	[75]
<i>Dendroctonus brevicornis</i>	Western pine beetle	<i>P. coulteri</i> , <i>P. ponderosa</i>	North America	[5, 184]
<i>Dendroctonus frontalis</i>	Southern pine beetle	<i>Pinus</i> spp., primarily <i>P. taeda</i> , <i>P. echinata</i> , <i>P. virginiana</i> , <i>P. rigida</i>	North America, central America	[185, 186]
<i>Dendroctonus ponderosae</i>	Mountain pine beetle	<i>P. contorta</i> var. <i>latifolia</i> , <i>P. lambertiana</i> , <i>P. monticola</i> , <i>P. ponderosa</i>	North America	[187]
<i>Dendroctonus terebrans</i>	Black turpentine beetle	<i>Pinus</i> spp. especially <i>P. elliotii</i> , <i>P. taeda</i>	North America	[188–190]
<i>Dendroctonus valens</i>	Red turpentine beetle	<i>P. tabuliformis</i> , <i>P. ponderosa</i> , <i>P. lambertiana</i> , <i>P. strobes</i> , <i>P. resinosa</i> , <i>P. bungeana</i>	China, North America, Mexico	[27]
<i>Hylastes ater</i>	Black pine bark beetle	<i>P. radiata</i> , <i>P. sylvestris</i>	Europe, Chile, New Zealand, Australia	[26, 191–193]
<i>Hylastes angustatus</i>		<i>P. sylvestris</i> , <i>P. rotundata</i> , <i>P. pinaster</i> , <i>P. nigra</i> , <i>P. pinea</i>	Central and South Europe, South Africa	[20, 194]
<i>Hylastes linearis</i>		<i>P. halepensis</i> , <i>P. pinaster</i> , <i>P. brutia</i> , <i>P. nigra</i> , <i>P. sylvestris</i>	South Africa, Russia, Tunisia, Algeria, Cyprus, Southern Europe, Canary Islands	[194, 195]
<i>Hylastes opacus</i>	Bark beetle	<i>P. sylvestris</i> , <i>P. resinosa</i>	Scandinavia, Russia, China, South Africa, North America	[22, 46, 195]
<i>Hylastes parallelus</i>	Pine bark beetle	<i>P. tabuliformis</i>	China, Korea	[196]
<i>Hylurgus ligniperda</i>	Goldenhaired bark beetle, red-haired pine bark beetle	<i>P. sylvestris</i> , <i>P. nigra</i> , <i>P. halepensis</i> , <i>P. brutia</i> , <i>P. pinaster</i> , <i>P. pinea</i> , <i>P. radiata</i>	Europe, Turkey, Algeria, Russia, New Zealand, Australia, South Africa, California, Chile, Brazil, Uruguay	[20, 191, 194, 197]
<i>Ips avulsus</i>	Small southern pine engraver	<i>P. strobes</i> , <i>P. taeda</i> , <i>P. palustris</i> , <i>P. rigida</i> , <i>P. serotina</i> , <i>P. clausa</i> , <i>P. echinata</i> , <i>P. elliotii</i> , <i>P. virginiana</i>	North America	[198, 199]
<i>Ips calligraphus</i>	Sixspined ips	<i>P. ponderosa</i> , <i>P. strobus</i>	North and central America, Caribbean, Philippines, south Africa	[199, 200]
<i>Ips grandicollis</i>	Eastern fivespined ips, five-spined bark beetle	<i>P. strobes</i> , <i>P. banksiana</i> , <i>P. taeda</i> , <i>P. palustris</i> , <i>P. rigida</i> , <i>P. serotina</i> , <i>P. clausa</i> , <i>P. sylvestris</i> , <i>P. echinata</i> , <i>P. elliotii</i> , <i>P. virginiana</i> , <i>P. palustris</i> , <i>P. caribaea</i> , <i>P. cubensis</i> , <i>P. kesiya</i> , <i>P. maestrensis</i> , <i>P. oocarpa</i> and <i>P. tropicalis</i> , <i>P. pinaster</i> , <i>P. radiata</i>	North America, Australia, Central America, Caribbean	[199, 201]
<i>Ips pini</i>	Pine engraver	<i>P. ponderosa</i> , <i>P. jeffreyi</i> , <i>P. contorta</i> var. <i>latifolia</i> , <i>P. banksiana</i> , <i>P. resinosa</i> , <i>P. nigra</i>	North America	[202]
<i>Ips sexdentatus</i>	Stenographer bark beetle, sixtoothed bark beetle, ips engraver beetle	<i>P. sylvestris</i> , <i>P. nigra</i> , <i>P. leucodermis</i> , <i>P. sibirica</i> , <i>P. koraiensis</i> , <i>P. brutia</i>	Europe, Caucasus, Turkey, Siberia, Korea, Japan, North China	[14, 194]
<i>Orthotomicus erosus</i>	Mediterranean pine engraver beetle	<i>P. halepensis</i> , <i>P. canariensis</i> , <i>P. brutia</i> , <i>P. pinaster</i> , <i>P. pinea</i> , <i>P. nigra</i> , <i>P. sylvestris</i>	Chile, Israel, South Africa, Central and South Europe, Israel, Morocco, Tunisia, Algeria, Crimea, Caucasus, North America	[20, 191, 194]

Table 1 (Cont.)

Species	Common names	Main <i>Pinus</i> host(s)	Regions affected	References
<i>Pityogenes calcaratus</i>	Bark beetle	<i>P. halepensis</i> , <i>P. brutia</i> , <i>P. pinaster</i> , <i>P. sylvestris</i>	Mediterranean countries, Portugal, Syria, Palestine, Algeria, Israel	[194]
<i>Tomicus destruens</i>	Pine Shoot Beetle	<i>P. halepensis</i> , <i>P. canariensis</i> , <i>P. brutia</i> , <i>P. pinaster</i> , <i>P. nigra</i> , <i>P. radiata</i>	Southern Europe, Cyprus, Algeria, Palestine, Israel	[194]
<i>Tomicus minor</i>	Lesser pine shoot beetle	<i>P. sylvestris</i> , <i>P. mugo</i> , <i>P. rotundata</i> , <i>P. strobus</i> , <i>P. nigra</i> , <i>P. halepensis</i> , <i>P. densiflora</i> , <i>P. brutia</i> , <i>P. koraiensis</i> , <i>P. thunbergiana</i> , <i>P. pinea</i>	Europe, Corsica, Caucasus, Turkey, Siberia, South China	[194, 203]
<i>Tomicus piniperda</i>	Pine shoot beetle, common shoot beetle, larger pine shoot beetle	<i>P. sylvestris</i> , <i>P. pinaster</i> , <i>P. uncinata</i> , <i>P. radiata</i>	Scandinavia, Europe, Georgia, Asia, North America, North Africa	[140, 204]

commercially significant tree genus in the world. Monocultures of *Pinus* spp. can provide very suitable environments for bark beetle outbreaks [8].

There are many bark beetle species that attack pine and cause significant damage (Table 1). The last decade has seen exceptional levels of tree mortality, with bark beetles reported as a significant factor, especially in North America [9, 10]. Species of *Dendroctonus* (e.g. *Dendroctonus ponderosae* Hopkins, *Dendroctonus frontalis* Zimmermann, *Dendroctonus valens* LeConte) are major pests in North and Central America, and China. In the southern USA, the southern pine beetle, *D. frontalis*, is the major insect pest of pine species, especially loblolly and shortleaf pine [11]. In western Canada, outbreaks of *D. ponderosae* are currently causing 'landscape-leveling' mortality of lodgepole pine, *Pinus contorta* var. *latifolia* [10]. The current epidemic is estimated to have resulted in a cumulative total loss of over 750 M cubic metres of timber, with over 17.5 Mha affected in British Columbia alone [12]. The leading edge of the epidemic has now crossed the Rocky Mountains into central Alberta, Canada, and there has been a host switch to jack pine, *Pinus banksiana* Lamb [13], threatening large forest areas. Attacks by other bark beetle species cause millions of dollars of damage each year. The Eurasian bark beetle, *Ips sexdentatus* (Boerner), has caused massive damage after disruption events. Storms in south-western France in 1999 [14, 15] caused 27 M cubic metres of fallen timber [16] and resulted in population outbreaks that allowed mass attack on standing trees. The 2009 storm 'Klaus' left 42.4 M cubic metres of fallen *Pinus pinaster* Ait. and is still affecting population levels [15]. Fire in Central Spain damaged over 12 000 ha of trees in 2005, leading to outbreaks of *I. sexdentatus* in the subsequent years [17]. The rare Torrey pine, *Pinus torreyana* Parry ex Carr., was decimated by *Ips paraconfusus* Lanier in California in 1988–92 [18]. These are a few examples of the massive damage bark beetles can cause in pines.

The sub-cortical life cycle of scolytids allows survival in transit, making them a globally important biosecurity threat. In many 'new world' countries, introduced pine beetles are the major pests of *Pinus* spp. plantations. For example, the red turpentine beetle, *D. valens*, was first found in China in the 1980s, and by 2005, more than 10 M *Pinus tabulaeformis* Carr. were killed or damaged by beetle attack [19]. The genus *Hylastes* contains species that have been accidentally introduced into several countries. These include *Hylastes angustatus* (Herbst), *Hylastes linearis* Er. and *Hylastes opacus* Er. into South Africa [20, 21], *H. opacus* into North America [22] and *Hylastes ater* (Paykull) into New Zealand [23, 24], Australia [25, 26] and Chile [27]. Where no external disturbances have occurred, *H. ater* has not been recorded as a pest; however, in 'second rotation' (i.e. replanting in the same location) populations can reach epidemic/economic levels [20, 23, 28], at times killing almost all seedlings [25–27, 29].

Vectors of disease

Fungi from 38 genera have been identified as being associated with conifer-killing bark beetles in North America alone [30]. Some of these fungi are phytopathogenic and play an important role in helping more aggressive bark beetles colonize and kill trees (e.g. members of genus *Dendroctonus*) [31, 32]. In this situation, fungi are introduced into the tree during the process of beetle colonization, and tree mortality probably occurs as a result of the combined stress caused by the feeding activity of the beetle and fungi colonizing the host tree. Once introduced into trees these fungi may colonize the sapwood and disrupt the flow of water to the crown, killing the tree. Host responses to beetle attack are more complicated when fungi are associated with bark beetles [33]. Most authors support the notion that beetles and fungi are mutualistic symbionts (e.g. [34]). Many scolytids have

specialized structures, or mycangia, which may be simple pits or more specialized morphological structures, found on the head, pronotum or elytral areas, that carry yeasts and other fungi that are nutritionally beneficial to bark beetles [34, 35].

Less aggressive scolytids have been demonstrated to vector non-phytopathogenic members of the Ophiostomataceae (including *Ophiostoma* spp.) that inhabit living or recently dead wood and are commonly found in the galleries of scolytids [36]. Ophiostomataceae can be the cause of sapstain in conifer wood. In New Zealand, surveys of beetles and larvae showed that ophiostomatoid fungi were associated with adults, larvae and pupae of both *H. ater* and another bark beetle, *Hylurgus ligniperda* (Fab.) [37–39]. *H. ater* was demonstrated to vector several ophiostomatoid species to *Pinus radiata* D. Don in a study assessing fungal colonization associated with *H. ater* feeding damage [37]. However, a subsequent study of the same sites, approximately 3 years following planting, found that no seedlings were infected with ophiostomatoids, indicating that fungi were unable to persist for extended periods in seedlings [37].

The relationship between scolytids and fungi has been considered a significant mechanism for the introduction of fungi into many countries, and is of concern in an age of increased global trade and alien species invasions, with exotic beetles potentially vectoring suites of fungi and other organisms (e.g. mites and nematodes) [40]. Even if the beetles themselves fail to establish, the associated fungi may be established in native species and the potential for unpredictable vectoring relationships exist [41].

Life cycle

The Scolytinae are one of the few insect subfamilies where the adult can penetrate the protective outer bark of woody plants. Most scolytids feed on the inner bark of dead woody plants [2], but different species have preferences for different age, species and portion of plants. This habitat niche provides some benefits, such as protection from environmental extremes and natural enemies [42]. With the exception of a brief period of short flight, scolytids complete their whole life cycle within the host plant [2]. The young of each generation usually reach their new host by migration as adults rather than minor movements [43, 44].

Bark beetles have adapted to rapidly increase numbers when suitable habitats are found [2, 20, 45–49]. The ability to find suitable breeding substrate is the limiting factor of all bark beetles in the natural environment, as the dispersal phase has been shown to account for up to 80% of mortality [20, 45, 46, 50]. The search for hosts is based on a number of behavioural mechanisms, which use visual [51], semiochemical [52] or gustatory cues [53]. Chemical cues signalling the presence of suitable substrates seems to play a major role during the selection phase [52].

Complementary hypotheses have been proposed in which the dispersing beetles would exploit semiochemicals to select between suitable habitats or host stands, as well as between non-hosts, suitable hosts or non-suitable hosts occupied by conspecifics or heterospecifics [54, 55].

Attraction to kairomones is thought to be a dominant cue to help beetles distinguish the most appropriate host [46]. For *D. valens*, the principal attraction monoterpene components in ponderosa pine are β -pinenes, 3-carene and an α -pinene [56]. Similarly, *Tomicus piniperda* (L.) uses α -pinene and other oleoresin volatiles to locate suitable brood material [57, 58]. Schroeder and Lindelöw [59] observed enhanced attraction by *Hylastes cunicularius* Er. and *Hylastes brunneus* Er. to α -pinene and ethanol. Attraction differed with varying rates of ethanol release, reflecting differences in breeding substrate. Volatiles released by non-hosts are also used as cues in the selection of appropriate breeding substrate [55].

In addition, bark beetles use aggregation pheromones, such as ipsdienol and lanierone produced by *Ips pini* [60], to attract conspecifics, produced both through modification of host compounds and *de novo*, and to coordinate mass attacks on host pine in order to overcome tree's defences [1, 52, 61, 62]. Aggregation pheromones were first discovered in bark beetles for *I. paraconfusus* [63] and have been described in many other species thereafter [61]. Anti-aggregation pheromones may also be released to prevent the overcrowding of colonized trees [11], such as verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) or MCH (methyl ciclo hexanone(3-methylcyclohex-2-en-1-one) [64, 65].

The interactions between beetles, pheromones and host volatiles can be complex. For example, *D. valens* is attracted to host volatiles more strongly in the presence of pheromones produced by *Dendroctonus brevicornis* and *Ips* spp., while pheromones of these species are weakly attractive to *D. valens* [31, 66]. Some host chemicals may be attractive at low, but not high concentrations, such as 4-allylanisole [1-methoxy-4-(2-propenyl) benzene] (present in oleoresin of various pines) to *D. valens* when released at low rates, but not high rates [19, 67].

Those few species that may colonize and kill healthy trees are termed 'aggressive' or 'primary' species, and are the first organisms to invade plant tissue that is otherwise un-infested and capable of mounting a defensive reaction [1, 26, 37]. 'Non-aggressive' or 'secondary' species, in turn, are those that colonize dead or dying trees, or trees that may have been previously attacked [31, 32, 45, 68]. Most Scolytinae are indeed saprophytic, and colonize dead trees or tree parts [1, 68].

Control Options

Scolytid beetles in pine are a constant and serious pest for many forests. Consequently, there have been many control options used or investigated. These may be divided

into the following approaches: management of forests, chemical pesticides, semiochemical-based and natural enemies.

Management to reduce beetle damage

Management is probably the most common approach for reducing bark beetle impacts. Management practices that contribute to the reduction of pest populations or damage include those that prevent potential outbreaks, methods to predict outbreaks, detection and monitoring of populations through to direct control. Sanitary felling of trees was the basic control strategy for bark beetles for hundreds of years and 'trap trees' were first recommended at the end of eighteenth century for *Ips typographus* L. in spruce [69]. This typical management approach is broadly practiced across the world, and basically consists of frequent search for new infestations, followed by felling and mass trapping, either using trap trees, sometimes treated with insecticides (i.e. 'lure and kill' [70]), or wood heaps or pheromone traps [69].

Stand thinning was proposed by Eaton [71] as a method to reduce beetle attack, theorizing that it would increase the vigour of trees by removing competition. A number of studies examined stand thinning for influence on beetle attack, as effects are variable (reviewed in [72]). Whitehead and Russo [72] examined trial sites in British Columbia that used stand thinning of lodgepole pine as a 'beetle-proofed' treatment for the mountain pine beetle (*D. ponderosae*). Unthinned stands required interventions to prevent outbreaks, but only one of five of the thinned stands needs such an intervention. They concluded that the effect of thinning was less a factor of tree vigour, and more a factor of inter-tree spacings over 4 m between trees reduced the frequency of attacks by beetles. However, several beetle species (i.e. *Ips* spp.) are attracted to trees during thinning operations, limiting the timing of thinning in some locations.

Prevention has also been a tool for reducing damage from bark beetles. Removal of breeding material, such as fallen trees, can prevent bark beetle population build up. Following large storms in France in 1999, the removal of wind-thrown trees to reduce breeding material was the only effective method [41]. However, log piles of removed material also contributed to subsequent outbreaks of *I. sexdentatus* [16]. Grégoire *et al.* [6] also noted that delays to tree removal (e.g. resulting from sale processes) could reduce the effectiveness of the approach of cutting and removal of infested material, as the infestation could increase before felling was able to take place. When the removal of infected material is not feasible, cut and leave tactics have been recommended for *D. frontalis*, but this results in breeding material remaining on site and may increase the risk of localized outbreaks [9].

Another method to reduce the availability of breeding material in sites is eliminating exposed roots and stumps.

One approach is the burning of slash and branches. However, a fire burn is also commonly used to reduce the accumulation of general burnable material [5] and, while it may help to control some insects and diseases, there is evidence that a burn can lead to increased bark beetle damage [5, 9]. Accidental fires which cause damage to large areas of pine forests results in many severely injured trees that are easily colonized by bark beetles, boosting their population levels, which in turn, leads to outbreaks that affect trees that would otherwise survive fire, and in extreme cases leads to infestation of nearby healthy stands [15]. Santolamazza-Carbone *et al.* [73] recommended removal of injured and dying pines after studying bark beetle and other insect colonization of *P. pinaster* after a fire in Spain. Mechanical methods for reducing fuel build up in managed forests, such as chipping or lopping and scattering of small trees, can also lead to higher bark beetle populations [74].

Prevention can also involve planting less susceptible species, decreasing rotation length and planting mixed species and differing age stands [9]. Tree species diversity has been found to result in reduced herbivory by insects, including bark beetles [8]. For prevention of *Dendroctonus adjunctus* Blandford, replacement of the Mexican pine *Pinus rudis* Endl. by less susceptible species (e.g. *Pinus ayacahuite* Ehrenb. ex. Schtdl or *Pinus pseudostrobus* Lindl.) and avoidance of fellings during the swarming season were recommended [75]. Trees may also be selected for bark beetle resistance [32, 76]. *Pinus* spp. defence mechanisms against bark beetles include oleoresins, a complex mixture of terpenoids consisting mainly of two fractions, the volatile turpentine and the more solid rosin fraction. Although many of the turpentine components have been shown to be toxic for insects and microbes, the crystallization of the rosin fraction provides the tree with a system that can potentially create a physical barrier around wounds, often trapping boring insects. As terpene composition is a heritable trait [77], it could be possible to select trees with higher levels of production of oleoresins. Many of the genes involved in resin-based defence mechanisms have been described and could potentially assist in generating transgenic conifers with increased defence capabilities [78]. As host monoterpenes may be used as kairomones (*sensu* Nordlund [79]), sometimes combined with aggregation pheromones to locate the plants both by bark beetles and their natural enemies [80, 81], or as their own pheromone precursors [61], more sophisticated strategies altering hosts oleoresin chemistry could also provide foresters with improved conifers. In any case, the relationship between specific terpenoids and tree resistance to insects is not well known [82]. Current selection processes for trees with better commercial production characteristics (i.e. for fast growth, form, etc.) may result in greater tree susceptibility, as such breeding may be at the expense of natural bark beetle defence systems.

For *D. frontalis* control in the USA, aerial surveys are used to detect infestations. Observing changes in crown colour can be used to detect beetle damage, with the obvious limitation that time of year and environmental influences can make such changes difficult to categorize [83].

The ability to predict outbreaks can significantly improve bark beetle control efforts. There have been attempts to model outbreaks with some success (e.g. [84–86]). Outbreaks of *D. frontalis* have been correlated with previous outbreaks in regions of the south-eastern USA [9], suggesting movement of adults is not expansive. Factors that influence bark beetle attack includes stand density, stand age and tree diameter [9, 11]. Nelson *et al.* [87] suggested that risk models for mountain pine beetle had been based on indices of stand susceptibility and lacked ecological understanding. They provided an approach that incorporated some ecological factors. Modelling and prediction have also included consideration of the effect of climate change on beetle outbreaks and distribution [88].

Chemical control

Chemical pesticides have been widely used for insect control in many agricultural and forestry situations. Use in pine forests is dependent on economics and practicalities of application and efficacy, and availability of products. The main chemicals reportedly used have been organophosphates, carbamates and pyrethroids.

Carbaryl (1-naphthyl methyl carbamate) has been used for 40 years in the western USA for control of bark beetles, particularly *D. ponderosae*. Hastings *et al.* [89] reviewed the research prior to 2000, reporting spray applications to individual trees were effective at reducing tree mortality associated with bark beetles. Application rates of 1–2% a.i. and at 18–28 litres/tree are used, applied with a hydraulic sprayer [90]. Carbaryl is not as effective in preventing attack of *D. frontalis* [91, 92]. Typically, 15–30 m no-spray buffers around waterways are recommended, as carbaryl has high toxicity to Plecoptera and Ephemeroptera [90]. Although carbaryl is considered one of the most effective, economically viable and ecologically compatible insecticides for protecting individual trees [93], future availability is not assured [94].

Other chemical pesticides, such as alphamethrin (a pyrethroid), have been used to spray infested log piles to kill emerging beetles and reduce subsequent colonisation [14]. Spraying sections of logs with permethrin, bifenthrin and carbaryl provided greater than 70% protection against the pine engraver, *I. pini* (Say) and other *Ips* spp. 13 months after treatment [95]. Chlorpyrifos (organophosphate) formulations have been used to prevent *D. frontalis* attack [83], but registration for this use has been cancelled in the USA [94]. Aluminium phosphide, a strong poison used to control rodents, has been used to

control *D. valens* in China, and dimethyl dichlorovinyl phosphate (DVVP) or omethoate (both organophosphates) have been injected into bark beetle galleries [19]. In China, during flight periods, direct control methods included spraying insecticides such as phorate, monocrotophos (organophosphates), cypermethrin (synthetic pyrethroid) and 'phoxime' have been attempted. Use of these insecticides for *D. valens* was reported to kill 90–98% of beetles, although no specific data were given [19].

Given the sub-cortical life history of bark beetles, the application of chemical control is very challenging, especially at the forest scale. Attempts to control emergence of beetles from trees were reviewed by Hastings *et al.* [89], with some success reported using diesel or toxic pesticides such as lindane, on trees that were infested with *Dendroctonus* spp.; however, these pesticides also affected non-target invertebrates. Carbaryl has some effect against emerging brood [89].

Neem, extracted from the seeds of *Azadirachta indica*, has been used against a number of insect pests. The active agent, azadirachtin, has been investigated as a systematic insecticide for *D. ponderosae* control. When applied to the xylem of *P. contorta*, Naumann and Rankin [96] found almost total prevention of development to adult of the beetle. However, surface treatment with neem-based insecticides did not repel or deter *D. ponderosae* [97].

Systemic insecticide application is a more environmentally safe alternative to broadcast spray. Grosman *et al.* [98] reported trunk injections with small amounts of emamectin benzoate (avermectin insecticide) and fipronil (phenylpyrazole insecticide) helped reduce *D. brevicomis* LeConte and *D. ponderosae* attack in ponderosa and lodgepole pines, respectively. The systemic application of fipronil was ineffective with high mortality of fipronil-treated trees in the third year, but emamectin benzoate in ponderosa pine was effective in the third year after application against *D. brevicomis*.

In general, because of the expense, safety and application issues, insecticides are more useful for protection of individual, high-value trees than whole forest stands [93]. Some chemical pesticides have been withdrawn (e.g. [94, 99]), or are currently under review as new evidence suggests unintentional effects [90, 100, 101]. For example, the US Environmental Protection Agency banned the uses of most organophosphates in 2001 for residential use and are currently expressing concerns over other applications. Agents that can be used directly against scolytid pests but are more environmentally benign and effective are being sought. For example, Fettig *et al.* [94] showed efficacy of two new 'reduced risk' insecticides, cyantraniliprole (Cyazypyr[®]) and chlorantraniliprole (Rynaxypyr[®]) to *D. ponderosae* in the laboratory. It is expected that more new compounds will be examined for use against bark beetles as they continue to grow as a problem, but clearly chemical control approaches have not been successful in reducing bark beetles as

threats to pines generally. Given the ecological impacts of broad-spectrum chemical insecticides, other approaches are likely to be favoured.

Semiochemical approach

Scolytid beetles have evolved a number of behavioural modifications to assist in the search for appropriate breeding substrates and overcoming of host tree defences, including release and response to semiochemicals. Given the importance of chemical cues in the behaviour of scolytids, their applied use for bark beetle control has been studied for a number of years [102, 103]. Together with the development of trapping technology and associated methodology (e.g. [104, 105]), multiple strategies using semiochemicals have arisen [106].

Usages of synthetic attractants (aggregation pheromones or host kairomones, e.g. α -pinene) include monitoring and mass trapping or tree baiting. Commercially available traps and lures are recognized as effective tools for monitoring both local and exotic bark beetles [103, 107, 108], and were found to be an economical substitute for traditional trap-tree methods [103]. The use of pheromone traps or pheromone-baited trees have been used to forecast beetles populations [109, 110]. Attempts to control epidemic outbreaks by means of mass trapping have shown that, alone, it has not been particularly successful [6, 111, 112], although using this method in an integrated pest management programme seems to reduce damage by bark beetles [111]. In selected situations, such as isolated plantings, pheromone-based trapping may be effective [18, 113]. Trapping was used to reduce *D. valens* attacks in China, with a blend of α -pinene, β -pinene and 3-carene successfully decreasing the average number of attacks per tree by 59% and area infested by 64.4% [19].

Aggregation pheromones have also been using in tree baiting strategies aiming at four operational applications for *D. ponderosae*: (i) detection and monitoring, (ii) containment and concentration, (iii) post-logging mop-up and (iv) spot suppression [114]. A modified usage of semiochemicals to aggregate beetles on breeding substrate has also been developed for such situations, where insects die upon landing, a strategy termed 'lure and kill' [115]. Thus, trap trees can be removed before new beetles emerge or treated with pesticides to reduce numbers or kill colonizing beetles [116].

Another method is to use repellent or inhibitory compounds signalling inappropriate hosts, to provide forest managers with tools for integrated pest management. Discovered soon after the descriptions of the first bark beetle pheromones, 'pheromonal masks' such as the MCH [117], or verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) [118] have attracted much interest in the study of semiochemical-based management of bark beetles. Verbenone is now recognized to have a general inhibitory effect on bark beetles [119]. It is produced

through a number of pathways, including auto-oxidation of α -pinene [120], by bark beetles themselves [121] or by the action of yeasts and other bark beetle associated micro-organisms [122]. Although the main role of verbenone in the population dynamics of bark beetles has not been completely clarified, it seems that its effect derives from linkage it may have with host tissue decay [123] or intraspecific competition [124]. This compound has been well studied, but inconsistent results (e.g. [125, 126]) slowed its practical application. Recent studies have found methods to overcome previous problems, and promising results have been obtained when dosages have been increased [15, 120, 127, 128]. The combined use with attractants in the strategy known as 'push and pull' [115], resulted in promising results for *D. ponderosae* [129] or the complete protection of a rare *P. torreyana* stand [18].

It is well known that compounds that may be part of the aggregative pheromonal blend of one species may repel the aggregation of close competitors. Thus, whereas ipsenol (a very common *lps* semiochemical) attracts *Pytiokteines curvidens*, *I. typographus* is repelled when this compound is used [103]. This type of response has been studied with the aim of controlling outbreaks through enhanced competition [130, 131] or by combined usage of other known inhibitors such as verbenone [132].

In addition to verbenone, volatiles that indicate the presence of non-host trees have been investigated for scolytid control [133]. These non-host volatiles (NHVs) have mainly been isolated from angiosperm trees for use against scolytids that attack conifers. The NHVs have shown repellent effects against a number of scolytids (e.g. [134–136]). For example, Jactel *et al.* [14] tested blends of green leaf and bark alcohols to disrupt attraction to pheromones of *I. sexdentatus*, showing that it was indeed repelled. The efficiency of NHVs has also been proven while protecting *P. contorta* [137]. The successful use of non-host tree volatiles may indicate that increased diversity of tree species does play a role in reducing forests susceptibility to bark beetle damage [14, 55].

Natural enemies

An attractive approach for control of pest insects, especially exotic invaders, has been the use of natural enemies: predators, parasites and pathogens. Natural enemies can maintain population levels at below damage thresholds in many natural situations [138, 139]. The lack of natural enemies in exotic environments can contribute to beetles reaching damaging populations. There have been many studies on natural enemies of bark beetles, but less on those affecting beetles on pines.

Predators and parasites

Moeck and Safranyik [138] and Kenis *et al.* [139] thoroughly reviewed the literature on predators and

parasites of all bark beetles, from natural occurrence through to their use in biological control. Several bird species (woodpeckers and passeriformes) [139] and small mammals [138] are known to consume bark beetles, but it is unlikely that vertebrates could be used as practical control agents given polyphagous feeding habits and other practical considerations. Among the insect predators, the clerid beetles (Coleoptera: Cleridae) are the most prevalent of the 24 Coleoptera families listed as associated with bark beetles [138]. Of the pine pests, the clerid, *Thanasimus dubius* (Fabr.), attacks *T. piniperda* adults and other pine scolytids such as *Ips* spp. in North America [140] and *Thanasimus formicarius* (L.) is a major bark beetle predator in Europe, including *T. piniperda* [141, 142]. Adult clerids are attracted by bark beetle pheromones, so will be attracted to heavily attacked trees [60, 143, 144]. Predacious beetles can also be attracted to tree volatiles, such as α -pinene and ethanol [145, 146]. Predators often appear on trees at the same time as bark beetles, whereas parasitoids arrive later [139]. Other important predators are found in the Trogositidae and Rhizophagidae (Coleoptera). Trogositid beetles prey on adults and larvae of some bark beetles and, like clerids, can be attracted to volatiles associated with bark beetles, but are less well studied than clerids [138].

Moeck and Safranyik [138] report 15 families of Diptera contain known predators. Ants, some bug species, spiders, mites, pseudoscorpions and dragonflies have also been reported as predators but have not been used in control efforts.

The impact of predation on bark beetle populations is rarely documented. The amount of prey capable of being eaten, fecundity rates and environmental constraints all affect predator success. As summarized in Kenis *et al.* [139], some species are voracious: *T. formicarius* can reduce brood by over 80% and one adult can consume three adult *Ips* per day. After outbreaks of *Ips acuminatus* (Gyll.) and *T. piniperda* in Scots pine in France in 1978–1979, 31 predators and 14 parasitoids were found associated with the populations, with three predators (*T. formicarius*, *Rhizophagus depressus* (Fab.) and *Medetera* spp.) abundant [142, 147]. *R. depressus* was found to reduce *T. piniperda* by 41% and *T. formicarius* by 81% in exclusion experiments [141]. Most of these predators attacked populations during early spring, while the other predators and parasites were active later in the season, suggesting a complementary action by a suite of natural enemies.

Parasitoids of bark beetles are contained in only a few families [138, 139]. The Braconidae (Hymenoptera) are the most prolific, and a few species of Pteromalidae (Hymenoptera), but there are few reports of species specifically acting on pine bark beetles. The bark beetle larval and pupal parasitoid, *Roptrocercus xylophagorum* (Ratzeburg), has a host range that includes pine-associated beetles in Europe and North America such as *I. typographus*, *T. piniperda*, *D. frontalis* and *D. brevicornis* [148].

This parasitoid was successfully introduced into Australia in the early 1980s as a biological control agent of *Ips grandicollis* Eichhoff [91].

There have been few other attempts to use predators and parasites for control of bark beetles which use some type of intervention, rather than relying on natural incidence [138, 139, 143]. There are several methods that could be employed: mass rearing and release [149], field collection and release, conservation management to enhance occurrence and even supplementary feeding, where the natural enemy is provided an alternate food source such as nectar for some parasitoids to extend their period of activity [83]. One successful programme utilizing a predator species has been the use of *Rhizophagus grandis* Gyll. for control of the spruce beetle, *Dendroctonus micans* (Kugelann). Although not a pine pest, this programme is a good example of use of a predator. As reviewed in Kenis *et al.* [139], the predator has been reared, released and established in Georgia, Turkey, France, Belgium and the UK.

In some cases, native predators can prey on introduced species. Yan *et al.* [19] listed a number of Chinese predator species for *D. valens*, with an adult Tenebrionidae species (Coleoptera) described as a highly effective predator of *D. valens* adults in the laboratory. However, this is not common. Therefore, importation and release of known natural enemies is a more common approach. *R. grandis* was imported into China in 2000, and is now an important predator of *D. valens* [150]. Several attempts to introduce natural enemies into New Zealand for control of *H. ater* have been unsuccessful [139]. A *Rhizophagus* species and a pteromalid, *Rhopalicus tutela* (Förster) were introduced to New Zealand [151]. *R. tutela* was also released in Canada in 1934, but also failed to establish [138].

Clerid beetles have been suggested as the most effective and promising predators for some scolytids [143, 152], but practical use in pines has not been successfully reported. For *D. ponderosae* in Canada, Moeck and Safranyik [138] recommended inundative releases of native Cleridae beetles against low populations. The predators *Enoclerus sphaegeus* F., *Enoclerus lecontei* Wolcott and *Thanasimus undatulus* (Say) were tested for ability to reduce populations of bark beetles, but because of cannibalism, rearing was difficult and expensive, and no inundative release was attempted [143]. Imported *T. formicarius* were not released as they could interbreed with *T. undatulus* and were likely to predate on the beneficial competing beetle, *I. pini*. The clerid *T. formicarius*, collected in Europe, was released against the southern pine beetle in the eastern USA in 1882 and 1883 and against *H. ater* and *H. ligniperda* in New Zealand, but has had little impact on population levels [151, 153].

Microbial pathogens

Microbes that are pathogenic to insects have been developed into practical control agents [154] and have

potential for scolytid control if (a) suitable agents can be found; (b) application methods that can target the insects in field situations can be developed and (c) the production and application of the microbe is economically viable. A number of fungal, protozoan, bacterial and nematode entomopathogens have been reported attacking pest scolytid species. Interestingly, occurrence of viral pathogens seems rare, with only some 'viral-like particles' and an entomopoxvirus reported [155, 156]. Herein, we concentrate on pathogens of pine-associated bark beetles, but there are substantial reviews of pathogens associated with scolytids (e.g. [157–160]).

Fungal pathogens in the genera *Beauveria*, *Metarhizium* and *Paecilomyces* are some of the most common and broad host range insect pathogenic microbes known. Unsurprisingly, representatives of these genera have been isolated from a range of scolytids that attack pines. *Beauveria bassiana* (Bals.) Vuill., *Beauveria brongniartii* (Sacc.) Petch, *Beauveria caledonica* Bissett & Widden, *Isaria farinosa* (Holmsk.) Fr (= *Paecilomyces farinosus*) *Isaria fumosorosea* Wize (= *Paecilomyces fumosoroseus*), *Paecilomyces viridis* Seg. et al. and *Metarhizium anisopliae* (Metsch.) Sorokin (Ascomycetes) have been described from various species in Europe (e.g. [157, 161–163]), China [19] and New Zealand [162, 164]. In North America, there are also reports of some of these species attacking bark beetles. For example, Safranyik et al. [152] reported on evaluation of *B. bassiana*, *P. farinosus* and *M. anisopliae* for control of *I. pini*. *B. bassiana* was further investigated as a potential biopesticide but found to lack the specificity needed to target a single bark beetle species [152]. *B. bassiana* has also been found to be pathogenic to predators of bark beetles, such as the predator, *T. formicarius*. However, field doses targeting and killing *I. sexdentatus* did not affect the predator, suggesting susceptibility was higher among bark beetles than the predator [165]. A benefit of using entomopathogenic fungi is that, as the mode of infection is via direct penetration of the cuticle and the infective stage does not need to be ingested, they can often kill larvae, pupae and adults. Most pathogens, such as bacteria, viruses and protozoa, act after infective propagules are ingested [159], meaning pupae can not be targeted. In addition to *B. bassiana*, *H. ater* in New Zealand are killed by two other entomopathogenic fungi, *Metarhizium flavoviride* var. *pemphigi* Driver & Milner and *Hirsutella guignardii* (Maheu) Samson et al. [166].

Use of fungi in the field is rarely reported for pine scolytids. In Poland, *B. bassiana* was sprayed during the early flight period of *T. piniperda* [167]. Scots pine trap trees were sprayed with the fungus but the infection rate in beetles trapped 2 months later was only 3–7%, although that was higher than in unsprayed trees ($\leq 1\%$) [167].

Isolation of bacteria from dead insects is common, so reports of bacterial pathogens need to be accompanied by demonstration of pathogenicity. Although Moore [168] recorded several potentially pathogenic bacteria from *D. frontalis*, bioassay found that only *Pseudomonas*

aeruginosa (Schröter) Migula, *Pseudomonas fluorescens* (Flügge) Migula and *Serratia marcescens* Bizio were pathogenic to *D. frontalis* [169]. In addition, generalist pathogens *Bacillus cereus* Frankland & Frankland, *Bacillus thuringiensis* Berliner and *B. thuringiensis* subsp. *kenyae* were pathogenic to *D. frontalis*. *B. thuringiensis* subsp. *thuringiensis* are the active agents in the largest number of biopesticides produced around the world and, although the *B. thuringiensis* has coleopteran-active toxins in some strains, there are very few reports of toxicity to bark beetles [170]. Cane et al. [171] found that no *B. thuringiensis*-based product with reported activity against Coleoptera was effective against adults of *Ips calligraphus* (Germar) and *D. frontalis* in laboratory bioassays.

Entomopathogenic nematodes, especially those in the genera *Steinernema* and *Heterorhabditis*, have been developed as commercially available biopesticides for pest insect species, including Coleoptera [172]. As with the fungal pathogens, a benefit of some nematodes is that they can attack non-feeding stages because they penetrate hosts directly. There are reports of bark beetle susceptibility to nematodes. *Steinernema ceratophorum* Jian et al. could cause 90% mortality of *D. valens* adults in the laboratory, but has not been recorded in the field in China [19]. Similarly, *Scolytus multistriatus* (Marsham) and *D. ponderosae* were susceptible to *Steinernema* (= *Neoalectana*) *carpocapsae* (Weiser), another common generalist entomopathogenic nematode [173]. In Italy, several species of steinernematid and heterorhabditid nematodes were active against *T. piniperda* [174]. Injection of *Heterorhabditis bacteriophora* into the entrance of bark beetle tunnels did lead to infection of beetles inside. However, field application data are lacking.

Protozoan pathogens have also been reported from bark beetles. Protozoan disease is usually slow to kill, but may exert some natural control on beetle populations (e.g. [156]). Takov et al. [175] listed 31 protozoan and microsporidian (sometimes classified as protozoan) from 14 genera pathogenic to bark beetles. The pathogen complex of the bark beetle species were 6% amoebae, 19% eugregarines, 26% neogregarines and 49% microsporidia. Microsporidia (such as *Nosema* spp.) are common pathogens of many insect groups and one of the most studied pathogen groups attacking scolytids, although not those species specifically associated with pines [175]. Among the pine pests, *Nosema calcarati* Purrini & Halperin was found attacking all life stages of *Pityogenes calcaratus* Eichhoff in Israel [176]. Protozoans are unlikely to be used in commercial biopesticide formulations given difficulties in production and that they are slow in killing.

Laboratory susceptibility to pathogens does not always translate into field control, given the cryptic habitats of the beetles. For example, *D. frontalis* is susceptible to nematodes *Steinernema* [*Neoalectana*] *feltiae* (Filipjev), *S. [N.] glaseri* (Steiner) and *H. bacteriophora* Poinar (= *Heterorhabditis heliothidis*), but no infections were found

after spray application onto pine bolts [177]. Innovative strategies for delivery would have to be developed, however, to circumvent the cryptic habits of the beetles [171]. One approach that has not been investigated but may have potential is the use of insect pathogens as endophytes of pines. The fungus *B. bassiana* has been found to persist endophytically in a number of plant species, including *P. radiata* [178] and *Pinus monticola* Douglas ex D. Don [179]. Effects of endophytes on insects feeding on pines has yet to be determined, but if the fungus presence can reduce beetle infestations it may be feasible to artificially inoculate pines to maintain an endophytic entomopathogenic fungus. Another strategy is to use the strong attraction of bark beetles to semiochemicals for a 'lure and infect' approach [180]. The ability of pathogens to move from a contaminated beetle to others through contact [181] suggests this method might be feasible for some bark beetle populations.

Conclusions

Scolytid beetles are a serious pest of production pine species around the world. Given their aggregation behaviour and vectoring ability of disease-causing microbes, they can cause massive tree losses worldwide. Management approaches, such as removal of trees and thinning, have been used to reduce damaging populations, but can be expensive or impractical in some situations. Chemical pesticides have been used for control, but are also expensive and can be associated with serious environmental and health concerns. Bark beetles use a range of semiochemicals to modify conspecific behaviour or find hosts and these pheromones and kairomones have shown promise as control tools. Natural enemies are known to regulate some beetle populations and have been investigated for introduction to where exotic pine species are infested with exotic species of bark beetle. Predator and parasitoid introductions have largely been unsuccessful. Many natural enemies lack specificity or have environmental requirements not met in non-native ranges. Predator rearing for release is labour-intensive and difficult, often expensive and impractical. Microbial pathogens have also shown promise, but the cryptic habitat of larvae and pupal stages within trees makes inoculation with microbes difficult.

It is likely that control will require a combination of agents and management practices to be successful. Some current methods can interfere with each other, such as control of bark beetle populations using pheromones can be destructive to coleopteran predator populations if not managed properly [182]. Novel methods and/or integrated approaches using the best available options is the most likely to succeed. A combination of careful management methods, semiochemical use and environmentally safe insect killing agents that can access cryptic habitats are required. It has been demonstrated that

predators can be selectively attracted to pines without attracting the bark beetle target and beetles can be trapped without attracting predators. For example, the predator *T. dubius* was attracted to frontalin plus α -pinene, but the bark beetle *I. pini* was not [182]. Conversely, increasing numbers of *I. pini* were trapped when increasing concentrations of lanierone plus ipsdienol were used, but trap catches of predators, including *T. dubius*, did not increase with this mixture [144]. There is potential, therefore, to selectively enhance predation and decrease trap catches of natural enemies. Timing of deployment of semiochemical traps for mass-trapping can also have a major impact on the pest to predator ratio in traps [183]. The success of verbenone is evidence of the potential of semiochemicals, but other compatible agents are required.

References

1. Raffa KF, Phillips TW, Salom SM. Mechanisms and strategies of host colonisation by bark beetles. In: Schowalter TO, Filip GM, editors. Interactions Among Bark Beetles, Pathogens, and Conifers in North American Forests. Academic Press Ltd, London, UK; 1993. p. 103–28.
2. Kirkendall LR, Kent DS, Raffa KF. Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behaviour. In: Choe JC, Cuespi BJ, editors. The Evolution of Social Behaviour in Insects and Arachnids. Cambridge University Press, Cambridge, UK; 1997. p. 181–215.
3. Byers JA. Host tree chemistry affecting colonization in bark beetles. In: Cardie RT, Bell WJ, editors. Chemical Ecology of Insects 2. Chapman and Hall, New York; 1995. p. 154–213.
4. Bueno A, Diez JJ, Fernández MM. Ophiostomatoid fungi transported by *Ips sexdentatus* (Coleoptera; Scolytidae) in *Pinus pinaster* in NW Spain. *Silva Fennica* 2010;44:387–97.
5. Fettig CJ, McKelvey SR, Cluck DR, Smith SL, Orosina WJ. Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in Ponderosa and Jeffrey Pine Forests in California, USA. *Forest Ecology and Management* 2010;260:207–18.
6. Grégoire JC, Salom S, Stephen F, Landmann G. Bark beetles and reforestation pests: facing a crisis. *Integrated Pest Management Reviews* 2001;6:vii–viii.
7. Richardson DM, Rundel PW. Ecology and biogeography of *Pinus*: an introduction. In: Richardson DM, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge; 1998. p. 3–48.
8. Jactel H, Brockerhoff EG. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 2007;10:835–48.
9. Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, et al. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management* 2007;238:24–53.
10. Klingenberg MD, Lindgren BS, Gillingham MP, Aukema BH. Management response to one insect pest may increase

- vulnerability to another. *Journal of Applied Ecology* 2010;47:566–74.
11. Duehl AJ, Koch F, Hain FP. Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history. *Forest Ecology and Management* 2011;261:473–9.
 12. British Columbia Ministry of Forests, Lands and Natural Resource. Infestation Information 2011. Available from: URL: http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/facts.htm
 13. Cullingham CI, Cooke JEK, Dang S, Davis CS, Cooke BJ, Coltman DW. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology* 2011;20:2157–71.
 14. Jactel H, Van Halder I, Menassieu P, Zhang QH, Schlyter F. Non-host volatiles disrupt the response of the stenographer bark beetle *Ips sexdentatus* (Coleoptera: Scolytidae), to pheromone-baited traps and maritime pine logs. *Integrated Pest Management Reviews* 2001;6:197–207.
 15. Etxebeste I, Pajares JA. Verbenone protects pine trees from colonization by the six-toothed pine bark beetle, *Ips sexdentatus* Boern (Col.: Scolytinae). *Journal of Applied Entomology* 2011;135:258–68.
 16. Rossi JP, Samalens JC, Guyon D, van Halder I, Jactel H, Menassieu P, *et al.* Multiscale spatial variation of the bark beetle *Ips sexdentatus* damage in a pine plantation forest (Landes de Gascogne, Southwestern France). *Forest Ecology and Management* 2009;257:1551–7.
 17. Sánchez G, González E, Vela Á, Ayuso S. Control de la población de *Ips sexdentatus* en el área afectada por el incendio del Rodenal: Consejería de Medio Ambiente y Desarrollo Rural de Castilla la Mancha. 2008.
 18. Shea PJ, Neustein M. Protection of a rare stand of Torrey pine from *Ips paraconfusus*. In: Applications of Semiochemicals for Management of Bark Beetle Infestations—Proceedings of An Informal Conference. General Technical Report – Intermountain Research Station, USDA Forest Service Issue: INT-318. 1995. p. 39–43.
 19. Yan Z, Sun J, Don O, Zhang Z. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. *Biodiversity and Conservation* 2005;14:1735–60.
 20. Tribe GD. Phenology of three exotic pine bark beetle species (Coleoptera: Scolytidae) colonising *Pinus radiata* logs in the South-western Cape Province. *South African Forestry Journal* 1991;57:27–31.
 21. Govender P, Wingfield MJ. Overview on the entomological research in the Mediterranean forest ecosystems of South Africa. In: Lieutier F, Ghaïoule D, editors. *Entomological Research in Mediterranean Forest Ecosystems*, INRA, Paris, France, 2005:43–52.
 22. Rabaglia RJ, Cavey JF. Note on the distribution of the immigrant bark beetle, *Hylastes opacus*, in North America (Coleoptera: Scolytidae). *Entomological News* 1994;105:277–9.
 23. Clark AF. The pine-bark beetle, *Hylastes ater*, in New Zealand. *New Zealand Journal of Science and Technology* 1932;14:1–20.
 24. Faulds W. *Hylastes ater* (Paykull), black pine bark beetle and *Hylurgus ligniperda* (Fabricius), golden haired bark beetle. In: Cameron PJ, Hill RL, Bain J, Thomas WP, editors. *A Review of Biological Control of Pests and Weeds in New Zealand 1874 to 1987*. Technical Communication No. 10. CAB International and DSIR, Wallingford, UK; 1989. p. 271–5.
 25. Boomsma CD, Adams AJS. The pine bark beetle (*Hylastes ater*) at Mount Burr, South Australia. *Australian Forestry* 1943;7:33–7.
 26. Neumann FG. Introduced bark beetles on exotic trees in Australia with special reference to *Ips grandicollis* in pine plantations. *Australian Forestry* 1987;50:166–78.
 27. Ciesla WM. Pine bark beetles: a new pest management challenge for Chilean foresters. *Journal of Forestry* 1988;86:27–31.
 28. Crowhurst PS. Observations on the breeding behaviour of *Hylastes ater* Paykull (Scolytidae: Coleoptera) at Eyrewell Forest. *Forest Entomology Report* (unpublished). New Zealand Forest Research Institute, Rotorua, New Zealand; 1969. 23p.
 29. Reay SD, Walsh PJ. The incidence of seedling attack and mortality by *Hylastes ater* (Coleoptera: Scolytidae) in second rotation *Pinus radiata* forests in the central North Island, New Zealand. *New Zealand Journal of Forestry* 2002;47:19–23.
 30. Stone C, Simpson JA. Species associations in *Ips grandicollis* galleries in *Pinus taeda*. *New Zealand Journal of Forestry Science* 1990;20:75–96.
 31. Raffa KF. Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones: *Ips pini* (Coleoptera: Scolytidae) in Wisconsin. *Environmental Entomology* 1991;20:1665–79.
 32. Paine TD, Raffa KF, Harrington TC. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 1997;42:179–206.
 33. Smalley EB, Raffa KF, Proctor RH, Klepzig KD. Tree responses to infection by species of *Ophiostoma* and *Ceratocystis*. In: Winfield MJ, Seifert KA, Webber JF, editors. *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*. American Phytopathological Society, St. Paul, MN; 1993. p. 207–17.
 34. Harrington TC. Diseases of conifers caused by species of *Ophiostoma* and *Leptographium*. In: Winfield MJ, Seifert KA, Webber JF, editors. *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*. American Phytopathological Society, St. Paul, MN; 1993. p. 161–72.
 35. Klepzig KD. Competition between a biological control fungus, *Ophiostoma piliferum*, and symbionts of the southern pine beetle. *Mycologia* 1998;90:69–75.
 36. Malloch D, Blackwell M. Dispersal biology of the ophiostomatoid fungi. In: Winfield MJ, Seifert KA, Webber JF, editors. *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*. American Phytopathological Society, St. Paul, MN; 1993. p. 195–205.
 37. Reay SD, Walsh PJ, Ram A, Farrell RL. The invasion of *Pinus radiata* seedlings by sapstain fungi, following attack by the black pine bark beetle, *Hylastes ater* (Coleoptera: Scolytidae). *Forest Ecology and Management* 2002;165:47–56.
 38. Reay SD, Thwaites JM, Farrell RL. A survey of *Ophiostoma* species vectored by *Hylastes ater* to pine seedlings in New Zealand. *Forest Pathology* 2005;35:105–13.
 39. Reay SD, Thwaites JM, Farrell RL. Survey of Ophiostomataceae associated with *Hylurgus ligniperda*

12 Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources

- (Curculionidae: Scolytinae) in New Zealand. *New Zealand Entomologist* 2006;29:21–6.
40. Reay SD, Thwaites JM, Farrell RL, Glare TR. The lack of persistence of Ophiostomataceae fungi in *Pinus radiata* three years after damage by the bark beetle *Hylastes ater*, and the subsequent colonization by *Sphareopsis sapinea*. *Forest Ecology and Management* 2006;233:149–52.
41. Humble LM, Allen EA. Forest biosecurity: alien invasive species and vectored organisms. *Canadian Journal of Plant Pathology* 2006;28:256–69.
42. Chararas C, Revolón C, Feinberg M, Ducauze C. Preference of certain scolytidae for different conifers: a statistical approach. *Journal of Chemical Ecology* 1982;8:1093–109.
43. Southwood TRE. Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 1962;37:171–214.
44. Atkins MD. Behavioural variation among Scolytids in relation to their habitat. *Canadian Entomologist* 1966;98:285–8.
45. Raffa KF, Berryman AA. The role of host plant resistance in the colonisation behaviour and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 1983;53:27–49.
46. Lindelöw Å. *Hylastes cunicularius*: host orientation, impact of feeding in spruce plantations, and population sizes in relation to seedling mortality (Coleoptera: Scolytidae) [PhD dissertation]. Sveriges Lantbruksuniversitet, Uppsala, Sweden; 1992.
47. Tribe GD. Phenology of *Pinus radiata* log colonisation by the pine bark beetle *Hylastes angustatus* (Herbst) (Coleoptera: Scolytidae) in the south-western Cape Province. *Journal of the Entomological Society of Southern Africa* 1990;53:93–100.
48. Wilson WL, Day KR. The comparative effectiveness of chemical traps, and fir, spruce and larch billets, for the estimation of pine weevil (*Hylobius abietis* L.). *Journal of Applied Entomology* 1995;119:157–60.
49. Rieske LK, Raffa KF. Baited pitfall traps and evaluation of dispensing methods for root weevils (Coleoptera: Curculionidae) in newly established pine plantations in Wisconsin. *Journal of Economic Entomology* 1999;92:439–44.
50. Byers JA. An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling* 1996;91:57–66.
51. Strom BL, Roton LM, Goyer RA, Meeker JR. Visual and semiochemical disruption of host finding in the southern pine beetle. *Ecological Applications* 1999;9:1028–38.
52. Wood DL. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review Entomology* 1982;27:411–46.
53. McNee WR, Bonello P, Storer AJ, Wood DL, Gordon TR. Feeding response of *Ips paraconfusus* to phloem and phloem metabolites of *Heterobasidion annosum* – inoculated ponderosa pine, *Pinus ponderosa*. *Journal of Chemical Ecology* 2003;29:183–1202.
54. Borden JH. Disruption of semiochemical-mediated aggregation in bark beetles. In: Cardé RT, Minks AK, editors. *Insect Pheromone Research: New Directions*. Chapman and Hall, New York; 1997. p. 421–38.
55. Zhang QH, Schlyter F. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology*. 2004;6:1–19.
56. Hobson KR, Wood DL, Cool LG, White PR, Toshikazu O, Isao K, *et al.* Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. *Journal of Chemical Ecology* 1993;19:1837–46.
57. Byers JA, Lanne BS, Schlyter F, Löfqvist J, Bergström G. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften* 1985;72:324–6.
58. Byers JA. Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. *Journal of Chemical Ecology* 1992;18:2385–402.
59. Schroeder LM, Lindelöw Å. Attraction of scolytids and associated beetles by different and absolute amounts and proportions of a-pinene and ethanol. *Journal of Chemical Ecology* 1989;15:807–17.
60. Raffa KF, Klepzig KD. Chiral escape of bark beetles from predators responding to a bark beetle pheromone. *Oecologia* 1989;80:566–9.
61. Blomquist GJ, Figueroa-Teran R, Aw M, Song MM, Gorzalski A, Abbott NL, *et al.* Pheromone production in bark beetles. *Insect Biochemistry and Molecular Biology* 2010;40:699–712.
62. Hodges JD, Elam WW, Watson WF, Nebeker TE. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. *Canadian Entomologist* 1979;111:889–96.
63. Silverstein RM, Rodin JO, Wood DL. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* 1966;154:509–10.
64. Ross DW, Gibson KE, Thier RW, Munson AS. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 1996;89:1204–7.
65. Gillette NE, Stein JD, Owen DR, Webster JN, Fiddler GO, Mori SR, *et al.* Verbenone-releasing flakes protect individual *Pinus contorta* trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). *Agricultural and Forest Entomology* 2006;8:243–51.
66. Erbilgin N, Raffa KF. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. *Journal of Chemical Ecology* 2000;26:2527–48.
67. Gladwin J, Kelsey RG, Peck RW, Niwa CG. Response of some scolytids to ethanol and 4-allylanisole in pine forest of central Oregon. *Journal of Chemical Ecology* 2001;27:697–715.
68. Rudinsky JA. Ecology of Scolytidae. *Annual Review of Entomology* 1962;7:327–48.
69. Niemeyer H. Integrated bark beetle control: experiences and problems in Northern Germany. In: Gregoire JC, Liebhold AM, Stephen FM, Day KR, Salom SM, editors. *Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests*. USDA, Washington, DC; 1997. p. 80–6.

70. Shea PJ, Haverty MI, Hall RC. Effectiveness of fenitrothion and permethrin for protecting ponderosa pine trees from attack by the western pine beetle. *Journal of the Georgia Entomological Society* 1984;19:427–33.
71. Eaton CB. Influence of the mountain pine beetle on the composition of mixed pole stands of ponderosa pine and white fir. *Journal of Forestry* 1941;39:710–3.
72. Whitehead RJ, Russo GL. 'Beetle-proofed' lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle. Information Report No. BC-X-402. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC; 2005. Available from: URL: <http://www.for.gov.bc.ca/hfd/library/documents/bib94728.pdf>
73. Santolamazza-Carbone S, Pestana M, Vega JA. Post-fire attractiveness of maritime pines (*Pinus pinaster* Ait.) to xylophagous insects. *Journal of Pest Science* 2011;84:343–53.
74. Fettig CJ, McMillin JD, Anhold JA, Hamud SM, Borys RR, Dabney CP, *et al.* The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *Forest Ecology and Management* 2006;230:55–68.
75. Schwerdtfeger F. Scolytidae on *Pinus* spp. in Central America. V. Mass outbreaks of *D. adjunctus* in Guatemala. *Zeitschrift für Angewandte Entomologie* 1960;46:1–33.
76. Nebeker TE, Hodges JD, Blanche CA. Host response to bark beetle and pathogen colonisation. In: Schowalter TD, Filip GM, editors. *Beetle-Pathogen Interactions in Conifer Forests*. Academic Press, London, UK; 1993. p. 157–71.
77. Smith R. Xylem monoterpenes of pines: distribution, variation, genetics, function. General Technical Report Issue: PSW-GTR-177. Pacific Southwest Research Station, USDA Forest Service, Albany, CA; 2000; 454 pp.
78. Phillips MA, Croteau RB. Resin-based defenses in conifers. *Trends on Plant Science* 1999;4:184–90.
79. Nordlund DA. Semiochemicals: a review of the terminology. In: Nordlund DA, Jones RL, Lewis WJ, editors. *Semiochemicals. Their Role in Pest Management*. John Wiley and Sons, New York; 1981. p. 13–28.
80. Raffa KF, Aukema BH, Erbilgin N, Klepzig KD, Wallin KF. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. In: Romeo J, editor. *Chemical Ecology and Phytochemistry of Forest Ecosystems*. Elsevier, Amsterdam; 2005. p. 79–118.
81. Mumm R, Hilker M. Direct and indirect chemical defence of pine against folivorous insects. *Trends in Plant Science* 2006;11:351–8.
82. Keeling CI, Bohlmann J. Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens. *New Phytologist* 2006;170:657–75.
83. Clarke S. Review of the operational IPM program for the southern pine beetle. *Integrated Pest Management Reviews* 2001;6:293–301.
84. Netherer S, Pennerstorfer J. Parameters relevant for modelling the potential development of *Ips typographus* (Coleoptera: Scolytidae). *Integrated Pest Management Reviews* 2001;6:177–84.
85. MacQuarrie CJK, Cooke BJ. Density-dependent population dynamics of mountain pine beetle in thinned and unthinned stands. *Canadian Journal of Forest Research* 2011;41:1031–46.
86. Aukema BH, Carroll AL, Zhu J, Raffa KF, Sickley TA, Taylor SW. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 2006;29:427–41.
87. Nelson WA, Potapov A, Lewis MA, Hundsdoerfer AE, He F. Balancing ecological complexity in predictive models: a reassessment of risk models in the mountain pine beetle system. *Journal of Applied Ecology* 2008;45:248–57.
88. Evangelista PH, Kumar S, Stohlgren TJ, Young NE. Assessing forest vulnerability and the potential distribution of pine beetles under current and future climate scenarios in the Interior West of the US. *Forest Ecology and Management* 2011;262:307–16.
89. Hastings FL, Holsten EH, Shea PJ, Werner RA. Carbaryl: a review of its use against bark beetles in coniferous forests of North America. *Environmental Entomology* 2001;30:803–10.
90. Fettig CJ, Munson AS, McKelvey SR. Spray deposition from ground-based applications of carbaryl to protect individual trees from bark beetle attack. *Journal of Environmental Quality* 2008;37:1170–9.
91. Berisford CW. Biological Control of Pine Bark Beetles: New Approaches to an Old Problem. Information Series. Virginia Polytechnic Institute and State University, College of Agriculture and Life Sciences 1991:91–2:57–66.
92. Zhong HE, Hastings HFL, Hain FP, Holsten EH, Werner RA. Rate of penetration and residual toxicokinetics of carbaryl on southern pine beetle and spruce beetle (Coleoptera: Scolytidae). *Journal of Economic Entomology* 1995;88:543–50.
93. Fettig CJ, Degomez TE, Gibson KE, Dabney CP, Borys RR. Effectiveness of permethrin plus-C (Masterline) and carbaryl (Sevin SL) for protecting individual, high-value pines (*Pinus*) from bark beetle attack. *Arboriculture and Urban Forestry* 2006;32:247–52.
94. Fettig CJ, Hayes CJ, McKelvey SR, Mori SR. Laboratory assays of select candidate insecticides for control of *Dendroctonus ponderosae*. *Pest Management Science* 2011;67:548–55.
95. De Gomez TE, Hayes CJ, Anhold JA, McMillin JD, Clancy KM, *et al.* Evaluation of insecticides for protecting southwestern ponderosa pines from attack by engraver beetles (Coleoptera:Curculionidae:Scolytinae). *Journal of Economic Entomology* 2006;99:393–400.
96. Naumann K, Rankin LJ. Pre-attack systemic applications of a neem-based insecticide for control of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* 1999;96:13–9.
97. Duthie-Holt MA, Borden JH. Treatment of lodgepole pine bark with neem demonstrates lack of repellency or feeding detergency to the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* 1999;96:21–4.
98. Grosman DM, Fettig CJ, Jorgensen CL, Munson AS. Effectiveness of two systemic insecticides for protecting

14 Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources

- western conifers from mortality due to bark beetle attack. *Western Journal of Applied Forestry* 2010;25:181–5.
99. Boobis AR, Ossendorp BC, Banasiak U, Hamey PY, Sebestyén I, Moretto A. Cumulative risk assessment of pesticide residues in food. *Toxicology Letters* 2008;180:137–50.
100. Jones RD, Steeger TM, Behl B. Environmental fate and ecological risk assessment for the re-registration of carbaryl. USEPA Office of Pesticide Programs, Environmental Fate and Effects Division, Washington, DC; 2003.
101. Dwyer FJ, Mayer FL, Sappington LC, Buckler DR, Bridges CM, Greer IE, *et al.* Assessing contaminant sensitivity of endangered and threatened aquatic species: Part I. Acute toxicity of five chemicals. *Archives of Environmental Contamination and Toxicology* 2005;48:143–54.
102. Bakke A, Sæther T, Kvamme T. Mass trapping of the spruce bark beetle *Ips typographus*: pheromone and trap technology. *Medd Norsk I Skogfor* 1983;38:35.
103. Vité JP, Baader E. Present and future use of semiochemicals in pest-management of bark beetles. *Journal of Chemical Ecology* 1990;16:3031–41.
104. Dodds KJ, Dubois GD, Hoebeke ER. Trap type, lure placement, and habitat effects on Cerambycidae and Scolytinae (Coleoptera) catches in the Northeastern United States. *Journal of Economic Entomology* 2010;103:698–707.
105. Lindgren BS. A multiple funnel trap for Scolytid beetles (Coleoptera). *Canadian Entomologist* 1983;115:299–302.
106. Borden JH. Strategies and tactics for the use of semiochemicals against forest insect pests in North America. In: Zumsde RD, Vaughn JL, editors. *Pest Management. Biologically Based Technologies*. American Chemical Society, Washington, DC; 1983. p. 265–79.
107. Brockerhoff EG, Bain J, Kimberley M, Knizek M. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research* 2006;36:289–98.
108. Seybold S, Huber D, Lee J, Graves A, Bohlmann J. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochemistry Reviews* 2006;5:143–78.
109. Wood DL, Stark RW, Waters WE, Bedard WD, Cobb Jr FW. Treatment tactics and strategies. In: Waters WE, Stark RW, Wood DL, editors. *Integrated Pest Management in Pine-bark Beetle Ecosystems*. John Wiley & Sons Inc., New York; 1985. p. 121–39.
110. Billings RF, Berisford CW, Salom SM, Payne TL. 1995. Applications of semiochemicals in the management of southern pine beetle infestations: current status of research. In: Salom SM, Hobson KR, editors. *Application of Semiochemicals for Management of Bark Beetle Infestations – Proceedings of an Informal Conference*. Annual Meeting of the Entomological Society of America. USDA, Forest Service, Intermountain Research Station, Indianapolis, IN; 1993. p. 30–8.
111. Weslien J. Effects of mass trapping on *Ips typographus* (L.) populations. *Journal of Applied Entomology* 1992;14:228–32.
112. Gokturk T, Aksu Y. Use of pheromone traps against *Tomicus piniperda* and *Tomicus minor* in the Kazbegi National Park, Georgian Republic. *African Journal of Agricultural Research* 2011;6:2430–5.
113. Schlyter F, Zhang QH, Liu GT, Ji LZ. A successful case of pheromone mass trapping of the bark beetle *Ips duplicatus* in a forest island, analysed by 20-year time-series data. *Integrated Pest Management Reviews* 2001;6:185–96.
114. Amman GD, Lindgren BS. Semiochemicals for management of mountain pine beetle: status of research and application. In: Salom SM, Hobson KR, editors. *Application of Semiochemicals for Management of Bark Beetle Infestations – Proceedings of an Informal Conference*. Annual Meeting of the Entomological Society of America. USDA, Forest Service, Intermountain Research Station, Indianapolis, IN; 1995. p. 14–22.
115. Cook SM, Khan ZR, Pickett JA. The use of push-pull strategies in integrated pest management. *Annual Review Entomology* 2007;52:375–400.
116. Smith DM. *The Practice of Silviculture*. John Wiley & Sons Inc., New York; 1986.
117. Rudinsky JA. Pheromone-mask by female *Dendroctonus pseudotsugae* Hopk an attraction regulator (Coleoptera – Scolytidae). *The Pan-Pac Entomologist* 1968;44:248–50.
118. Pitman GB, Vité JP. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera – Scolytidae) in response to chemical messengers. *Canadian Entomologist* 1969;101:143–9.
119. Borden JH, Chong LJ, Earle TJ, Huber DPW. Protection of lodgepole pine from attack by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using high doses of verbenone in combination with nonhost bark volatiles. *Forestry Chronicle* 2003;79:685–91.
120. Flechtmann CAH, Dalusky MJ, Berisford CW. Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. *Environmental Entomology* 1999;28:638–48.
121. Rudinsky JA, Morgan ME, Libbey LM, Putnam TB. Antiaggregative-rivalry pheromone for the mountain pine beetle, and a new arrestant of the southern pine beetle. *Environmental Entomology* 1974;3:90–8.
122. Leufven A, Bergstrom G, Falsen E. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *Journal of Chemical Ecology* 1984;10:1349–61.
123. Lindgren BS, Miller DR. Effect of verbenone on five species of bark beetles (Coleoptera: Scolytidae) in lodgepole pine forests. *Environmental Entomology* 2002;31:759–65.
124. Borden JH, Ryker LC, Chong LJ, Pierce HD, Johnston BD, Oehlschlager AC. Response of the mountain pine-beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera-Scolytidae), to 5 semiochemicals in British-Columbia lodgepole pine forests. *Canadian Journal of Forest Research* 1987;17:118–28.
125. Amman GD, Thier RW, Weatherby JC, Rasmussen LA, Munson AS. Optimum dosage of verbenone to reduce infestation of mountain pine-beetle in lodgepole pine stands of central Idaho. USDA Forest Service Intermountain Research Station Research Paper; 1991. p. 1–6.
126. Bentz BJ, Lister CK, Schmid JM, Mata SA, Rasmussen LA, Haneman D. Does verbenone reduce pine beetle attacks in

- susceptible stands of ponderosa pine? USDA Forest Service Research Note, RM-485; 1989.
127. Bentz BJ, Kegley S, Gibson K, Thier R. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) attacks. *Journal of Economic Entomology* 2005;98:1614–21.
 128. Progar RA. Verbenone reduces mountain pine beetle attack in lodgepole pine. *Western Journal of Applied Forestry* 2003;18:229–32.
 129. Lindgren BS, Borden JH. Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera, Scolytidae), in response to their antiaggregation and aggregation pheromones. *Canadian Journal of Forest Research* 1993;23:286–90.
 130. Byers JA, Wood DL. Interspecific effects of pheromones on the attraction of the bark beetles, *Dendroctonus brevicornis* and *Ips paraconfusus* (Coleoptera, Scolytidae) in the laboratory. *Journal of Chemical Ecology* 1981;7:9–18.
 131. Poland TM, Borden JH. Semiochemical-based communication in interspecific interactions between *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera, Scolytidae) in lodgepole pine. *Canadian Entomologist* 1994;126:269–76.
 132. Devlin DR, Borden JH. Efficacy of antiaggregants for the pine engraver, *Ips pini* (Coleoptera, Scolytidae). *Canadian Journal of Forest Research* 1994;24:2469–76.
 133. Wilson IM, Borden JH, Gries R, Gries G. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 1996;22:1861–75.
 134. Poland TM, De Groot P, Burke S, Wakarchuk D, Haack RA, Nott R. Semiochemical disruption of the pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae). *Environmental Entomology* 2004;33:221–6.
 135. Zhang QH, Birgersson G, Zhu JW, Lofstedt C, Lofqvist J, Schlyter F. Leaf volatiles from nonhost deciduous trees: variation by tree species, season and temperature, and electrophysiological activity in *Ips typographus*. *Journal of Chemical Ecology* 1999;25:1923–43.
 136. Zhang QH, Schlyter F. Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. *Oikos* 2003;101:299–310.
 137. Huber DPW, Borden JH. Angiosperm bark volatiles disrupt response of Douglas-fir beetle, *Dendroctonus pseudotsugae*, to attractant-baited traps. *Journal of Chemical Ecology* 2001;27:217–33.
 138. Moeck HA, Safranyik L. Assessment of predator and parasitoid control of bark beetles. Information Report BC-X-248. Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre; 1984.
 139. Kenis M, Wermelinger B, Grégoire JC. Research on parasitoids and predators of Scolytidae – a review. In: Lieutier F, Day K, Battisti A, Grégoire JC, Evans HF, editors. *European Bark and Wood Boring Insects in Living Trees. A Synthesis*. Kluwer, Dordrecht; 2004. p. 237–90.
 140. Kennedy AA, McCullough DG. Phenology of the larger European pine shoot beetle *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in relation to native bark beetles and natural enemies in pine stands. *Environmental Entomology* 2002;31:261–72.
 141. Schroeder LM. Attraction of the bark beetle *Tomicus piniperda* and some other bark- and wood-living beetles to the host volatiles alpha-pinene and ethanol. *Entomologia Experimentalis et Applicata* 1988;46:203–10.
 142. Herard F, Mercadier G. Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col., Scolytidae) on *Pinus sylvestris* near Orleans, France: temporal occurrence and relative abundance, and notes on eight predatory species. *Entomophaga* 1996;41:183–210.
 143. Dahlsten DL. Relationships between bark beetles and their natural enemies. In: Mitton JB, Sturgeon KB, editors. *Bark Beetles in North American Conifers – A System for the Study of Evolutionary Biology*. University of Texas Press, Austin, TX; 1982. p. 140–82.
 144. Aukema BH, Raffa KF. Chemically mediated predator-free space: herbivores can synergize intraspecific communication without increasing risk of predation. *Journal of Chemical Ecology* 2000;26:1923–39.
 145. Raffa KF. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology* 2001;11:49–65.
 146. Gallego D, Galian J, Diez JJ, Pajares JA. Kairomonal responses of *Tomicus destruens* (Col., Scolytidae) to host volatiles alpha-pinene and ethanol. *Journal of Applied Entomology* 2008;132:654–62.
 147. Warzee N, Gilbert M, Gregoire JC. Predator/prey ratios: a measure of bark-beetle population status influenced by stand composition in different French stands after the 1999 storms. *Annals of Forest Science* 2006;63:301–8.
 148. Sullivan BT, Pettersson EM, Seltmann KC, Berisford CW. Attraction of the bark beetle parasitoid *Roptrocercus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. *Environmental Entomology* 2000;29:1138–51.
 149. Sullivan BT, Seltmann KC, Berisford CW. A simple continuous-rearing technique for the bark beetle parasitoid, *Roptrocercus xylophagorum* (Ratzeburg). *Journal of Entomological Science* 1999;34:260–4.
 150. Wei JR, Ding BF, Tang YL, Zhao JX, Yang ZQ. Study on the relationship between growth and environmental temperature of *Rhizophagus grandis* (Coleoptera: Rhizophagidae), an important predator of *Dendroctonus valens* (Coleoptera: Scolytidae). *Forest Research, Beijing* 2010;23:478–81.
 151. Zondag R. Breeding of the clerid *Thanasimus formicarius* for the control of the bark beetles *Hylastes ater* and *Hylurgus ligniperda* in New Zealand. *New Zealand Journal of Forestry Science* 1979;9:125–32.
 152. Safranyik L, Shore TL, Moeck HA, Whitney HS. *Dendroctonus ponderosae* Hopkins, mountain pine beetle (Coleoptera: Scolytidae). In: Mason PG, Huber JT, editors. *Biological Control Programmes in Canada, 1981–2000*. CABI, Oxfordshire, UK; 2001. p. 104–9.
 153. Milligan RH. *Hylastes ater* (Paykull) (Coleoptera: Scolytidae): black pine beetle. *Forest and Timber Insects in New Zealand No. 29*. Forest Research Institute, New Zealand Forest Service, Rotorua, New Zealand; 1978.
 154. Goettel MS, Eilenberg J, Glare TR. Entomopathogenic fungi and their role in regulation of insect. In: Gilbert LI,

16 Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources

- Gill SS, editors. Insect Control: Biological and Synthetic Agents. Academic Press, San Diego, CA; 2010. p. 387–432.
155. Wegensteiner R, Weiser J. A new entomopox virus in bark beetle *Ips typographus* (Coleoptera: Scolytidae). *Journal of Invertebrate Pathology* 1995;65:203–5.
156. Händel U, Wegensteiner R, Weiser J, Zizka Z. Occurrence of pathogens in associated living bark beetles (Col., Scolytidae) from different spruce stands in Austria. *Journal of Pest Science* 2003;76:22–32.
157. Wegensteiner R. Pathogens in bark beetles. In: Lieutier F, Day KR, Battisti A, Gregoire JC, Evans HF, editors. *Bark and Wood Boring Insects in Living Trees in Europe: A Synthesis*. Springer Publishing, Dordrecht, The Netherlands; 2004. p. 291–313.
158. Burjanadze M, Lortkipanidze M, Supatashvili A, Gorgadze O. Occurrence of pathogens and nematodes of bark beetles (Coleoptera, Scolytidae) from coniferous forest in different region of Georgia. In: *Proceedings of the IOPC/WPRS Working Group "Insect Pathogens and Entomopathogenic Nematodes"*, Innsbruck, Austria, 19–23 June 2011. p. 351–4.
159. Fuxa JR, Ayyappath R, Goyer RA. *Pathogens and Microbial Control of North American Forest Insect Pests*. USDA Forest Health Technology Enterprise Team Publication; 1998. 97–27, 235 p.
160. Kaya HK. Nematode parasites of bark beetles. In: Nickle WR, editor. *Plant and Insect Nematodes*. Marcel Dekker, New York; 1984. p. 727–54.
161. Pabst GS, Sikorowski PP. Susceptibility of southern pine beetle (*Dendroctonus frontalis*) on oligidic medium to *Paecilomyces viridis* and also *Beauveria bassiana*, and *Metarhizium anisopliae*. *Journal of the Georgia Entomological Society* 1980;15:235–40.
162. Glare TR, Reay SD, Nelson TL, Moore R. *Beauveria caledonica* is a naturally occurring pathogen of the forest pests *Hylastes ater* and *Hylurgus ligniperda* (Coleoptera: Scolytidae) in New Zealand and *Hyllobius abietis* (Coleoptera: Curculionidae) in the United Kingdom. *Mycological Research* 2008;112:352–60.
163. Draganova SA, Takov DI, Doychev DD. Naturally-occurring entomopathogenic fungi on three bark beetle species (Coleoptera: Curculionidae) in Bulgaria. *Pesticides and Phytomedicine (Belgrade)* 2010;25:59–63.
164. Reay SD, Brownbridge M, Cummings NJ, Nelson TL, Souffre B, Lignon C, *et al.* Isolation and characterisation of *Beauveria* spp. associated with exotic bark beetles in New Zealand *Pinus radiata* plantation forests. *Biological Control* 2008;46:484–94.
165. Steinwender BM, Krenn HW, Wegensteiner R. Different effects of the insect pathogenic fungus *Beauveria bassiana* (Deuteromycota) on the bark beetle *Ips sexdentatus* (Coleoptera: Curculionidae) and on its predator *Thanasimus formicarius* (Coleoptera: Cleridae). *Journal of Plant Diseases and Protection* 2010;117:33–8.
166. Brownbridge M, Reay SD, Cummings NJ. Association of entomopathogenic fungi with exotic bark beetles in New Zealand pine plantations. *Mycopathologia* 2010;169:75–80.
167. Bychawska S, Swiezynska H. Attempts to control *Myelophilus piniperda* by means of the entomopathogenic fungus *Beauveria bassiana*. *Sylwan* 1979;123:59–64.
168. Moore GE. Mortality factors caused by pathogenic bacteria and fungi of the southern pine beetle in North Carolina. *Journal of Invertebrate Pathology* 1971;17:28–37.
169. Moore GE. Pathogenicity of ten strains of bacteria to larvae of the southern pine beetle. *Journal of Invertebrate Pathology* 1972;20:11–45.
170. Glare TR, O'Callaghan M. *Bacillus thuringiensis*; Biology, Ecology and Safety. John Wiley and Sons, Chichester, UK; 2000.
171. Cane JH, Cox HE, Moar WJ. Susceptibility of *Ips calligraphus* (Germar) and *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) to coleopteran-active *Bacillus thuringiensis*, a *Bacillus* metabolite, and avermectin B1. *Canadian Entomologist* 1995;127:831–7.
172. Bedding RA. Entomopathogenic nematodes from discovery to application. *Biopesticides International* 2006;2:87–119.
173. MacVean CM, Brewer JW. Suitability of *Scolytus multistriatus* and *Dendroctonus ponderosae* as hosts for the entomogenous nematode *Neoaplectana carpocapsae*. *Journal of Economic Entomology* 1981;74:601–7.
174. Triggiani O. Susceptibility of *Tomicus (Blastophagus) piniperda* L. (Col. Scolytidae) to nematodes of the family Steinernematidae and Heterorhabditidae. *Entomologica* 1983;18:215–23.
175. Takov D, Pilarska D, Wegensteiner R. List of protozoan and microsporidian pathogens of economically important bark beetle species (Coleoptera: Curculionidae: Scolytinae) in Europe. *Acta Zoologica Bulgarica* 2010;62:201–9.
176. Purrini K, Halperin J. *Nosema calcarati* n.sp. (Microsporidia), a new parasite of *Pityogenes calcaratus* Eichhoff (Col., Scolytidae). *Zeitschrift für Angewandte Entomologie* 1982;94:87–92.
177. Kard BM. Inability of three entomogenous nematodes to locate and infect *Dendroctonus frontalis* (Coleoptera: Scolytidae) larvae in beetle infested loblolly pine bolts. *Florida Entomologist* 1991;74:156–8.
178. Reay SD, Brownbridge M, Gicquel B, Cummings NJ, Nelson TL. Isolation and characterization of endophytic *Beauveria* spp. (Ascomycota:Hypocreales) from *Pinus radiata* in New Zealand forests. *Biological Control* 2010;54:52–60.
179. Ganley RJ, Newcombe G. Fungal endophytes in seeds and needles of *Pinus monticola*. *Mycological Research* 2005;110:318–27.
180. Zhang LW, Liu YJ, Yao JA, Wang B, Huang B, Li ZZ, *et al.* Evaluation of *Beauveria bassiana* (Hyphomycetes) isolates as potential agents for control of *Dendroctonus valens*. *Insect Science* 2011;18:209–16.
181. Kreutz J, Zimmermann G, Vaupel O. Horizontal transmission of the entomopathogenic fungus *Beauveria bassiana* among the spruce bark beetle, *Ips typographus* (Col., Scolytidae) in the laboratory and under field conditions. *Biocontrol Science and Technology* 2004;14:837–48.
182. Aukema BH, Raffa KF. Selective manipulation of predators using pheromones: responses to frontalin and ipsdienol pheromone components of bark beetles in the Great Lakes region. *Agricultural and Forest Entomology* 2005;7:193–200.
183. Aukema BH, Dahlsten DL, Raffa KF. Exploiting behavioral disparities among predators and prey to selectively remove

- pests: maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology* 2000;29:651–60.
184. EPPO. *Dendroctonus brevicomis*. Data Sheets on Quarantine Pests. Available from: URL: http://www.eppo.org/QUARANTINE/insects/Dendroctonus_brevicomis/DENCBR_ds.pdf, 2006. 5pp.
 185. Haack RA, Paiz-Schwartz G. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 1997;108:67–76.
 186. Ungerer MJ, Ayres MP, Lombardero MJ. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography* 1999;26:1133–45.
 187. CABI/EPPO. *Dendroctonus ponderosae*. Distribution Maps of Plant Pests No. 635. CABI Head Office, Wallingford, UK; 2002.
 188. Price TS. Insect Enemies of Slash Pine. General Technical Report SRS-76. Southern Research Station, USDA Forest Service, Albany, CA; 2004. p. 84–6.
 189. Zanzot JW, Matusick G, Eckhardt LG. Ecology of root-feeding beetles and their associated fungi on longleaf pine in Georgia. *Environmental Entomology* 2010;39:415–23.
 190. USDA Forest Service. Insects of Eastern Forests. Miscellaneous Publication No. 1426. USDA Forest Service, Washington, DC; 1985. 608 p.
 191. Ruiz CG, Lanfranco DL. Bark beetles in Chile: a review of the current situation and its effects in the international trade. *Bosque* 2008;29:109–14.
 192. Global Invasive Species Database. 2010 *Hylastes ater* [cited September 2011]. Available from: URL: <http://www.issg.org/database/species/ecology.asp>
 193. Leahy MJA, Oliver TH, Leather SR. Feeding behaviour of the black pine beetle, *Hylastes ater* (Coleoptera: Scolytidae). *Agricultural and Forest Entomology* 2007;9:115–24.
 194. Sarkaya O, Avc M. Bark beetle fauna (Coleoptera: Scolytinae) of the coniferous forests in the Mediterranean region of Western Turkey, with a new record for Turkish fauna. *Turkish Journal of Zoology* 2011;35:33–47.
 195. Wingfield MJ, Swart WJ. Integrated management of forest tree diseases in South Africa. *Forest Ecology and Management* 1994;65:11–6.
 196. Lu M, Miller DR, Sun J-H. Cross-attraction between an exotic and a native pine bark beetle: a novel invasion mechanism? *PLoS ONE* 2007;2(12):e1302.
 197. CABI/EPPO. *Hylurgus ligniperda*. Distribution Maps of Plant Pests No. 740. CABI Head Office, Wallingford, UK; 2010.
 198. Furniss RL, Carolin VM. Western Forest Insects. Miscellaneous Publication No. 1339. U.S. Department of Agriculture, Forest Service, Washington, DC; 1977.
 199. Connor MD, Robert Wilkinson RC. Ips Bark Beetles in the South. Forest Insect & Disease Leaflet 129. USDA Forest Service, Albany, CA; 1983.
 200. CABI/EPPO. *Ips calligraphus*. Distribution Maps of Plant Pests No. 720. CABI Head Office, Wallingford, UK; 2009.
 201. CABI/EPPO. *Ips grandicollis*. Distribution Maps of Plant Pests No. 691. CABI Head Office, Wallingford, UK; 2007.
 202. Sartwell C, Schmitz RF, Buckhorn WJ. Pine engraver, *Ips pini*, in the western States. Forest Pest Leaflet No. 122. USDA Forest Service, Albany, CA; 1971.
 203. Borkowski A. A method of estimation of the total density of infestation of Scots pine stems by the lesser pine shoot beetle (*Tomicus minor*). *Electronic Journal of Polish Agricultural Universities* 2010;13:art 14.
 204. Horn A, Stauffer C, Lieutier F, Kerdelhue C. Complex postglacial history of the temperate bark beetle *Tomicus piniperda* L. (Coleoptera, Scolytinae). *Heredity* 2009;103:238–47.