



Review

A review of semiochemicals associated with bark beetle (Coleoptera: Curculionidae: Scolytinae) pests of coniferous trees: A focus on beetle interactions with other pests and their associates

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ABSTRACT

Bark beetles (Curculionidae) have assumed increasing prominence as pests of coniferous trees and wood products. Some species of *Ips* and *Dendroctonus* introduce blue stain fungi that cause damage to trees and downgrading of wood products. In forest ecosystems, bark beetles respond to fire, frost, drought, lightning or windstorms, all of which can initiate tree stress. Silvicultural practices that improve tree vigour are widely used to manage these pests. Pruning, disposing of infested limbs and salvage logging following storm damage are also frequently employed. Systemic insecticide applications can be used to protect trees from beetle attack for several months to a year. Insecticides are also frequently used to protect trees of high value in landscape settings, seedlings in nurseries and can be used as bole sprays where trees may be treated during outbreaks. Insecticides are, however, often uneconomical in natural and commercial forests, particularly in broad acre landscapes. Options for better management could involve the wider use of semiochemicals (pheromones and kairomones) that influence beetle behaviour such as feeding, mating and oviposition. Currently, semiochemicals are used extensively for monitoring bark beetle populations and for optimising timing of silviculture treatments. Semiochemical use for protecting trees using 'push-pull' strategies are promising and, in some cases, effective strategies for control of scolytines. Recent research shows that volatiles from unsuitable and non-host tree species could impede bark beetle attack on conifer trees. Applications of bark beetle pheromone components, such as verbenone, when used as a blend with non-host volatiles can deter scolytine bark beetles from trees. The use of semiochemicals and non-host volatiles in the management of bark beetles is, however, complicated when other insect pests and their associates are present together with bark beetles. Effective management of bark beetles under these circumstances will depend on a better understanding of the key chemical ecology stimuli of relevance to each pest. We review semiochemicals of bark beetles and their use as interruptants or inhibitors when used together with non-host volatiles. Implications of using semiochemicals when scolytine bark beetles attack trees together with other tree pests is discussed with an example of interactions between a wood wasp and an *Ips* species presented.

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1. Introduction

Scolytine bark beetle species have been accidentally introduced in Europe (Lieutier et al., 2004), North America (Mattson et al., 1994) and Australia (Neumann, 1987). The presence of bark beetles is of concern as they are capable of killing even healthy trees in natural and commercial forests (Schowalter et al., 1981; Paine et al., 1997; Raffa et al., 2005), resulting in considerable economic impact (Lieutier et al., 2004). Aside from impact on cosmopolitan forestry species such as *Pinus radiata* D. Dons, beetles may also undergo a host switch to attack native tree species, with potentially serious ecological consequences (Six and Paine, 1999). The impacts of bark beetles in natural forests leads to the loss of native trees with adverse effects on ecosystem services such as water purification, stabilising slopes, carbon sequestration, conservation of wildlife and soil formation. Outbreaks may result in host replacement by other tree species and new plant associations that may impact timber and fibre production, fuels and fire behaviour, and aesthetics, recreation, grazing capacity, real estate values, biodiversity, carbon storage, cultural and other resources.

Approximately 3700 of the 7500 species in the weevil (Curculionidae) subfamily Scolytinae attack forest trees (Bright, 1993; Marvaldi et al., 2002). Scolytine bark beetles generally attack stressed trees and can lead to tree death (Kausrud et al., 2012). Beetle-related tree deaths subsequently cause openings in the forest canopy which increase the amount of sunlight reaching the understory below. Changes in sunlight alter both the canopy and understory species that grow back after beetle attack (Collins et al., 2011). Canopy reduction changes water dynamics and hence tree physiology (Jactel et al., 2009). In plantations and natural forests, trees attacked by bark beetles deteriorate leading to reduction in volume of timber harvested (Raymond, 2008). Investigations of many possible management tactics arising from semiochemical strategies have led to operational management programs such as suppression of bark beetle populations through the utilisation of semiochemical-baited traps and inhibitors to protect vulnerable host trees from attack. This review focuses on these applications and scolytines chemical ecology, especially on how semiochemicals from the beetles, their hosts or from non-host plants might be exploited for better management of this important group of forestry pests. Interactions between bark beetles and their associates are also discussed.

2. Impacts of bark beetles

In outbreak situations, bark beetle infestations can directly kill trees (Amman and Lindgren, 1995), while less severe attack may predispose trees to subsequent invasion by other pests or to reinvasion by subsequent generations (Klepzig et al., 1991). Primary bark beetles, those that attack healthy trees and overcome tree defences by a mass aggregation strategy, successfully establish on host trees through pheromone-mediated mass attacks (Paine et al., 1997). The beetles introduce fungi that help them overcome the tree defences (Aukema et al., 2010). Secondary bark beetles on the other hand attack stressed trees and use ethanol from decaying host trees (Klimetzek et al., 1986) as a kairomone attractant

(Moeck et al., 1981; Gilbert et al., 2001). Healthy trees are attacked by primary bark beetles such as *Dendroctonus ponderosae* Hopkins, *D. frontalis* (Zimmermann) and *Ips typographus* (Linnaeus) which cause tree mortality as a result of mass colonisation (Byers, 1989). Secondary bark beetles (e.g., *I. pini* Say, *Scolytus ventralis* LeConte, *D. simplex* LeConte, and *Tomicus piniperda* (Linnaeus)), colonise weakened, stressed, and recently killed trees (Klepzig et al., 1991; Langstrom and Hellqvist, 1993). Bark beetles have significant effects on the decomposition of trees, as plant pathogen vectors and as the initial decomposers of tree debris (Edmonds and Eglitis, 1989). Equally important and not easily measured are the ecological consequences for affected ecosystems. These may include changes in ecosystem structure and interspecies dynamics, and changes in biological diversity, especially if the beetles are invasive species (Neumann, 1987).

Abiotic and biotic stress predisposes forest trees to infestation by insect herbivores and fungal diseases (Wargo and Harrington, 1991; Williams and Liebhold, 1995). In outbreak conditions, mass beetle attack can overwhelm tree defences. Outbreaks often occur after wind damage, fire or drought (Wermelinger, 2004; Aukema et al., 2008; Carnegie, 2008; Ivković et al., 2010; Kausrud et al., 2012; Marini et al., 2012; Simard et al., 2012) and can have significant adverse effects on nutrient cycling, water quality and quantity, carbon sequestration, and biodiversity (Ayres and Lombardero, 2000; Kurz et al., 2008). For example, *Ips grandicollis* (Eichhoff) caused serious damage to *P. radiata* in South Australia in the 1940s (Morgan and Griffith, 1989) and is currently causing tree mortality in New South Wales, Australia (Carnegie, 2008; Carnegie and Loch, 2010). Nevertheless, outbreaks of scolytine beetles may help regenerate natural forests by killing older trees as well as encouraging the decomposition of dead wood. Following the outbreaks of *I. typographus* in Germany (Müller et al., 2008), the administration of the Bavarian national park decided against management of the areas affected to allow for forest succession and regeneration (Müller and Job, 2009).

3. Life cycle and symbionts

Scolytine bark beetles generally mate and tunnel within the phloem where they construct galleries and oviposit. The extent of damage due to the beetles' activity depends largely on the numbers attacking as well as favourable climatic and forest conditions coinciding in time and space. A few scolytine species are near-obligate parasites (e.g., *D. micans* (Kugelann) in Europe and *D. terebrans* (Olivier) and *D. valens* LeConte in North America) which rarely kill their host trees. Some non-aggregating species colonise the base of trees that are often weakened by injury or root diseases (Raffa et al., 2005) while some like *D. valens* aggregate almost exclusively at the base of trees (Wood, 1982). The larvae of these beetles are gregarious and feed in large chambers in the inner bark. Scolytines have two feeding strategies, those that feed on the xylem (ambrosia beetles; subfamily Scolytinae) and those that feed on the phloem (phloeophagous) (Paine et al., 1997).

Xylem feeders introduce an ascomycete fungus, usually an *Ambrosiella* sp., on which they feed. Infestation of trees by the fungi lowers the economic value of wood by causing undesirable colour

(Orbay et al., 1994). Phloem feeders lay eggs, larvae hatch in about a week and feed on the living phloem or inner bark. The latter can attack living trees in large numbers causing tree mortality (Ayres et al., 2000) and are often associated with blue-stain fungi such as *Ceratocystis polonica* (Siem.) C. Moreau, *Ophiostoma polonicum* Robinson-Jeffrey and Davidson, *O. ips* Wingfield (Christiansen and Solheim, 1990; Ghaïoule et al., 2007; Adams et al., 2009) among others. Fungi associated with tree-killing bark beetles have been known to overwhelm tree defenses and subsequently cause substantial host tree mortality (Christiansen and Solheim, 1990). However, a recent review by Six and Wingfield (2011), suggests that phytopathogenicity from the fungi may mediate competitive interactions and support beetle survival and efficient resource gain from host trees.

4. Management of bark beetles

Control of scolytine bark beetles is difficult because of their largely cryptic feeding habit and the often extensive nature of forests. Silvicultural practices that minimise bark beetle attack are commonly applied in commercial forestry. They involve thinning, pruning and implementation of short planting cycles as well as precise timing of harvesting operations which are synchronised outside the beetle flight period (Christiansen and Fjone, 1993). Debarking cut timber and destroying infested trees by chipping, burning or burying removes the beetle broods and prevents further attack (Jactel et al., 2009). Clearing wind-thrown timber to reduce breeding material is an important preventive method (Grégoire and Evans, 2004) with varying success, e.g., the method is sometimes ineffective in western North America (Wickman, 1987). Some silvicultural methods involve direct control techniques such as cut-and-remove or cut-and-leave. The effectiveness of these methods varies among bark beetle species with differing life cycle and patterns of attack. Tree density can affect the incidence and severity of bark beetle infestations and thinning has been advocated as a preventative measure that reduces bark beetle induced tree mortality (Fettig et al., 2007a). Some studies on the efficacy of thinning have, however, failed to detect significant benefit and some bark beetles are attracted to thinning residues (Cochran, 1998).

Mass trapping of bark beetles by pheromone traps or standing live trap trees is used to reduce population densities to levels below the critical threshold (El-Sayed et al., 2006; Hansen et al., 2006; Schiebe et al., 2011). Studies have shown that traps might provide more effective control of bark beetles (Raty et al., 1995; Faccoli and Stergulc, 2008). Use of traps is important for preventing attack by primary bark beetles as numbers of beetles caught in traps or trap trees may be well used as an identification of specific beetles or flight seasons (Billings, 1988). The trapping technique should have good selectivity and a reduced impact on the natural enemies and should also be ecologically safe. A serious problem with mass trapping, however, is the inadvertent removal of natural enemies that respond to baits as kairomones (Aukema et al., 2000). An integrated beetle management approach is important as numbers of beetles caught in traps at a given place and time is not exclusively decisive for the attack on trees (Faccoli and Stergulc, 2008; Raty et al., 1995; Wermelinger, 2004).

Predators, parasitoids and competitors of bark beetles have potential as biological control agents of scolytine bark beetles. Bark beetle predators and parasitoids have been shown to detect aggregating pheromones of prey beetles (Hayes and Strom, 1994). Classical biocontrol has been attempted for introduced scolytine beetles. For example, a common predator of scolytine bark beetles, *Thanasimus dubius* (F.) (Coleoptera: Cleridae) was introduced against *I. grandicollis* in Australia (Lawson and Morgan, 1992) though establishment of the parasitoids is not yet known. Inundative releases are used against beetles at low intensity

outbreaks, e.g., *T. dubius* has been used against several native species of *Dendroctonus* (Miller et al., 1987). Entomopathogenic microorganisms such as bacteria, viruses, fungi, protozoa and nematodes play a major role in population dynamics of forest pests. Bacteria also are potential biocontrol agents against scolytine bark beetles. A study by Sevim et al. (2012) showed that strains of *Pseudomonas fluorescens* Flügge (Pseudomonadales: Pseudomonadaceae) can be modified to express insecticidal toxins and other detrimental substances against *I. sexdentatus* (Boern). Biocontrol agents are strongly r-selected and hence able to disperse in time and space in extensive areas and biological control is hence, generally a desirable approach and theoretically possible to management of scolytine bark beetles. Challenges lie in identifying difficulties in identifying effective agents and constraints to introduction of exotic agents to new locations.

Chemical control is a strategy that has been used to combat both the xylem (Damon, 2000; Pena et al., 2011) and phloem feeding bark beetles (Fettig et al. 2006; Stone and Simpson, 1991; Grosman et al., 2010.) The method employs insecticides which are used to protect high-value trees in recreational grounds (e.g., campgrounds, resorts) or administrative sites from bark beetle attack. Protection of individual trees has previously involved applications of liquid formulations of contact insecticides to the tree bole using hydraulic sprayers (Haverty et al., 1997). Recently, environmentally safe alternatives have examined the effectiveness of injecting small quantities of systemic insecticides directly into trees (Grosman et al., 2010). Some insecticides, e.g., oxydemeton methyl (Metasystox-R) used for protecting individual trees from attack by several western bark beetle species, but it has been shown to be largely ineffective and is not recommended (Haverty et al., 1997). Lack of efficacy may be attributed to the type of insecticide used, resin flow by the tree may prevent uptake, chemical mobility into or through phloem tissue may be obstructed or the tree could be water stressed. Insecticides may have detrimental effects on natural enemies. Given this, it is thus important to look into the chemical ecology of scolytines bark beetles and explore the development of semiochemicals as an alternative pest management method.

5. Semiochemicals of scolytine bark beetles

Most insects use semiochemicals to communicate and to interact with their hosts and other species (Norin, 2007). Semiochemicals have been shown to influence various aspects of scolytine bark beetle biology (Borden, 1989). Signals effective intraspecifically (within a single species) are referred to as pheromones. For instance, alarm, sex and food trail pheromones affect behaviour or physiology of individuals within the same species (van Tol et al., 2001). Signals between different species are allelochemicals. Depending on their respective biological function, allelochemicals are classified as allomones (those that benefit the emitter), kairomones (those that benefit the recipient), synomones (those that benefit both the emitter and recipient) or apneumones (those from non-living sources) (Nordlund, 1982). Of course a given semiochemical may function in more than one of these categories depending on the receiving species. Within a given scolytine species, communication is based on pheromones which are made up of single, or more commonly mixtures of compounds. The qualitative and quantitative composition of the pheromones is unique within bark beetle species as they are used for reproduction, isolation and aggregation of conspecifics (van Tol et al., 2001). Most bark beetles also produce acoustic signals that have been implicated in defence, courtship, aggression and species location and recognition (Ryker and Rudinsky, 1976). Despite the ubiquity of acoustic signalling in bark beetles, there is little information available on the characteristics and function of these signals in

different species, how these signals are received and transmitted through either the air or wood and potential for their use in pest management. Accordingly, the following sections discuss current knowledge on chemical communication in host selection and colonisation by scolytine bark beetles in forests.

5.1. Host selection and colonisation

The most important determinant of fitness for bark beetles is location of a suitable host (Raffa, 2001). Many scolytine species avoid the costs of having to land to determine host identity and quality by responding to olfactory cues while in flight (Raffa et al., 1993; Byers et al., 1985). Initial host location by some species is mediated by volatiles from host tree semiochemicals (Wallin and Raffa, 2002; Erbilgin et al., 2003). For example, the Douglas-fir beetle, *D. pseudotsugae* Hopkins is attracted to synthetic blends of Douglas-fir foliage and tree trunk monoterpenes, although *D. ponderosae* Hopkins is not (Pureswaran and Borden, 2005). Foraging bark beetles perceive their environment through different sensory modes such as olfaction, vision or taste (Moeck et al., 1981; Byers, 1989). Cues used at any particular time vary in both cost of assessment such as events following landing versus flight and, in precision. These factors affect the sensory mode used during host selection (Fawcett and Johnstone, 2003).

Cues such as substrate colour, texture, form and contrast are usually synchronised with olfaction (Prokopy and Owens, 1983; Borden et al., 1986; Campbell and Borden, 2006). Goyer et al. (2004) found that the total number of *Ips* spp. arriving at *Pinus taeda* L. pine logs was significantly affected by colour; fewer *Ips* spp. were caught at logs painted white than those painted a dark colour. Strom et al. (1999) showed that visual and semiochemical treatments, especially used in combination, disrupted host finding by *D. frontalis*. By using a combination of treatments with the antiaggregation pheromone verbenone, or the repellent host compound 4-allylanisole in addition to the attractant, few *D. frontalis* were caught in traps. Visual cues may enable precise approach to the tree, enabling beetles to orientate and land on suitable host trees, while semiochemicals enable the beetles to colonise the host. Recent evidence shows that other cues enable beetles to accept host trees. Walter et al. (2010) showed that host acceptance by *Orthotomicus erosus* (Wollaston) (Coleoptera: Curculionidae) is determined by both gustatory and non-gustatory cues rather than bark and phloem volatiles.

Bark beetle pheromones in combination with kairomones (host derived volatiles) enable the insects to coordinate attack on specific host trees (Byers, 1989; Seybold et al., 2000). For example, alpha-pinene together with frontalin (a pheromone of bark beetles) arrests beetle flight orientating them to trees (Adams et al., 2011). Pine monoterpenes occurring in the oleoresin, a mixture of oil and resin found in pine, function as behaviourally active kairomones for bark beetles. Some monoterpenes are essential co-attractants for pine bark beetle aggregation pheromones (Table 1). Monoterpenes can, however, be physiologically toxic to bark beetles at high vapour concentrations and are considered an important component of tree defence process (Seybold et al., 2006).

5.2. Aggregation

Aggregation pheromones are usually released after feeding and the production of faecal material by pioneer beetles (Vité et al., 1972). Once the first individuals of the pioneer sex (males of *Ips* and *Pityogenes* or females of *Dendroctonus* and *Tomicus*) arrive at the tree, they begin boring into the bark (Byers, 1989; Byers, 1992) hence producing a feeding stimulant. In the genus *Dendroctonus*, the pioneer females make a hole through the bark and release a pheromone to which both males and females

respond. The responding females land and initiate new attacks. In contrast, *Ips* spp. are polygamous. The males make the initial attack, initiate boring and release the pheromone which attracts several females. Feeding stimulants, such as frass, trigger the boring process (Wood, 1982). Studies using an artificial diet for *I. paracon-fusus* Lanier (Coleoptera: Curculionidae) showed that sucrose together with host phloem particles stimulated boring more strongly than did sucrose alone (Hynum and Berryman, 1980). Ethanol has also been shown to act as a boring stimulant (Moeck et al., 1981).

Several semiochemicals are involved in aggregation and these differ between species (Table 1). In *Ips* spp., the aggregation pheromone is a synergistic blend of three components, *ipsenol*, *ipsdienol* and verbenone (Silverstein, 1979) (Table 1). *Ipsenol* and *ipsdienol* are released by males and increase in a logarithmic relationship with host tree monoterpene. Myrcene, a host volatile that has been found to be synergistic when presented with the aggregation pheromone components of some conifer-infesting bark beetles, accumulates when *Ips* spp. males are exposed to vapours of the tree volatiles (Byers and Wood, 1981). Myrcene is converted to the pheromone components *ipsdienol* and *ipsenol* in most *Ips* species except *I. amitinus* (Eichhoff) which converts myrcene to *amitinol* (Byers and Birgersson, 1990) (Table 1). *Ips* spp. males acquire alpha-pinene from vapour absorbed while in the galleries and also from ingested phloem and then convert it to verbenone (Klimetzek and Francke, 1980) depending on the population of beetles at breeding sites. Verbenone is known to play a role in reducing intraspecific competition at breeding areas (Allison et al., 2012) and can deter additional adults from entering the host tree when fully occupied. Verbenone is produced by the beetles themselves (Byers et al., 1984), by auto-oxidation of the host monoterpenes, alpha-pinene via the intermediary compounds *cis*- and *trans*-verbenol (Hunt et al., 1989; Hunt and Borden, 1990) and most probably through degradation of host material by associated microorganisms (Leufvén et al., 1984). Verbenone can also be attractive to some species e.g., *D. frontalis* and *D. brevicomis* LeConte, at low concentrations (Byers et al., 1984). Some beetle species have evolved to recognise verbenone as an indication of unsuitable host material and produce verbenone as a by-product of gallery feeding (Raffa et al., 2008).

Attraction to trees by scolytine bark beetles stops when the galleries are congested and presence of verbenone acts as a deterrent, functioning as a species-specific indicator to beetles attempting to colonise already occupied hosts (Huber and Borden, 2001; Etebeste and Pajares, 2011). Some species have evolved mechanisms that help them avoid host material occupied by different species producing verbenone. The anti-aggregation behaviour is controlled by pheromones (Table 1) and verbenone has been trialled as an inhibitor in management of scolytines. Studies on bark beetle caught in traps baited with attractant pheromone showed that beetle arrival increased with pheromone concentration up to a point, then declined (Birch, 1978). An increase of certain male pheromones facilitates termination of aggregation, spacing and short range dispersal to new trees (Table 1), thus as production of the local anti-aggregation pheromone increases, attacks shift to adjacent host trees. As a result of this semiochemical-mediated behaviour, trees are often killed in groups rather than in isolation (Hovorka et al., 2005). In *D. ponderosae*, dispersal occurs in response to high concentrations of the pheromones *exo*-brevicomin and frontalin (Borden et al., 1986). Males of *D. frontalis* produce (–)-*endo*-brevicomin that interrupts the responses of aggregating beetles to the female-produced pheromone (Sullivan et al., 2007). Verbenone, produced by both sexes of *Dendroctonus* (Borden et al., 1986; Borden et al., 2006; Etebeste and Pajares, 2011), has an inhibitory or interruptive effect on most scolytine bark beetle species (Wood, 1982). *Dendroctonus pseudotsugae*

Table 1
Semi-chemicals involved at different stages of attack by scolytine bark beetles.

Semiochemical notes.	Emitter	Recipient	Stage of attack	Function	Species	References
<i>Pheromones</i> (-)-endo-brevicomine (Synthesized by males in small quantities).	Males	Females	Post-landing	Acts as a population regulator. It also enhances the attractiveness of frontalin and host plant volatiles when released in low concentrations by males during mass attack. It interrupts the response of aggregating beetles to frontalin.	<i>D. frontalis</i>	Sullivan et al. (2007), Payne et al. (1988)
(+)-Sulcatol	Males	Females	Aggregation	Causes aggregation.	<i>Gnathotrichus sulcatus</i> (LeConte) <i>I. sexdentatus</i>	Francke et al. (1995)
4,6,6-Lineatin	Female	Males	Aggregation	Causes aggregation	<i>Trypodendron lineatum</i> (Olivier)	Francke et al. (1995)
Exo-brevicomine	Males	Females	Post-landing	Acts as a population regulator and enhances attractiveness of females when released in low concentrations.	<i>D. terebrans</i>	Borden et al. (1986)
Frontalin (found in the hindguts of newly emerged females)	Female	Con-specific beetles of both sexes	Aggregation	Dual role: as sex and aggregation pheromone to both sexes. It also causes close-range communication, bringing individual beetles together in sufficient numbers to overcome host tree defenses. Its produced in frass and also when females land on a tree and determined the tree to be a suitable host. It also helps to reduce rivalry fighting and competition with other males	<i>D. ponderosae</i> <i>D. brevicomis</i> <i>D. frontalis</i>	Coster and Vité (1972), McCarty et al. (1980),and Payne et al. (1988)
Ipsdienol	Male	Both sexes	Aggregation	Attracts females to mate and both sexes to aggregate. Performs in a blend together with plant volatiles.	<i>D. rufipennis</i> <i>D. brevicomis</i> <i>D. pseudotsugae</i> <i>D. terebrans</i> <i>Ips calligraphus</i> (Germar) <i>Ips pini</i> <i>Ips duplicatus</i> (Sahlberg) <i>Ips avulsus</i> <i>Ips paraconfusus</i> (Lanier) <i>Ips grandicollis</i> <i>Ips perturbatus</i> <i>Ips grandicollis</i>	Vité et al. (1972), Byers and Birgersson (1990), and Allison et al. (2012)
Ipsenol	Male	Both sexes	Aggregation	Attracts females to mate and both sexes to aggregate. Performs in a blend together with plant volatiles.	<i>Ips paraconfusus</i> <i>Ips duplicatus</i> <i>D. pseudotsugae</i>	Vité and Renwick (1971), Vité et al. (1972)
Trans-verbenol (results from the oxidation of alpha-pinene after beetles feed on phloem material or are exposed to vapours while in the host)	Hindgut of newly emerged female	Both sexes	Initial attack and landing	Produced outside the beetle by autoxidation of alpha-pinene upon exposure to air. Metabolised internally from alpha-pinene by bacteria in the beetle gut and externally by other microbial activity. As with alpha-pinene, trans-verbenol alone is unattractive to walking and flying beetles.	<i>D. ponderosae</i> <i>D. frontalis</i>	Payne et al. (1978), Hunt and Borden (1990), Pureswaran and Borden (2004)
Verbenone	Males and females	Both males and females	Post-landing, anti-aggregation	Regulates local beetle densities. Derived from alpha-pinene upon the oxidation of trans-verbenol. It is also produced outside the beetle by autoxidation of trans-verbenol in presence of air and by symbiotic fungi introduced into the host tree by bark beetles. It is the primary anti-aggregation pheromone of some bark beetle species.	<i>D. ponderosae</i> <i>D. frontalis</i> <i>D. brevicomis</i> <i>D. ponderosae</i> <i>I. typographus</i>	Leufvén et al. (1984), Payne et al. (1988), Borden (1989), Hunt and Borden (1990), Huber and Borden (2001), Borden et al. (2003), and Borden et al. (2006)

Table 1 (continued)

Semiochemical notes.	Emitter	Recipient	Stage of attack	Function	Species	References
<i>Tree-derived kairomones</i>						
Alpha-pinene (A monoterpene and major component of resin)	Phloem tissues of host trees	Both sexes	Initial attack	Functions as a kairomone arrestant in combination with frontalinal, a pheromone that draws beetles to the tree. It causes arrestment of walking beetles on the trees.	Produced by most conifer species.	Renwick and Vité (1969), Byers et al. (1985), Payne et al. (1978), and Hofstetter et al. (2008)
<i>p</i> -Cymene	Host trees	Both sexes	Attraction	Enhances attractiveness to host trees.	Produced by deciduous and conifer species	Andersson et al. (2009)
Ethanol	Host trees	Both sexes	Attraction	Secondary bark beetles are attracted to ethanol released from stressed or decaying wood as a result of microbial activity.	Produced by stressed and decaying wood tissue	Byers et al. (1985), Raffa et al. (2005), and Byers (1992)
Myrcene	Host trees	Both sexes	Attraction	Primary attraction to host trees and also enhances bark beetles' response to aggregation pheromone	Produced by most conifer species	Byers (1992) and Hofstetter et al. (2008)
B-pinene	Host trees	Both sexes	Attraction	Primary attraction to host trees and also enhances bark beetles' response to aggregation pheromone	Produced by most conifer species	Byers (1992)
(+)-3-carene	Host trees	Both sexes	Attraction	Primary attraction to host trees and also enhances bark beetles' response to aggregation pheromone	Produced by most conifer species	Byers (1992) and Erbilgin and Raffa (2000)
Terpinolene	Host trees	Both sexes	Attraction	Primary attraction to host trees and also enhances bark beetles' response to aggregation pheromone	Produced by most conifer species	Byers et al. (1985) and Byers (1992)

regulates its densities by stridulatory sounds produced by males which induce the females to release an anti-aggregation pheromone that counteracts the attractiveness of other pheromones (Alcock, 1982). This anti-aggregation behaviour ensures that a suitable density of beetles within galleries can be supported from the host resources during mass attacks.

5.3. Semiochemicals and management of scolytine bark beetles in forest ecosystems

Semiochemicals are important in monitoring pest populations to determine when and where control is warranted and for decision making that would lead to appropriate management intervention (Norin, 2007). For practical detection purposes, pheromone traps have been extensively used for monitoring and management of bark beetles because of their easy handling, specificity and sensitivity. Successful cases in the use of synthetic semiochemicals are, however, rare (Hayes et al., 2009). Aggregation pheromones have been developed as high release lures for specific species. Verbenone has been used to protect the lodgepole pine, *Pinus contorta* var. *latifolia* Engelm, from attack by *D. ponderosae* and *D. valens* (Borden, 1997; Rappaport et al., 2001). Green leaf volatiles together with verbenone have been shown to interrupt responses to aggregation pheromones of bark beetles which infest pines in the United States such as *D. frontalis*, *Ips avulsus* (Eichhoff) and *I. grandicollis* (Zhang and Schlyter, 2004), *D. brevicomis* and *D. valens* (Fettig et al., 2008) and *D. ponderosae* (Huber and Borden, 2001).

Models have been developed for predicting tree losses based on trap catches of *I. typographus* (Faccoli and Stergulc, 2004, 2006) in Italy and *D. rufipennis* Kirby (Hansen et al., 2006) and *D. frontalis* in the USA (Billings 1988). The use of baited traps is common during the early spring dispersal phase to give an estimate of population density. This use of semiochemicals has proven useful in scolytine management as monitoring during this critical phase of the pest's seasonal activity leaves time for planning and applying management over the summer and can avoid the material and labour costs associated with a longer-running monitoring period. Furthermore, semiochemical-baited traps have considerable potential for the detection and monitoring of scolytines, particularly at sea ports and other potential points of entry. The detection of exotic bark beetles is one of the major functions of quarantine detection programs (McMaugh, 2005), because the global planting of a small number of softwood species has provided an almost unlimited source of host material for many of the primary bark beetle species outside the natural range of their natural enemies (Humble, 1999). Large-scale trapping programs for the detection of species such as *I. typographus* and *D. ponderosae* are in place at most of the major trading ports in the world, for example in China (Lui and Dai, 2006), Australia (Bashford, 2012) and USA (Haack, 2006).

Several additional techniques that employ semiochemicals have been used against bark beetles of forest trees. "Push-pull" has been adopted as a direct control strategy (Gillette and Munson, 2009) where the "push" part involves a known anti-aggregation pheromone (e.g., lures of verbenone for *D. ponderosae*) (Borden et al., 2006), and the "pull" part involves intercept panel traps, baited with beetle pheromone such as *ipsenol*, *ipsdienol* or host volatiles such as alpha-pinene, placed near trees of interest or treatment plots. Push-pull components using aggregants and antiaggregants from the same species can significantly reduce numbers of beetles caught in traps, e.g., in protection of lodgepole and whitebark pine from *D. ponderosae* in Washington, USA (Gillette et al., 2012). Herbicide-treated trees can also be used as a "pull" and a non-host volatile used as a disruptant or interruptant (Dodds and Miller, 2010). In the latter case, multiple

types of negative stimuli such as green leaf volatiles from non-host plants and verbenone are used to create chemical stimuli that indicate that conspecifics have mass attacked an unsuitable and potentially lethal non-host habitat or tree (Lindgren and Borden, 1993), sending a strong message that deters bark beetles.

There are, however, unsuccessful attempts and obstacles to verbenone being a solution to management of these pests (Fettig et al., 2009b; Shea et al., 1992), most notably ineffectiveness at the stand scale for several conifer species (Bentz et al., 1989; Strom et al., 2004) and breakdown to the inactive compound chrysanthenone when subjected to ultraviolet radiation (Francke et al., 1995). A study by Fettig et al. (2009a) revealed that using verbenone alone did not protect Ponderosa pine stands from *D. brevicomis* and the authors suggested that verbenone is best utilised in combination with other semiochemicals and at high doses. Lack of efficacy was attributed to low levels of inhibition so larger numbers of release pouches are required to achieve maximum protection at the stand level. The same study suggested that low stand densities and elevated temperatures may result in unstable layers and multi-directional traces that dilute synthetic verbenone plumes in forest stands (Fettig et al., 2009b). On the other hand, verbenone can enhance the activity of biocontrol agents. A study by Fettig et al. (2007b) showed that *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), a common bark beetle predator, is attracted to high release rates of verbenone which points to potential utility for optimising biological control of the north American bark beetle *D. valens*.

In the 'lure-and-kill' strategy, beetles are attracted to a killing agent, which eliminates them from the population (El-Sayed et al., 2009). Mass trapping uses species-specific synthetic chemical lures to attract insects to a trap. Sex attractant, food or aggregation pheromones are used to lure beetles to traps where they are confined and eventually die (Byers, 1989; El-Sayed et al., 2006). Trap trees that are treated with a herbicide may also act as "traps" for bark beetles. They are eventually burnt (Bakke, 1983, 1989) to kill all life stages under the bark (Werner et al., 1986). The continued development and use of suitable semiochemicals, with low non-target impact in urban and forest monitoring systems has provided a tool to determine the arrival of exotic insect pests, providing an early warning system enabling managers to take steps for eradication or containment (Bashford, 2003). Development of commercial, generic and specific semiochemicals has made the use of lures a viable option for monitoring programs. By using generic 'bark beetle' lures or combinations of different compatible lures per trap a large number of species can be detected. Once detected and identified, catch data for that species can be utilised to determine changes in relative abundance and distribution (Schwalbe and Mastro, 1988).

As scolytines aggregate in large numbers, trap catches may reach biologically significant levels, making mass-trapping with synthetic attractants a viable pest management tactic (El-Sayed et al., 2006). Semiochemicals may be used to monitor scolytine population flights to schedule movement of high risk or high value logs so as to minimize potential losses. Harvested logs that may be infested have potential to spread beetles outside their native range resulting in economic and ecological risks. Semiochemicals that inhibit oviposition might also be used to protect high value logs for short periods of time. Verbenone and *trans-conophthorin* have been shown to be effective for inhibiting *I. perturbatus* (Eichhoff) attacks on live trees in Alaska (Graves et al. 2008) and on decked, unscored logs by reducing host colonisation during localised outbreaks (Fettig et al., 2013).

5.4. Use of volatiles from non-hosts in the management of bark beetles

The use of non-host volatiles provides another non-insecticidal opportunity for protection of forest trees (Table 2). Volatile green

leaf alcohols and aldehydes are ubiquitous among numerous plant species and many insects use these chemicals to find specific tree hosts (Zhang, 2003). Though monoterpenes are commonly known as volatiles of conifer bark and foliage and are used in host selection by bark beetles, they are also common in the tissues of non-host angiosperm trees (Byers, 2000; Huber et al., 2000). Green leaf volatiles, especially alcohols with six carbon atom chains, derived from leaves and sometimes from the bark of non-host angiosperm trees, may represent non-host odour signals at the habitat level. Specific bark volatiles such as *trans-conophthorin* (*E*)-7-methyl-1,6-dioxaspiro[4.5]decane), leaf alcohols with eight carbon atom chains and some aromatic compounds, may indicate non-hosts at the tree species level (Zhang and Schlyter, 2004). Several studies have yielded promising results for the management of some bark beetle species (Table 2) where a blend of non-host volatiles has been capable of reducing attraction of beetles to lured traps and logs.

Non-host volatiles have been shown to interrupt attraction of bark beetles, especially when used alone or in a blend together with verbenone (Campbell and Borden, 2006; Dodds and Miller, 2010; Etxebeeste and Pajares, 2011) (Table 2). Studies by Wilson et al. (1996) showed that a combination of two non-host angiosperm volatiles, (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol, significantly reduced attack of *D. ponderosae* on pheromone-baited lodgepole pine in British Columbia. Fettig et al. (2008) showed that applications of verbenone with a blend of non-host volatiles protected ponderosa pines from attack by *D. brevicomis* and *D. valens*. Etxebeeste and Pajares (2011) recently showed that efficiency of verbenone in repelling bark beetles from trees is enhanced when blended with *trans-conophthorin*. Presently, the most promising use of non-host volatiles together with mass trapping in the management of bark beetles has been for *I. typographus* in natural reserves, forest camping grounds and urban forests where it is more acceptable than insecticide use. This method reduces the numbers of dispersing beetles as they are captured by pheromone trap barriers giving the trees a chance to defend themselves against subsequent attacks. Protecting forest trees from attack by bark beetles by application of non-host volatiles is still too expensive for use in commercial forests, but could be viable for high-value (e.g., nature conservation reserves). Use of non-host volatiles may be viable for the protection of small areas of "trap trees" such as those used for introducing biological control agents such as the nematode agents for *Sirex noctilio* (F.) (Bedding, 2009).

In mixed forests, bark beetles will encounter unsuitable hosts and non-host trees as well as their odours. The decision to occupy unsuitable trees may be based on disparities of certain tree characteristics and inhibitory responses to some non-host stimuli or volatiles (Shepherd et al., 2007). This is supported by the semiochemical diversity hypothesis, which states that mixed habitats with high plant biodiversity are more stable due to the abundance of non-host volatiles which interferes with host-selection by specialised herbivores (Zhang and Schlyter, 2004). In these mixed habitats, non-host volatiles may negatively influence host selection enabling natural protection of forest trees. This could be due to the richer plant communities releasing more diverse plant odours that may disrupt olfactory-guided host choice. Some beetles also use defensive compounds that are emitted by trees to avoid predation (Byers et al., 2004).

6. Role of semiochemicals in integrated management of scolytine bark beetles

Silvicultural practices promote individual tree and stand resistance, protect stand sites and minimises bark beetle and disease incidence as well as competition. The practice may involve intensive forest management such as thinning, pruning and short

Table 2
Volatiles from non-host tree families that have been shown to reduce attack on trees by scolytine bark beetles.

Volatile compound	Family of non-host species	Scolytine bark beetle controlled or tested	Effect	References
(E)-(±)-conophthorin	Betulaceae	<i>D. brevicomis</i> <i>I. perturbatus</i> <i>I. pini</i> <i>I. grandicollis</i>	Combined with verbenone, the non-host angiosperm volatile protects trees from attacks by bark beetles. The compound alone does not reduce numbers of <i>I. pini</i> or <i>I. grandicollis</i> arriving on trap trees.	Graves et al. (2008), Dodds and Miller (2010), Dallara et al. (2000), López et al. (2012), Fettig et al. (2012)
(E)-2-hexenal	Betulaceae	Ambrosia beetles	Active as a non-host volatile in inhibiting attack by some ambrosia beetles	Borden (1997), Deglow and Borden (1998), Poland et al. (1998), and Fettig et al. (2012)
(Z)-3-hexen-1-ol	Salicaceae	<i>D. brevicomis</i> <i>D. rufipennis</i> <i>Dendroctonus</i> spp.	Disrupts beetle response to aggregation pheromones in baited traps.	Borden et al. (1998), Zhang et al., 2000, Pureswaran and Borden (2004), and Fettig et al., 2012)
(E)-2-hexen-1-ol	Common green leaf volatile of Betulaceae	<i>I. pini</i> <i>I. typographus</i> <i>D. brevicomis</i>	Inhibits attack on trees by beetles	Poland et al. (1998), Fettig et al. (2012)
(Z)-2-hexen-1-ol	Betulaceae	<i>D. rufipennis</i> <i>D. brevicomis</i>	Inhibits attack on trees by beetles	Poland et al. (1998), and Fettig et al. (2012)
(Z)-3-hexenyl acetate	Betulaceae	<i>D. rufipennis</i> <i>I. typographus</i>	Disrupts <i>D. ponderosae</i> , response to aggregation pheromones.	Wilson et al. (1996), Borden et al. (1998), and Zhang et al. (2000)
1-Hexanol	Salicaceae Common green leaf volatile of Salicaceae	<i>D. ponderosae</i> Various <i>Dendroctonus</i> spp.	A repellent non-host volatile in various bark beetles. Also interrupts pheromonal communication in bark beetles.	Dickens et al. (1992), Borden et al. (1998), Huber and Borden (2003)
Hexanal	Many Angiosperms	<i>D. brevicomis</i> <i>D. rufipennis</i> <i>I. grandicollis</i> <i>I. avulsus</i>	Reduced attraction of the bark beetles to attractant-baited traps.	Dickens et al. (1992) and Poland et al. (1998)
1-Octen-3-ol	Betulaceae	<i>Dendroctonus</i> spp.	A non-host volatile tested with success against bark beetles in genus <i>Dendroctonus</i> and <i>Ips</i> .	Zhang et al. (2000), and Pureswaran and Borden (2004)
3-Carene	Betulaceae	<i>Ips pini</i> <i>I. typographus</i> <i>P. bidentatus</i>	Present in volatiles of numerous conifers.	Zhang et al. (1999) and Huber et al. (2000)
3-Octanol	Betulaceae	<i>Dendroctonus</i> spp.	A non-host volatile tested with success against bark beetles in genus <i>Dendroctonus</i> and <i>Ips</i> .	Zhang et al. (2000) and Pureswaran and Borden (2004)
4-Allylanisole	Cycadaceae	<i>Ips pini</i> <i>I. typographus</i> <i>D. rufipennis</i>	Significantly reduced catches of beetles on traps.	Hayes and Strom (1994), Werner (1995), Faccoli and Stergulc (2004), and Snyder and Bower (2005)
Acetophenone	Pinaceae	<i>D. ponderosae</i> <i>I. pini</i> <i>I. typographus</i> <i>D. pseudotsugae</i>	Anti-attractants. The compound significantly decreased catches of beetles in aggregation pheromone-baited traps.	Pureswaran and Borden (2004), Erbilgin et al. (2007), and Fettig et al. (2012)
Alpha-pinene	Present in volatiles of numerous conifers such as Betulaceae, Salicaceae	<i>D. ponderosae</i> <i>D. rufipennis</i> <i>D. brevicomis</i> Ambrosia beetles (Scolytinae)	Common attractant host kairomone for coniferophagous bark beetles.	Schroeder and Lindelow (1989), and Huber et al. (2000)
Benzaldehyde	Salicaceae	<i>D. ponderosae</i>	Disruptive to aggregation of <i>D. ponderosae</i> .	Borden et al. (1998)
Benzyl alcohol	Salicaceae	<i>D. ponderosae</i>	Disruptive to aggregation of <i>D. ponderosae</i> .	Borden et al. (1998)
Beta-pinene	Betulaceae	<i>P. bidentatus</i> (Herbst)	Present in volatiles of numerous conifers	Zhang et al. (1999), and Huber et al. (2000)
Blend of α-zingiberene and α-santalene,	Betulaceae	<i>I. typographus</i>	Volatiles found in bark chips of birches which are long-range olfactory cues for beetles causing them to discriminate between its conifer host and non-hosts.	Zhang et al. (2000)

Table 2 (continued)

Volatiles compound	Family of non-host species	Scolytine bark beetle controlled or tested	Effect	References
Fenchyl alcohol	Salicaceae Pinaceae	<i>D. brevicomis</i>	Compound reduced trap catches of beetles in aggregation pheromone-baited traps.	Erbilgin et al. (2007)
Nonanal	Volatile chemicals that are associated with foliage and/or bark of angiosperm trees	<i>D. frontalis</i>	Significantly inhibited response of male <i>D. frontalis</i> beetles when used as a blend with benzaldehyde.	Sullivan et al. (2007)
<i>Trans</i> -conophthorin	Betulaceae	<i>Pityophthorus pubescens</i> (Marsham)	A non-host volatile commonly found on bark chips of birches that reduces catches of <i>Ips</i> spp.	Zhang and Schlyter (2004), Etxebeste and Pajares (2011), López et al. (2012)
β -Pinene	Salicaceae Present in volatiles of numerous conifers such as Betulaceae, Salicaceae	<i>I. sexdentatus</i> <i>D. ponderosae</i>	Common attractant host kairomone for coniferophagous bark beetles.	Huber et al. (2000)
Verbenone Plus (a four-component semiochemical blend)	Blend composed of acetophenone, (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol, and (-)-verbenone]	<i>D. pseudotsugae</i> <i>D. rufipennis</i> <i>Dryocoetes confusus</i> (Swaine) <i>I. pini</i> <i>D. brevicomis</i>	Verbenone Plus significantly reduce the proportion of trees mass attacked by <i>D. brevicomis</i>	Fettig et al. (2012)

rotation cycles and has traditionally been considered a method of control for bark beetles (Christiansen and Fjone, 1993; Wermelinger, 2004). This kind of forest hygiene also decreases the risk of outbreaks especially in situations where trees are deliberately weakened, e.g., trap tree plots, and thus could be pre-disposed to beetle attack. Thistle et al. (2004) showed that bark beetle pheromone plumes remained concentrated and directional in high density stands while low density stands resulted in unstable layers and multi-directional traces of diluted pheromone concentrations. This can, in part, result in reduced attack on trees in well managed density stands, which emphasises the natural role of semiochemical communication in forests.

On the other hand, intensive management may actually give opportunities for pest populations to increase (Schowalter and Filip, 1993). Regularly managed and thinned stands are relatively open and have a more favourable microclimate for certain primary scolytines such as *I. typographus* (Väisänen et al., 1993). Managed stands, which typically have only one age class of one tree species, tend to favour scolytine species as they contain a less varied spectrum of host species than stands in natural condition (Martikainen et al., 1999; Jactel et al., 2009). Managed forests can also be more favourable to certain bark beetle species as there are minimal interactions and interferences between allomonal effects of semiochemicals released by attacking beetles. Mixed forests on the other hand have greater semiochemical diversity than pure host stands as non-host angiosperms would disturb olfaction-guided host selection and hence reduce the likelihood of outbreaks of conifer-infesting bark beetles (Huber and Borden, 2001; Zhang et al., 2001). Schowalter and Turchin (1993) showed that a mixed stand of deciduous species may decrease the spread of *D. frontalis* while homogenous stands experience outbreaks of forest insect pests more often than heterogeneous stands (Jactel et al., 2002). Research is required to explore whether such effects could be practicable in pine forests. In the context of pest management, a diverse array of chemical cues and signals may disrupt bark beetles searching more than high doses of a single semiochemical (e.g., verbenone) or even mixtures of semiochemicals intended to mimic one type of signal (e.g., anti-aggregation pheromones), because

they represent heterogeneous stand conditions to searching insects.

7. Interactions between scolytines and associated species

Interactions between scolytine bark beetles, other pest species, their host trees and associated microorganisms form an intricate system in forest ecosystems. For instance, the arthropod complex associated with *I. typographus* includes about 140 species (Weslien, 1992). As mentioned previously, bark beetles can colonise living conifers when attacking in large numbers. As the beetles are frequently associated with fungi that are carried in specialised structures or on their body surfaces (Paine et al., 1997), the spores are actively or passively introduced into trees. The association between micro-organisms and beetles is complex as the former may compete for the same substrates (Slippers et al., 2012). Micro-organisms such as fungi clearly benefit from the association with bark beetles by transportation to new host trees but, less obviously, the beetles may benefit by feeding on the fungi (and associates) after it has colonised wood. The microbes may also affect tree physiology through mycelial penetration of host tissue or toxin release (Weslien and Martin Schroeder, 1999) to the beetles' advantage. Stress to trees caused by physical wounding, introduced chemicals or pathogens and insects attacking trees and the strategy of attack strongly influence volatile emissions from hosts (Parè and Tumlinson, 1996). Differences between systems and how tree species respond and interact in different environmental conditions make it difficult to generalise about the importance of the separate biological components in successful communications and host colonisation in forest ecosystems. This leads to predicaments when deciding upon a management strategy as is illustrated in the following case study.

7.1. Case study of *I. grandicollis* and the *Sirex* wood wasp in Australia

In Australia, softwood plantation covers 1.02 million hectares (Garvan and Parsons, 2011). *Sirex noctilio* F. (Hymenoptera: Siricidae) is a major pest that attacks pine species throughout the

northern and southern hemispheres (Slippers et al., 2012). During oviposition, female adults deposit a phytotoxic mucus as well as a wood-decaying fungus *Amylostereum areolatum* (Chaillat ex Fr.) Boidin (Coutts, 1969a; Coutts, 1969b,c). The main injury to trees attacked by *S. noctilio* is from the symbiotic fungus which is injected by the female wasp within the oviposition puncture. The hyphae attack the living tissue of the wood and the portion of the tree above the puncture dies due to cut of water supply within the tree. The fungus causes a white rot on the wood and causes the wood to decay rapidly (Slippers et al., 2012). Trees attacked by the wasps subsequently die due to a combination of toxicity of the mucus and wood rot by the fungus (Coutts, 1969b,c). Several major outbreaks of *S. noctilio* have occurred in Australia since it established six decades ago, including one in the late 1980s where over five million trees were killed (Haugen and Underwood, 1990). Sporadic outbreaks have occurred since (Carnegie and Bashford, 2012).

Mating of *S. noctilio* is facilitated by a sex pheromone that is released from the cuticle of females (Böröczky et al., 2009). The pheromone induces males to copulate and also facilitates the formation of male swarms which females fly through to mate. Strong antennal responses are elicited by the components of the synthetic pheromones, but, Böröczky et al. (2009) showed that host-derived compounds are also perceived by the male antenna. These plant odours play a role in the attraction of wasps to pine plantations. Migrating *S. noctilio* adults are attracted to alpha-pinene volatiles emitted from stressed trees in a *Pinus* spp. plantation. Studies have shown that beta-pinene, a host derived compound, plays a major role in attracting *S. noctilio* females into a plantation and then alpha-pinene leads the wasps to a specific tree (Simpson, 1976; Simpson and McQuilkin, 1976). Simpson and McQuilkin (1976) showed that volatiles emanating from *P. radiata* show minor changes after felling. However, attractiveness of the wood wasp to the felled timber declines markedly over the first three weeks.

A long-established, successful biocontrol program that uses the nematode *Beddingia* (= *Deladenus*) *siricidicola* Bedding (Sphaerulariidae) has been widely used in the management of *S. noctilio* (Bedding, 2009). In this technique, a group of approximately 10 'trap' trees are trunk-injected with herbicide to stress them so that they become attractive to *S. noctilio* for oviposition (Carnegie and Bashford, 2012). At the completion of *S. noctilio* flight season, the trees are felled and inoculated with nematodes. The nematodes then breed within the logs, infest *Sirex* larvae and migrate to the ovaries of developing females, thus making them sterile (Bedding, 2009). The female wasp emerges and deposits nematodes in the next tree, reducing *Sirex* numbers in subsequent generations.

Trap trees release volatiles that are not only attractive to the wasp, but also to *I. grandicollis*. This effect is feared to threaten the biocontrol program because the beetles hasten tree death, so reducing the period over which they are attractive to *S. noctilio* females (Carnegie, 2008). Gitau (unpublished data) found that trap trees that were attacked by *I. grandicollis* are not attractive to *S. noctilio*. *Ips grandicollis* has been present in Australia for over seven decades and has been associated with significant mortality of trees in commercial plantations of *P. radiata*. Studies in some regions of Australia have revealed an increase in *Ips*-related tree mortality (Carnegie, 2008) and beetle attack on trap trees, with coincident decrease in *S. noctilio* parasitism (Carnegie and Loch, 2010). Semiochemicals released by beetles may act in an allomonal manner to deter attack by competing species (Borden, 1989). For bark beetle management, allomonal inhibition and competition (i.e., presence of aggregation pheromone of one species reduces aggregation in another) can be risky in terms of trading one potential source of tree mortality for another (Paine and Hanlon, 1991).

The magnitude and mechanisms of *I. grandicollis* and its associates in disrupting the development of *S. noctilio* in trees and interference with the infectivity of the wasp's larvae by the *B. siricidicola*

is yet to be elucidated. Carnegie and Loch (2010) trialled a "push-pull" strategy with verbenone as the "push" and trap trees as the "pull". They found that verbenone was not effective in inhibiting *I. grandicollis* attacks on trap trees. As the chemical ecology of both species becomes better understood, semiochemicals of both pine pests could have utility not only on trap trees, but in open forests. Use of disruptants or interruptants to protect wood wasp trap trees might include blends that keep the wasp attracted but push the bark beetles away. Since the semiochemicals produced by *S. noctilio* and *I. grandicollis* are very different, there is scope to develop a selective semiochemical management strategy based on a compound which is repellent to the bark beetle but inactive against (or even attractive to) *S. noctilio*.

8. Conclusions and priorities for future research

This review highlights the need to consider responses of bark beetles and their associates, as well as other pests, to ecologically relevant cues of both hosts and non-hosts in multiple sensory modes when evaluating appropriate management strategies for scolytine bark beetles. Presently, semiochemicals are mainly used in forest protection for monitoring pest species to determine presence and the optimal time for applying treatments. "Lure" and "kill" has not been successfully exploited for scolytine bark beetles. The "push" and "pull" strategy has been used against bark beetles of the genera *Dendroctonus* (Borden et al., 2006; Gillette and Munson, 2009) where the anti-aggregation pheromone verbenone, green leaf volatiles and a non-host volatile blend are utilised. Trials have, however, yielded mixed results in different scolytine beetles which impede the exploitation of this strategy in management of conifer scolytine pests. Since phytophagous insects benefit both by identifying and avoiding non-hosts, as well as orienting to suitable hosts, further studies would involve establishing how sensory integration operates during each process, especially when bark beetles are associated with other organisms such as fungi, bacteria and nematodes as well as other pests. Furthermore, integration and synergism between modes of stimuli would best use factorial designs that allow comparisons among all combination of stimuli such that detection of synergistic interactions among volatiles of hosts, bark beetles and their associates is recognised.

Stands are managed by ensuring that freshly cut logs are kept away from trees that remain on thinned sites to prevent further infestations while for individual trees already showing signs of infestation, direct control methods involve removal of infested trees and use of insecticides. Research on scolytine bark beetles is not fully explored because their attack on trees although ecologically critical, does not always result in serious economic loss. Experimental work with scolytines is also challenging because in many cases the behaviour elicited by semiochemicals is complex and obtaining sufficient live insects for exhaustive laboratory experiments can be difficult. It is clear that beetle life history and behaviour are intricately mediated by semiochemicals and much more needs to be learned before the full scope for the use of these chemicals in pest management is realised. Tree resistance to successful bark beetle attack has been studied in Europe for several *Pinus* species but this has not been included in tree breeding programs since most provenance work has shown that tree resistance to insect attack correlates with poor wood quality and growth rates (Lieutier, 2002). Host resistance factors include increased production of phenolics at attack sites, increased resin flow and oleoresin pressure at time of increased tree stress, increased bark thickness, high levels of calcium oxalate crystals in the phloem, and resin blisters (Hudgins et al., 2003). Most of these factors are partially genetically dependent (Nebeker et al., 1992). Scolytine bark beetles counter these defences by utilising strategies such as mass aggre-

gation, gallery orientation, timing of attack and associations with phytopathogenic fungi. Research to determine weak links in some of these aspects for specific pest species is needed in order to reduce economic losses specifically where the host is being grown off-site or as an introduced plantation species.

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