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Management of Western North American Bark Beetles with Semiochemicals

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Abstract

We summarize the status of semiochemical-based management of the major bark beetle species in western North America. The conifer forests of this region have a long history of profound impacts by phloem-feeding bark beetles, and species such as the mountain pine beetle (*Dendroctonus ponderosae*) and the spruce beetle (*D. rufipennis*) have recently undergone epic outbreaks linked to changing climate. At the same time, great strides are being made in the application of semiochemicals to the integrated pest management of bark beetles. In this review, we synthesize and interpret these recent advances in applied chemical ecology of bark beetles for scientists and land managers.

INTRODUCTION AND BACKGROUND

Semiochemical: a chemical emitted by one organism that affects the behavior of another organism, either within or among species

Pheromone: a semiochemical that mediates intraspecific interactions

Allelochemical: a semiochemical that mediates interspecific interactions

Native bark beetles are among the most important disturbance agents in western North American forests (8), with landscape-level impacts on the carbon cycle and interactions with climate change (12, 111). Over the last three decades, outbreaks of two widespread species, the mountain pine beetle, *Dendroctonus ponderosae*, and the spruce beetle, *D. rufipennis*, have caused unprecedented damage (14, 86, 203). Other species, such as the western pine beetle (*D. brevicomis*), Douglas-fir beetle (*D. pseudotsugae*), fir engraver (*Scolytus ventralis*), western balsam bark beetle (*Dryocoetes confusus*), and pine engravers (*Ips* spp.), are locally important, killing trees at significant levels (120, 195, 203). The outbreaks have been of such magnitude that they have attracted the attention of not only biologists, but also physical scientists/geographers, social scientists, and policy makers (83, 85, 126). Management of populations of these bark beetles is challenging, given the rapid development and extreme spatial scale of the outbreaks (46, 207). Two approaches have been used: indirect or silvicultural treatments that increase stand resilience to beetle attack and direct control measures that target reductions in beetle population density (207). Silvicultural treatments may be the most effective and long-lasting approach, but they are expensive, time consuming, and logistically complex (47, 74). Direct control tactics include sanitation harvesting [used extensively in western Canada (208)], as well as treatment with insecticides or behavioral chemicals. The use of insecticides is constrained by risks to nontarget organisms such as fish, amphibians, birds, pollinators, and insect natural enemies of bark beetles and other forest insects (45, 140). These constraints and the structural and biotic complexity of forest ecosystems make the use of behavioral chemicals to interrupt host and mate location by bark beetles an attractive approach for management (186). This likely motivated the pioneers of chemical ecology to isolate some of the first insect pheromones from bark beetles, such as the California fivespined ips (*Ips paraconfusus*) (188) and *D. brevicomis* (187).

Behavioral chemicals of many other ecologically and economically significant western North American bark beetles have since been isolated and identified (40, 189), and over the last several decades, tactics using these chemicals have been developed to detect, monitor, and manipulate populations of native and invasive species. In this synthesis, we discuss recent advances in the use of semiochemicals for management of bark beetles in western North America. We emphasize case studies of the management of a suite of prominent native coniferophagous species and the enhanced detection of a small, but growing, number of invasive species, some of which damage hardwood trees.

OVERVIEW: SEMIOCHEMICALS AND APPLIED CHEMICAL ECOLOGY OF BARK BEETLES

The development of the discipline of chemical ecology has been replete with examples based on bark beetles, their insect associates, and their host and nonhost trees. Discoveries from the ecological interactions within these forest communities have led to strategies for the management of bark beetles with semiochemicals.

Semiochemicals: Definitions and Characteristics

Semiochemicals are chemicals emitted by one organism that can affect the behavior of another organism (57, 128). The term is derived from the Greek *semeion*, which means “signal.” Similar terms encountered in the literature include infochemicals, signaling chemicals, and behavioral or behavior-modifying chemicals. Semiochemicals that act within a species are called pheromones (57), and those that act among species are referred to as allelochemicals (128). Allelochemicals that benefit the sending organism are called allomones (from the Greek *allos*, "other"), and those that benefit the receiving organism are called kairomones (from the Greek *kairos*, "opportunist"). Those that benefit both the sender and receiver are called synomones.

A few characteristics of semiochemicals are important when considering their applications in integrated pest management (IPM) of bark beetles. First, most semiochemicals are multifunctional; they are typically attractive when released into the forest airspace at low to intermediate rates and repellent when released at high rates. Second, most semiochemicals function in the context of multicomponent blends. In these blends, the components may each be electrophysiologically active but elicit behavioral activity only in combination (i.e., behaviorally synergistic). Some blends involve contributions from one sex of a bark beetle species, from both sexes of a species, or from the host and from the beetle. Third, semiochemical specificity may rely on blends of optical or geometric isomers of the components. In some instances, substantial amounts of both an enantiomer and its antipode, or *cis*- and *trans*-isomers [(*Z*)- and (*E*)-isomers], are required to elicit the full behavioral response, whereas in other cases, the opposite isomer may be inactive. With some bark beetle species (169), the antipode interrupts the flight response to the enantiomer. Fourth, for widely distributed species, there can be variability in the production and response to semiochemicals among populations, such that there are in essence olfactory dialects in different parts of the range (34, 145, 164, 174). Such variation has been poorly studied and is not understood for most species. Thus, before developing a semiochemical-based management strategy for bark beetles, it is crucial to have knowledge of (*a*) all the major semiochemical components, including synergists; (*b*) an understanding of the most efficacious blends, ratios, and release rates; (*c*) the most effective isomeric combinations; and (*d*) the regional appropriateness of the semiochemical mixture.

Allomone: a semiochemical that mediates interspecific interactions to the benefit of the emitter but not the receiver

Kairomone: a semiochemical that mediates interspecific interactions to the benefit of the receiver but not the emitter

Synomone: a semiochemical that mediates interspecific interactions to the benefit of both the emitter and the receiver

IPM: integrated pest management; a systematic approach to manage pest damage that minimizes pesticide use and impacts to human and environmental health

Types of Semiochemicals Relevant to Bark Beetles

Bark beetles utilize pheromones, kairomones, allomones, and synomones when locating and colonizing host trees, mating, and interacting with competitors and mutualists (17, 18, 75, 205). For example, aggregation pheromones produced by either sex or both sexes provide a very strong host selection cue at relatively low airborne concentrations (release rates of 0.1 to 10 mg/day from formulated materials). The status of certain signals as sex pheromones for bark beetles is generally considered to reflect incomplete knowledge of the aggregation pheromone. Bark beetle aggregation pheromones may also function as synomones, deterring potential rival species and thus benefitting both firstcomers and rivals by avoiding competition for limited real estate in the inner bark. Regular spacing of entrance holes to galleries in the inner bark (28) suggests a close-range spacing (epideictic) pheromone. During later stages of host colonization, bark beetles may produce compounds that deter further landing and colonization of the host (29), which perhaps reflects an epideictic pheromone active over a longer range. Such signals may cause incoming beetles to land on nearby host trees that are in an earlier stage of colonization. The classical and relatively universal example of such an antiaggregation pheromone for bark beetles is verbenone, which is a monoterpene ketone derived from α-pinene (149, 178). (See the sidebar titled Chemical Nomenclature of Semiochemicals of Western North American Bark Beetles.)

For many coniferophagous bark beetles, host monoterpenes can function independently as attractant kairomones (87, 143) or as coattractants with pheromone components (173). Ethanol emanating from fermenting tree tissue due to damage from fire, flooding, or other causes (106) also can act as a kairomonal cue for host location. However, in nearly all instances, the beetles that respond to this cue are closely allied ambrosia beetles or so-called secondary bark beetles, the latter of which rarely merit consideration for management (102, 106). Another group of plant-derived

CHEMICAL NOMENCLATURE OF SEMIOCHEMICALS OF WESTERN NORTH AMERICAN BARK BEETLES

Semiochemicals of bark beetles are identified both by their trivial names and by their formal or IUPAC (International Union of Pure and Applied Chemistry) names. Both names for some of the most prominent semiochemicals noted in this review are presented and organized below by their most probable biogenetic origin (178).

- Isoprenoid-derived semiochemicals of bark beetles: verbenone [(*1R*)-*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one]; verbenene (4-methylene-6,6-dimethylbicyclo[3.1.1]hept-2-ene); frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane); *cis*- or *trans*-verbenol (*cis*- or *trans*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol); (+)- or (−)-ipsdienol [(4*S*)- or (4*R*)-2-methyl-6-methylene-2,7-octadien-4-ol)]; (−)-α-pinene: [(1*S*,5*S*)-2,6,6-trimethylbicyclo[3.1.1]hept-2-ene]; myrcene (7-methyl-3-methylene-1,6-octadiene); terpinolene [1-methyl-4-(1-methylethylidene)-1-cyclohexene]; sulcatone (6-methyl-5-hepten-2-one); 3-methyl-2-buten-1-ol; 2-methyl-3-buten-2-ol.
- Fatty acid–derived semiochemicals of bark beetles: (+)-*exo*-brevicomin [(1*R*,5*S*,7*R*)-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane]; (+)-*endo*-brevicomin [(1*R*,5*S*,7*S*)-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane]; *trans*-conophthorin [(*E*)-7-methyl-1,6-dioxaspiro[4.5]decane]; nonanal; leaf aldehyde [(*E*)-2-hexenal]; leaf alcohols [(*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol].
- Amino acid–derived semiochemicals of bark beetles: acetophenone (1-phenylethan-1-one); benzyl alcohol (phenylmethanol); benzaldehyde; guaiacol (2-methoxyphenol); 2-phenylethanol (2-phenylethan-1-ol); salicylaldehyde (2-hydroxybenzaldehyde).
- Semiochemicals of bark beetles of unknown biosynthetic origin: ethanol; methylcyclohexenone (MCH) or seudenone (3-methylcyclohex-2-en-1-one); methylcyclohexenol (MCOL) (1-methylcyclohex-2-en-1-ol); seudenol (3-methylcyclohex-2-en-1-ol).

kairomones for coniferophagous bark beetles are nonhost volatiles (NHVs), which are thought to signify to beetles that the trees they are encountering are outside of their host range and thus are unsuitable hosts for brood development (18, 209). Like pheromones, NHVs may also function as synomones because the beetles avoid wasted interactions with the nonhost trees, whereas nonhosts avoid injury from colonization attempts by the beetles. NHVs include compounds characteristic of angiosperm foliage (e.g., various saturated or unsaturated C_6 aldehydes and alcohols) and bark (e.g., conophthorin, benzaldehyde, benzyl alcohol, salicylaldehyde, nonanal, and guaiacol) (95, 96, 98). Kairomonal or coattractant compounds generally require much higher release rates (100 to 1,000 mg/day) than pheromones to affect bark beetle behavior.

The complex communities of bark and ambrosia beetles associated with western conifers are likely regulated spatially and temporally on the host trees through behavioral interactions guided by allomones and synomones. There is evidence for these interactions in communities among multiple genera of bark beetles in ponderosa pine (*Pinus ponderosa*) (16), lodgepole pine (*P. contorta*) (22, 134), and white spruce (*Picea glauca*) (135). These effects provide potential semiochemical tools that can be exploited to interrupt the host-finding behavior of target pest species (18).

NHV: nonhost volatile; includes green leaf volatiles or angiosperm bark volatiles like conophthorin emitted by trees that are not hosts of conifer bark beetles

Although semiochemicals can influence bark beetle behavior in numerous ways, we focus herein on two generalized types of behavior: attraction (elicited by aggregation pheromones and/or host kairomones) and antiattraction (elicited by antiaggregation pheromones, allomones, and/or NHVs). In the bark beetle literature, antiattraction has also been described as disruption, inhibition, interruption, or repellency [see footnote on p. 1814 of Reference 169 for a discussion of these terms].

Semiochemical-Based Management Strategies

Semiochemicals have played an increasingly important role in bark beetle IPM (18). Silverstein (186) categorized the practical applications of pheromones as (*a*) monitoring and surveying (i.e., used in lures for trapping insects to identify newly infested areas and/or to estimate size of insect populations); (*b*) luring insects to specific areas for targeted use of insecticides or pathogens; (*c*) mass trapping for population suppression; and (*d*) mating or aggregation disruption (also for population suppression). The general tenor of these prescriptions was to use pheromones to optimize application of insecticides as part of the larger IPM framework (200). Today, these concepts are being extended beyond pheromones to include the larger universe of ecologically available semiochemicals in management strategies for bark beetles.

Monitoring and Detection. Central to IPM is the capacity to ascertain the presence, location, and population density of the pest. Key elements for semiochemical-based monitoring are traps (1) and trap lures. Trap lures normally consist of a slow-release formulation of aggregation pheromones combined with coattractant or synergistic host volatiles (173). They are attached to multiple-funnel, panel, or vane traps (**Figure 1**). Release devices for the attractive lures include bubble capsules (bubble caps), vials, pouches, or solid polymer tubing (72) (**Figure 2**). Semiochemical-baited traps are particularly valuable for detecting incipient populations of invasive bark beetles (see the sidebar titled Detection of Invasive Bark Beetles in Western North

Figure 1

(*a*) Multiple funnel traps or (*b*) panel traps are key elements for monitoring the flight of or trapping out bark beetles with semiochemicals. Image *a* courtesy of R.A. Progar; image *b* courtesy of Gaylord Briggs, Jefferson Resource, Redding, CA.

Figure 2

Release devices for bark beetle semiochemicals include (*a*) Synergy methylcyclohexenone (MCH) bubble capsules (bubble caps), (*b*) Synergy verbenone pouch, (*c*) Hercon Disrupt Bio-Flakes, and (*d*) SPLAT containing verbenone (17.5 g/day) applied to the bark surface of lodgepole pine (*Pinus contorta*); image *d* inset is a 5.5-cm × 2.2-cm SPLAT dollop. Images *a* and *b* courtesy of R.A. Progar; image *c* courtesy of William Murray, Department of Biological Sciences, San Jose State University, San Jose, CA; image *d* courtesy of C.J. Fettig.

America with Semiochemical-Baited Traps). When used for monitoring, baited traps should be placed at least 20 to 25 m (and sometimes farther) away from susceptible hosts and generally in an elevated and shaded position. Baited traps have been used to monitor seasonal and diurnal periodicity of bark beetle flight (63); although when populations are at low levels, the utility of these traps may be limited (7). Moreover, although no correlation has been established between trap catches and numbers of trees killed, trap catches can be used to discriminate between endemic and epidemic populations (79).

Placing trap lures (without host kairomones) on host trees to induce attack can provide a much more sensitive detection tool than a baited trap, possibly because of an attractive visual signal presented by the upright bole of the tree or the presence of a complete blend of host volatiles. Baited trees are used to monitor the eastward advance of the invasive mountain pine beetle in northern Alberta and Saskatchewan, where exceedingly small numbers of beetles may be present at the extreme front of the invasion (110). This tactic demands that all attacked trees be removed, burned, or debarked after the beetle flight is over, lest the detection tool create an infestation in its own right. Baited traps and trees are also necessary experimentally as positive controls for the

DETECTION OF INVASIVE BARK BEETLES IN WESTERN NORTH AMERICA WITH SEMIOCHEMICAL-BAITED TRAPS

Invasive bark beetles and related species are being detected with increasing frequency in North America (112, 113). In California alone, six invasive hardwood bark beetles and four invasive coniferophagous bark beetles have been reported (175). Kairomones (e.g., ethanol and monoterpenes) have been employed as trap lures in US screening surveys that have resulted in the detection of a large number of targeted as well as unexpected organisms (146). However, these generic lures result in complex trap catches of many insect species that have to be sorted and identified. Aggregation pheromone–baited traps provide a more efficient and species-specific detection tool for invasive bark beetles. Two male-produced hemiterpenoid pheromone components, 3-methyl-2-buten-1-ol and 2-methyl-3-buten-2-ol, provide some of the specificity for respective survey traps that target the walnut twig beetle, *Pityophthorus juglandis* (170, 171), and the Mediterranean pine engraver, *Orthotomicus erosus* (172, 173). The aggregation pheromone of *P. juglandis* has also been used experimentally to attract populations of these beetles for further study of wood and bark sanitation techniques to minimize pest damage (122). The pheromone of *O. erosus* also includes another male-produced monoterpenoid component [(−)-ipsdienol] and a host coattractant (α-pinene). Both of these beetle species have been the focus of detection surveys because of their potential as invasive forest pests in North America and internationally.

development of insecticides (45) and repellents (see the next subsection titled Treatments and the four case studies in the section titled Examples of Semiochemicals in Integrated Pest Management of Native Western North American Bark Beetles) to protect trees. The techniques of precisely timing an experimental insecticide application based on beetle response to pheromone-baited traps and challenging trees by placing pheromone lures on the stems of treated trees have been used for a wide range of bark beetles (45). When formulated as trap lures or tree baits, bark beetle semiochemicals do not need to be registered with the U.S. Environmental Protection Agency (EPA) or Canada's Pest Management Regulatory Agency (PMRA).

Treatments. Suppression of bark beetle populations is another key element of IPM that involves application of semiochemicals. Bark beetles can be removed from a population by killing them after luring them with attractants (5). This can be accomplished with traps (as described above for monitoring); with standing or felled trap trees; or through attract-and-kill techniques that also involve strategically applied insecticides. Trap-tree and attract-and-kill techniques use large diameter trees in shaded sites that have been baited with an aggregation pheromone. Tree baits are stapled to or near the host tree bole, whereby the host tree is presumed to augment the pheromone by releasing synergistic monoterpenes or other plant-derived synergists. Adjacent hosts are also often attacked. All attacked trees must be disposed of to prevent initiation or exacerbation of an infestation.

A second treatment tactic is host protection achieved by applying semiochemicals to or near the host to cause dispersal away from the protected trees (interruption or inhibition of aggregation or host location) (75). Repellents can be applied to the bark surface or to nearby substrates in slow-release devices, including bubble caps, pouches, vials, semisolids, or flakes (**Figure 2**). Bubble caps, pouches, and vials range in size from 2.5 to 10 cm and are attached manually by staple or nail, and the release rate of the semiochemicals will vary with changes in temperature and humidity, as well as time since deployment. In practice, these variations may not be important, because bark beetle emergence and flight activity also vary in tandem with release rate as temperature and humidity change.

SPLAT: Specialized Pheromone and Lure Application Technology; an emulsion used as a controlled-release technology for semiochemicals

Researchers have focused on development of biodegradable formulations of repellents and other formulations that can be broadcast from the ground or applied aerially by helicopter or fixed-wing aircraft. Repellent flakes (**Figure 2*c***) are relatively small (3–6 mm) pieces of plastic impregnated with semiochemicals. They can be applied dry, so that they fall to the forest floor, or with a liquid sticking agent that makes them adhere to the tree trunk or forest canopy. Flakes can also be distributed with a handheld fertilizer spreader to cover small land areas and can also be used in aerial application to cover large forested landscapes. Pheromone-releasing flakes have been used for decades to disrupt mating by the gypsy moth (179), and tests since 2005 have shown promise for the use of flakes with semiochemicals of bark beetles (67–71, 73). A relatively new formulation for repellent bark beetle semiochemicals is SPLAT (Specialized Pheromone and Lure Application Technology) (**Figure 2*d***) (121), which is a hand-applied, flowable, and biodegradable emulsion that allows the user to adjust the size of each release point (dollop) according to desired distribution and probable rate of emission in the field (54). With one product (SPLAT Verb; see the sidebar titled Semiochemical Products for Management of Western North American Bark Beetles), dollops biodegrade within ~1 year of application; the inert ingredients have been certified as food-safe by the EPA; and the product is classed as organic by the United States Department of Agriculture (USDA) (121).

Sales and use of repellent semiochemicals are regulated in Canada by the PMRA and in the United States by federal (EPA) and state (e.g., California Department of Pesticide Regulation) agencies. Therefore, product availability and use vary by state. In 1999, the first repellent semiochemical–based tools for management of bark beetles were registered in the United States, a bubble cap for *D. pseudotsugae* in the western United States (156) and a pouch for the southern pine beetle, *D. frontalis*, in the southeastern United States (33). Both contained antiaggregation pheromones. Three biodegradable formulations of the antiaggregation pheromone verbenone have also been registered at one time in the United States, including the Disrupt Bio-Flake verbenone (Hercon Environmental, Emigsville, PA) in 2010, the Disrupt Bio-Dispenser BB (Hercon Environmental) in 2013, and SPLAT Verb in 2013 (see the sidebar titled Semiochemical Products for Management of Western North American Bark Beetles).

SEMIOCHEMICAL PRODUCTS FOR MANAGEMENT OF WESTERN NORTH AMERICAN BARK BEETLES

The range of products available and their registration status change rapidly, but these are among the products available commercially as of August 2017.

- Verbenone products: Beetleblock Verbenone (Chem Tica USA, Durant, OK); Disrupt Micro-Flake Verbenone (Hercon Environmental, Emigsville, PA); Synergy Shield Verbenone pouch and bubblecap (Synergy Semiochemical Corporation, Burnaby, BC, Canada); Verbenone Pine Beetle Repellent Pouch (The Scotts Company LLC, Longmont, CO); Verbenone SPLAT Verb bark beetle repellent (ISCA Technologies, Inc., Riverside, CA).
- Methylcyclohexenone (MCH) products: Beetleblock MCH (Chem Tica USA); Disrupt MCH HA, a hand-applied MCH dispenser (Hercon Environmental); Disrupt Bio-Flake Verbenone (Hercon Environmental); Disrupt Micro-Flake MCH (Hercon Environmental); MCH Douglas-fir and Spruce Beetle Repellent Bubblecap (The Scotts Company); Synergy Shield MCH single and double bubblecap (Synergy Semiochemical Corporation). ISCA Technologies, Inc., plans to apply for registration for SPLAT MCH bark beetle repellent (56).

A third treatment tactic for managing bark beetle populations with semiochemicals is called push–pull, which causes dispersal away from a stand of protected trees with a combination of a repellent within the stand and an attractant at the perimeter. Beetles are pushed away from protected trees and pulled to traps or trap trees at the periphery. Thus, this technique combines the repellency and trap-out methods, but it has had variable success (19, 71, 81, 196).

EXAMPLES OF SEMIOCHEMICALS IN INTEGRATED PEST MANAGEMENT OF NATIVE WESTERN NORTH AMERICAN BARK BEETLES

Four prominent species of bark beetles native to western North America provide case studies for the role of semiochemicals in the IPM of bark beetles.

Mountain Pine Beetle, *Dendroctonus ponderosae*

D. ponderosae is the most damaging forest insect in North America (86). Outbreaks between the early 1990s and 2014 have exceeded historic twentieth century limits, causing devastating damage to commercial timber and huge losses of ecological goods and services at broad spatial scales. In general, outbreaks occur at the convergence of favorable forest age- and size-class structure and climate patterns (47, 201). This beetle colonizes the majority of pine species within its range, including *Pinus contorta*, *P. ponderosa*, and various high-elevation white pines such as limber pine (*P. flexilis*) and whitebark pine (*P. albicaulis*) (65). Development is temperature dependent, and a single generation is completed per year (i.e., univoltine) in most locations, although two years (i.e., semivoltine) may be required at high elevations (13).

Female *D. ponderosae* initiate host colonization, and males and additional females respond to two α-pinene derivatives, *trans*- and *cis*-verbenol, released by pioneering females (124, 197, 198). Both sexes produce *exo*-brevicomin, which is attractive mainly to males at low concentrations but inhibitory at high concentrations (144, 162). However, *trans*-verbenol increases the attraction of females to *exo*-brevicomin (124). Attraction is synergized by host monoterpenes such as α-pinene (132) and myrcene and terpinolene (24, 26). As the abundance of colonizing males increases, concentrations of *trans*- and *cis*-verbenol and host monoterpene coattractants decline (150) and increasing levels of male-secreted *exo*-brevicomin and frontalin reduce the attractiveness of the tree to colonizing beetles (21, 26, 30, 147, 165, 166).

During later stages of tree colonization, verbenone is produced by autoxidation (100) and/or biological oxidation of α-pinene, primarily by microbes that inhabit the gut or the gallery system (99, 133, 162). Verbenone inhibits additional *D. ponderosae* from colonizing the original tree, thereby restricting gallery density and increasing the likelihood of brood survival (2). Attacks switch to surrounding trees when $<50\%$ of total attacks have occurred on a tree, suggesting that verbenone and other inhibitory pheromones may function at a local scale (11), possibly around an adult entrance hole (147). Reorientation to adjacent trees allows host colonization to continue at a broader spatial scale (64).

Semiochemical-based tools and tactics for *D. ponderosae* include application of aggregation pheromones and coattractants for survey and detection; aggregation pheromones and coattractants for trap-out, trap-tree, or push–pull treatments to reduce population density and overall levels of tree mortality (e.g., 19, 71, 76, 196); and semiochemical repellents (see the next paragraph). The use of attractants entails the risk of inducing infestation of nearby trees (130). Nevertheless, if coupled with sanitation harvesting, tactics involving attractants, particularly to contain and concentrate infestations prior to harvesting, have sometimes been effective in reducing the infestation of adjacent stands (e.g., 76, 116, 190, 196).

Repellents to disrupt *D. ponderosae* colonization have been employed frequently in research and practice. Verbenone has been tested exhaustively for protecting individual trees (25, 73) and small stands of pines [<20 hectares (ha)] (9, 19, 20, 25, 43, 67, 68, 94, 115, 116, 127, 137–139, 181, 185, 204). While verbenone can protect most pine species successfully from attack (67–69), it has not been effective for protecting *P. ponderosa* stands without adjuvants (127). Initial efforts with verbenone involved simple bubble caps and pouch release devices stapled in spring at ∼2 m in height on the north aspect of boles of individual pines or applied in a grid pattern to achieve uniform coverage. Verbenone bubble caps (with lower release rates than pouches) have not been registered with the EPA or the PMRA, but several pouch formulations and a similar dispenser (Disrupt Bio-Dispenser BB) are or were at one time registered (see the sidebar titled Semiochemical Products for Management of Western North American Bark Beetles). In addition, several flake formulations are registered for ground and aerial application (140).

GLV: green leaf volatile; includes C_6 or C_7 alcohols, aldehydes, or esters like (*E*)-2-hexenal or (*Z*)-3-hexen-1-ol that characterize the odor profile of angiosperm leaves

In some instances, application of verbenone has not caused significant reductions in levels of tree mortality (9, 66, 137, 138, 181), particularly in stands of *P. ponderosa* (e.g., 10, 119, 127). These negative outcomes have been linked to high beetle population density (139), high stand density (47), low verbenone release rates, and limitations in the range of inhibition (123) (reviewed in 140). At outbreak population levels, population density may overwhelm the repellent signal, and verbenone may be ineffective (138). Fettig et al. (54) developed and tested a SPLAT formulation of (−)-verbenone (ISCA Technologies Inc., Riverside, CA) (see the sidebar titled Semiochemical Products for Management of Western North American Bark Beetles) for protecting individual trees and forest stands from *D. ponderosae*.

Host location and colonization behaviors of *D. ponderosae* might be exploited further by combining verbenone with NHVs, which enhance the repellent message to host-seeking beetles that the first colonizers have attacked an unsuitable host that should be avoided. Further enhancement might be achieved by adding the repellent pheromone signal (in this case a synomone) of a heterospecific bark beetle competitor, conveying the message that a suitable host tree or stand is already occupied by that competitor (18, 75, 167, 184, 209). NHVs, especially acetophenone and some green leaf volatiles (GLVs), are capable of reducing aggregation in *Dendroctonus* spp. (41, 209). Wilson et al. (204), Borden et al. (27), and Huber & Borden (94) reported that combinations of GLVs and angiosperm bark volatiles significantly reduced attack densities of *D. ponderosae* on attractant-baited *P. contorta* in British Columbia, Canada. Similarly, Kegley & Gibson (104) reported significant reductions in levels of tree mortality when *P. albicaulis*, *P. contorta*, and *P. ponderosa* were treated with a combination of verbenone and GLVs in Montana. However, Kegley et al. (105) reported that verbenone flakes, pouches, and a combination of verbenone and two GLVs were equally effective at protecting individual *P. contorta* from *D. ponderosae* in Montana. Gillette et al. (69) showed that two GLVs did not significantly increase the efficacy of verbenone for protection of *P. albicaulis* and *P. flexilis*. With a combination of verbenone and NHVs, Fettig et al. (43) demonstrated a 78% reduction in tree mortality attributed to *D. ponderosae* in stands of *P. albicaulis* in California. Despite this success, no product containing a combination of verbenone and NHVs has been registered for protecting trees from colonization by *D. ponderosae*.

Douglas-Fir Beetle, *Dendroctonus pseudotsugae*

D. pseudotsugae is the most damaging bark beetle on Douglas-fir, *Pseudotsuga menziesii*, in North America (61). Western larch, *Larix occidentalis*, can also be attacked. Populations are univoltine and increase when beetles attack weakened and downed trees in fire-, wind-, and/or avalanche-affected areas (62, 92). *D. pseudotsugae* is especially damaging in Mexico, where Douglas-fir is protected and survives primarily in small, isolated stands (32).

Semiochemical-based management of *D. pseudotsugae* has been an early success story in applied chemical ecology. During the early 1970s, frontalin (107, 131), seudenol (199), and 1-methylcyclohex-2-en-1-ol (MCOL) (114) were identified as potential attractants that might be useful for monitoring or trap out. A blend containing MCOL is most effective in British Columbia (118), whereas interior Oregon populations respond most strongly to blends containing seudenol (154). Concurrent with other research into *D. pseudotsugae* attractants, Kinzer et al. (107) demonstrated that methylcyclohexenone (MCH) is an attractant at very low release rates. Subsequent research demonstrated that at high release rates, MCH inhibits aggregation (60, 161), and for operational purposes it has been utilized solely for antiaggregation. Huber & Borden (93) suggested that NHVs (e.g., conophthorin) might increase the antiaggregative efficacy of MCH, but the combined interruptants have not been tested, as MCH is extremely effective as a single component, and most current field applications rely on MCH alone (70, 156).

Trap-out applications with attractant semiochemicals to concentrate Douglas-fir beetles into traps or trees slated for harvesting (141, 160) have had variable success. Disruption with MCH, in contrast, has been extremely effective with several different release devices. Bubble caps (**Figure 2*a***) deployed at the rate of about 75–100/ha to standing trees or wind- or avalanche-thrown trees have been used for decades with good success for relatively small areas, particularly in recreation sites or administrative areas (153, 155, 156). Individual trees can be protected effectively with two MCH bubble caps per tree. The use of bubble caps is limited by the cost of labor for hand application, inefficiency in treating remote or steep terrain by hand, and (in some cases) the need to remove the bubble caps at the end of the season. The latter limitation has been overcome with the development of biodegradable SPLAT MCH (10% active ingredient), which has comparable efficacy to that of bubble caps (56) and has no regulatory requirement for removal at season's end.

There have been several attempts to develop aerially applied MCH products for treatment of large, remote, and/or steep areas. Furniss et al. (59) demonstrated that aerially applied granular controlled-release formulations were successful in area-wide trials. Initial tests of biodegradable flake formulations (produced by Hercon Environmental) for treatment of large areas with fixed-wing aircraft or helicopters provided good results with 370 g of MCH/ha (70).

When *D. pseudotsugae* populations are very high because stands of host trees are extremely stressed, or windstorms, avalanches, or fire have killed or damaged many trees, it may be advisable to use a push–pull tactic (153), in which healthy stands are treated with MCH-releasing bubble caps or flake, whereas the perimeter, especially near fallen or damaged trees, is treated with funnel traps baited with seudenol (or MCOL), frontalin, and ethanol. Care must be taken to place baited traps far enough from healthy trees to avoid spillover attack from beetles attracted to the baited traps.

Various formulations of MCH are currently registered with the EPA and the PMRA, including bubble caps (several registrants) and the Disrupt Micro-Flake MCH (Hercon Environmental). The MCH bubble cap is used to treat several thousand hectares of forest each year (159). Concerns that MCH and structurally related compounds may repel bees (168) appear to be unfounded, at least for the western honey bee, *Apis mellifera*, in Idaho and Montana (56).

Spruce Beetle, *Dendroctonus rufipennis*

D. rufipennis is the most important disturbance agent of mature spruce trees, *Picea* spp., with primary impacts from the southern Rocky Mountains in New Mexico to the Yukon Territory and

Alaska (89). Under endemic conditions, *D. rufipennis* typically colonize isolated standing trees or fallen trees from wind throw, logging activity, or other causes. Following larger-scale disturbance events, rapid population growth can occur (62), followed by aggregation on and attack of standing live trees. This can be exacerbated by susceptible stands, favorable weather, and drought stress (14, 151). The life cycle ranges 1–3 years depending on local temperature. Females initiate attacks during early summer by using host kairomones and pheromones to locate suitable hosts, find mates, and attract conspecifics to overwhelm host defenses (101). As for *D. pseudotsugae*, various methylcyclohexene derivatives of unknown biogenic origin affect these behaviors.

Attractive semiochemicals for *D. rufipennis* have been used to predict local population levels (79) and in push–pull suppression efforts (80). Dyer & Chapman (37) first suggested that frontalin and α-pinene may play a role as *D. rufipennis* attractants. Frontalin (78), seudenol (199), verbenene (77), and MCOL (23) were later isolated from feeding females. Commercially available lures used in western North America have typically included frontalin, α-pinene, and MCOL, although MCOL can have a region-dependent additive or inhibitory effect (23, 158). Augmenting α-pinene with a more complete host terpene blend may further improve attractiveness (82). Frontalin alone is typically sufficient to initiate attacks on live trees, as might be desirable to create trap trees (39).

Rudinsky et al. (163) first demonstrated that MCH was repellent to *D. rufipennis*. Subsequently, MCH has been shown to reduce attraction to pheromone-baited traps (117); to logs infested with unmated females (58, 109); and to reduce colonization of stumps, wind-thrown trees, and felled trees (38, 91). Other tests with downed host material have had variable success, presumably because the release devices were improperly calibrated for local temperatures (e.g., 90).

Tests of MCH to protect live standing spruce from *D. rufipennis* were unsuccessful in Alaska (202) and Utah (157). These tests relied on passive release from devices whose elution rate depended on temperature and time since deployment (2–10 mg/day at 22–25°C for fresh devices). The first successful test of MCH to protect live trees used a microinfusion pump to emit MCH at a metered rate (2.6–5.0 mg/day regardless of temperature) (88). This Alaskan test deployed the release devices at >120/ha and resulted in >80% reduction in new attacks in 0.2-ha blocks.

Trapping experiments in Utah revealed that a high-dose passive MCH releaser (1,000-mg bubble cap, releasing MCH at 12 mg/day at 25°C) reduced captures in traps baited with MCOL, frontalin, and spruce monoterpenes (Synergy Semiochemical, Burnaby, BC, Canada) by ~96% (80). These assays also identified isophorone plus sulcatone (I+S) and a maple, *Acer* sp., kairomone blend (AKB) as *D. rufipennis* repellents. Hansen et al. (81) found that mass attacks on live spruce were ~15 times more likely in blocks in which lethal trap trees were sprayed with carbaryl than in similar blocks that were also treated with a grid of MCH and I+S release devices. In a 2016 study in Utah and New Mexico, MCH treatment caused an ~50% reduction in attack rates on live spruce within 0.64-ha plots, with no difference in MCH doses of 20, 40, or 80 g/ha (80). In nearby single-tree protection trials, 24 of 32 spruces baited with the Synergy attractant were mass attacked, compared to 10 of 30 baited trees treated with MCH, 11 of 30 baited trees treated with AKB, and 0 of 32 baited trees treated with MCH plus AKB.

Overall, MCH has been proven to be an effective tool to protect living spruce from *D. rufipennis*. Efficacy has been associated with temperature, beetle population density, MCH concentration and release rate, co-occurring secondary bark beetle semiochemicals, release device type, and spatial distribution of treatment (210). Testing in Utah and New Mexico suggested that MCH alone is marginally effective (80), but deploying additional semiochemicals with MCH may protect trees with greater efficacy. MCH is currently registered with the EPA for use against *D. rufipennis*. Registering improved formulations of MCH with additive/synergizing semiochemicals may delay commercial availability.

Western Pine Beetle, *Dendroctonus brevicomis*

D. brevicomis is a major cause of *P. ponderosa* mortality in much of western North America, especially California and Oregon. Coulter pine, *P. coulteri*, is also a frequent host, but its distribution is restricted to the mountains of Southern California and northern Baja California. *D. brevicomis* prefers large diameter trees (>50 cm at 1.37 m) but under certain conditions may attack and kill apparently healthy trees of all ages and size classes (125). There are typically 2–4 generations per year, depending on location and weather.

During early stages of tree colonization, female *D. brevicomis* release *exo*-brevicomin, which attracts conspecifics when combined with the host monoterpene myrcene (4). Populations east of the Great Basin produce primarily *endo*-brevicomin, and this isomer is more attractive to males than *exo*-brevicomin is in traps baited with α-pinene and frontalin (145). Frontalin, which is produced by males (108), enhances attraction, and mass attack ensues (206). These volatiles are now commercially produced and are effective attractants for survey, detection, and induction of mass attack on individual trees. They have also been used to induce attack and create biologically rich snags of *P. ponderosa* that provide feeding substrates, nesting sites, and habitat for a variety of invertebrates and vertebrates (180). Trap-out and trap-tree methods, however, have not been well investigated as means of control for *D. brevicomis* (191). Later in the colonization process, verbenone is produced by autoxidation of the host monoterpene α-pinene via the intermediary compounds *cis*- and *trans*-verbenol (100), by the beetles themselves (29), and presumably by microorganisms associated with *D. brevicomis*. Verbenone has been demonstrated to disrupt the response of *D. brevicomis* to attractant-baited traps in many studies (3, 6, 15, 41, 42, 48, 129, 183, 194) but not in all cases (84).

Verbenone was the focus of early efforts to protect *P. ponderosa* from attack by *D. brevicomis*. Bertram & Paine (15) found that applications of verbenone and (+)-ipsdienol, an aggregation pheromone component produced by several species of *Ips* (169) and an antiaggregation pheromone component produced by male *D. brevicomis* (176), significantly reduced numbers of *D. brevicomis* landing on and attacking *P. ponderosa*, but tree mortality rates were not determined. Verbenone flakes applied to the stem of individual *P. ponderosa* were ineffective for preventing *D. brevicomis* attacks in California (73). Furthermore, Fettig et al. (48) found no differences in levels of tree mortality attributed to *D. brevicomis* between verbenone-treated (5-g pouch) and untreated plots during a three-year study in California. Thus, verbenone alone is ineffective for protecting *P. ponderosa* trees and stands from attack by *D. brevicomis*, despite the availability of several products labeled for this use.

In field trapping experiments in British Columbia, Poland et al. (136) found that the GLVs (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol reduced captures of male *D. brevicomis*, and (*Z*)-2-hexen-1-ol also reduced captures of females. However, Fettig et al. (52) reported that these three GLVs combined with several nonhost bark volatiles [benzaldehyde, benzyl alcohol, *trans*-conophthorin, guaiacol, nonanal, and salicylaldehyde] did not affect responses to attractant-baited traps in California. However, when the NHVs were combined with verbenone, trap catches were reduced to levels below those of verbenone alone (52). Acetophenone, a common plant volatile that is also produced by some bark beetles (142), also reduces captures in attractant-baited traps (41).

Using a blend of NHVs [benzyl alcohol, benzaldehyde, guaiacol, nonanal, salicylaldehyde, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol] and verbenone, Fettig et al. (44, 49) demonstrated the successful protection of *P. ponderosa* from mortality attributed to *D. brevicomis*. Later, Fettig et al. (50, 51) developed Verbenone Plus [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (−)-verbenone] that protected *P. ponderosa* trees and stands from mortality attributed to

D. brevicomis in the United States and Canada. To date, Verbenone Plus has not been registered and commercialized.

CONCLUSIONS AND FUTURE DIRECTIONS

Several management tactics can be used to reduce bark beetle–associated tree mortality. Indirect control is preventive and is designed to reduce future bark beetle infestations within treated areas by manipulating stand structure through thinning, prescribed burning, and altering age classes and species composition (46). This stand manipulation reduces the number of susceptible hosts. Direct control, in contrast, involves short-term tactics designed to address current infestations by manipulating beetle populations. Semiochemicals are an integral component of direct control. Although repellents may not provide the same level of tree protection as toxic insecticides, they can be applied with less restriction and fewer regulatory concerns, and more easily than conventional insecticides in rugged terrain. For example, SPLAT technology and pouches are used by the USDA Forest Service to apply verbenone to protect white pine blister rust–resistant *P. lambertiana* (55) and *P. albicaulis* (103) seed trees from attack by *D. ponderosae* in California and in the Greater Yellowstone Ecosystem and similar high-elevation sites, respectively. Campground treatments with Verbenone Disrupt Micro-Flakes for *D. ponderosae* in Montana, Colorado, and Washington also significantly reduced attack rates on *P. albicaulis* and *P. flexilis* (69), whether applied to individual trees or broadcast on the landscape.

We have outlined experimental evidence in four western North American bark beetle–host systems for the efficacy of population management by semiochemical applications. The scope of these experimental treatments has ranged from individual trees to stands of approximately 100 ha (the maximum allowable for experimental studies). Attempts to demonstrate operational-scale efficacy of these treatments have been either uncontrolled, unreplicated, or both (e.g., 182). These case studies are also often poorly documented in the literature. Thus, the extent of the operational use of these treatments in western North America remains unquantified. Further, we know of no systematic cost–benefit analyses for such treatments. These analyses have likely not been conducted because of the high degree of variability in beetle response and thus efficacy of treatment, in any given year and place (207). Sources of variability include differences in stand species composition and structure, beetle population levels, weather patterns, and semiochemical release devices.

Semiochemicals may also be integrated with other resource management tactics. For example, prescribed fire and mechanical fuel treatments are increasingly used in western North America to reduce forest fuels, but bark beetles can cause significant posttreatment tree mortality, particularly 1–2 years following treatment (35, 53). In these cases, repellent semiochemicals could be used to protect residual trees until short-term stressors have dissipated.

Complete integration of semiochemical-based approaches into bark beetle IPM has also not yet been achieved. However, this is an active area of research, and new tree-protectant products—both active ingredients and release devices—are constantly emerging in the marketplace. Much of what is known about semiochemicals and their role in bark beetle dynamics derives from small-scale studies (<20 ha), whereas operational management decisions are usually made at the landscape level. Landscapes have diverse spatial patterns of structure and composition that influence the behavioral dynamics of bark beetles (31) and the dispersion and longevity of semiochemical aerosols (173) in ways that are not fully understood. Other factors that affect risk of bark beetle infestation—such as host species composition and age distribution (152), environmental conditions that increase host vulnerability (148), beetle population density, and distribution of semiochemical plumes (193), in particular NHVs—are not uniformly distributed across forested areas. Complete coverage of large areas with semiochemicals is practically impossible, and wise use of limited pheromone release sources is paramount. Guidelines will be needed to direct optimal semiochemical deployment, alone or as part of IPM efforts. In some instances, robotic or drone-based delivery of repellents to the upper portions of tree boles might improve the efficacy of semiochemical treatments.

Another challenge to scientists and land managers is the availability and purity of bark beetle semiochemicals. One possible answer to this challenge is to develop bioproduction technology. During the last 20 years, great strides have been made in understanding the biosynthesis of western bark beetle pheromones (177). The key genes and enzymes from the de novo synthesis could be exploited commercially for the production of monoterpene alcohol and bicyclic acetal pheromones of high stereochemical purity for applications in management. The cytochrome P450 genes that mediate the biochemical interactions between bark beetles and their host conifers have been isolated and characterized from *I. paraconfusus* (97). These discoveries could lead to the development of commercial bioproduction of bark beetle semiochemicals in microbes or plants. There are models for bioproduction in related systems (36, 192) that could guide this development for bark beetles.

Bark beetle population dynamics are significantly influenced by climate and weather. Shifts in thermal and precipitation patterns associated with climate change are driving large-scale outbreaks across western North America (12). Warming temperatures increase overwintering beetle survival and reduce the time required to complete a generation; both can enhance population growth. Trees at the margins of their ranges, both in elevation and latitude, are particularly susceptible to climate-induced stress, and these locations are also predicted to have increasingly favorable thermal conditions for beetle population growth. Reduced precipitation weakens host-tree defenses, which also facilitates increases in bark beetle populations. Semiochemicals will be valuable tools for tree protection in climate-stressed and high-value stands during periods of temporary vulnerability. Recent developments in understanding bark beetle chemical ecology, discovery of key genes that influence host tree and bark beetle interactions, and strategies for applying newfound knowledge within an IPM framework show promise for improved efficacy of bark beetle management at a variety of spatial scales.

FUTURE ISSUES

1. More efficacious repellent blends are needed for most bark beetle species, especially for use in landscape-level applications. Research to identify and field test new semiochemical components and compositions is encouraged.
2. Most forest lands in western North America are publicly managed through regulation by national, state, provincial, or local government policies. There is a need for biodegradable release devices and products that do not leave residues of concern on these public (and private) lands. Further development of such products is also encouraged.
3. Semiochemical cost and purity present obstacles to their deployment over large forested acreages. New developments in microbial synthesis (192), however, offer the promise of less expensive semiochemicals with greater optical purity.
4. Drone technologies offer hope for more widespread and precise application of semiochemicals in steep and remote terrain, previously inaccessible by most methods. Fixed-wing aircraft are generally inappropriate for use in such environments, and most applications today are made by helicopter. Drone applications, while currently limited in the payloads that can be delivered, have promise for future applications that involve newer and lighter-weight release devices.

5. Research has demonstrated that semiochemical blends are effective for limiting levels of tree mortality attributed to several species of bark beetles in western North America. However, none of the compositions have been registered because of the substantial required investment contraposed with the relatively low market value of the crop (i.e., firs, pines, and spruces). Some of this is a consequence of well-meaning legislation both in Canada and the United States designed primarily to regulate the use of conventional toxic insecticides. Until this regulatory issue is addressed, the use of novel, potentially efficacious semiochemicals and their blends for the management of bark beetles will be limited.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. Mention of a product or service does not constitute recommendation for its use by the USDA Forest Service or the authors.

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