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].

Scolytsids 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.

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

---

**Table 1** (Cont.)

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

**References**

[140, 204]
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 monoterpane components in ponderosa pine are β-pinene, 3-carene and an α-pinene [56]. Similarly, *Tamiaspis 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 curriculatus* 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-2-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 brevicomis* 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 4,4-dimethylbicyclo[3.1.1] hept-2-en-2-one (4,6,6-trimethylbicyclo[3.1.1.]hept-2-en-2-one) [64, 65].

**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

http://www.cabi.org/cabreviews
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 radiata* 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.

http://www.cabi.org/cabreviews
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 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].

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 *lps* 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 phosphate, a strong poison used to control rodents, has been phosphided to control *D. valens* in China, and dimethyl dichlorovinyl phosphate (DVVP) or omeothoate (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 ponderosae 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 used 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 repellant 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 Ips 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 repellant 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. cantora [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 Medeteria 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 parasitoids 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, Roptrocerus 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 parasitoids 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 Tenebrionid 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 sphæreas 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 there 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 & Widd., Isaria farinosa (Holm.) Frank (= Paecilomyces fumosoroseus) 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 L. 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 cannot 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 (≤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 carpocapsae (=Neodera 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 beetles 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 calcarius Eichhoff in Israel [176]. Protozoan 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 [Neodera] feltiae (Filipjev), S. [N.] glaseni (Steiner) and H. bacteriophora Poinar (=Heterorhabditis helathidis), but no infections were found.

http://www.cabi.org/cabreviews
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 *l. 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**

10. Klingenber MD, Lindgren BS, Gillingham MP, Aukema BH. Management response to one insect pest may increase

http://www.cabi.org/cabreviews


Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources


http://www.cabi.org/cabreviews


92. Fettig CJ, Degomez TE, Gibson KE, Dabney CP, Borys RR. Effectiveness of permethrin plus-C (Masterline) and carbaryl (Sevin SL) for protecting individual trees from bark beetle attack. Journal of Environmental Quality 2008;37:1170–9.


126. Bentz BJ, Lister CK, Schmid JM, Mata SA, Rasmussen LA, Haneman D. Does verbenone reduce pine beetle attacks in...


131. Poland TM, Borden JH. Semiochemical-based communication in interspecific interactions between *ips pini* (Say) and *Phyogenes knechti* (Swaine) (Coleoptera, Scolytidae) in lodgepole pine. Canadian Entomologist 1994;126:269–76.


154. Goettel MS, Eilenberg J, Giare TR. Entomopathogenic fungi and their role in regulation of insect. In: Gilbert LI,


pests: maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out.


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.


http://www.cabi.org/cabreviews