

The Western Bark Beetle Research Group: A Unique Collaboration With Forest Health Protection

Proceedings of a Symposium at the 2007
Society of American Foresters Conference

October 23–28, 2007, Portland, Oregon

J.L. Hayes and J.E. Lundquist, compilers



U.S. Department of Agriculture, Forest Service
Pacific Northwest Research Station
Portland, Oregon
General Technical Report PNW-GTR-784
April 2009

Semiochemical Sabotage: Behavioral Chemicals for Protection of Western Conifers From Bark Beetles¹

Nancy E. Gillette and A. Steve Munson²

Abstract

The discovery and elucidation of volatile behavioral chemicals used by bark beetles to locate hosts and mates has revealed a rich potential for humans to sabotage beetle host-finding and reproduction. Here, we present a description of currently available semiochemical methods for use in monitoring and controlling bark beetle pests in western conifer forests. Delivery systems include hand-applied methods, such as semiochemical-releasing bubblecaps, pouches, and “puffers,” as well as products that can be applied by aircraft such as semiochemical-releasing flakes. Descriptions of both attractant-based (“pull”) and anti-attractant-based (“push”) strategies are provided. Examples are provided for the major bark beetle pests in western North America, including the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), western pine beetle (*Dendroctonus brevicomis* LeConte), the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), the spruce beetle [*Dendroctonus rufipennis* (Kirby)], and the red turpentine beetle (*Dendroctonus valens* LeConte),.

Keywords: Pheromones, allomones, kairomones, IPM, trap-out, trap trees, push-pull, pine, Douglas-fir, spruce.

¹ The genesis of this manuscript was a presentation by the authors at the Western Bark Beetle Research Group—A Unique Collaboration with Forest Health Protection Symposium, Society of American Foresters Conference, 23–28 October 2007, Portland, OR.

² **Nancy E. Gillette** is a Research Entomologist, USDA Forest Service, Pacific SW Research Station, 800 Buchanan Street, Albany, CA 94710; e-mail ngillette@fs.fed.us. **A. Steve Munson** is an Entomologist, USDA Forest Service, Forest Health Protection, 4746 S. 1900 E., Ogden, UT 84403; e-mail smunson@fs.fed.us.

Introduction

Background

Bark beetles are the most damaging insect pests of conifer forests in western North America (Furniss and Carolin, 1977) and outbreaks are increasing (Hicke et al. 2006, Hicke and Jenkins 2008, Logan and Powell 2001). For example, a current epic outbreak of mountain pine beetle in British Columbia, Canada, has affected over 9.2 million hectares of ponderosa pine (*Pinus contorta* Dougl.) (Westfall 2007) and has breached the Continental Divide, spilling over into interior Canada (Wilent 2005). This bark beetle outbreak is the largest ever documented, and is expected to continue until either the host is depleted or severe cold weather reduces beetle populations (Ebata 2004). Outbreaks of this magnitude have the potential to convert large regions of boreal and temperate forest from carbon sinks to carbon sources, exacerbating global warming (Kurz et al. 2008a, 2008b). The MPB could infest millions of hectares of jack pine (*Pinus banksiana* Lamb.) in the vast boreal forests of Canada and the north central United States, and climate change may favor *D. ponderosae* range extensions into this habitat (Carroll et al. 2003, Logan and Powell 2001, Ono 2004). Heavily stocked or old growth stands are particularly at risk (Shore et al. 2000, Wood et al. 1985), with extensive outbreaks predicted for many locations in the western United States (Krist et al. 2007). Forest managers have therefore sought methods to mitigate the effects of these pests. To this end, efforts have focused on the development of better methods to prevent losses of forest trees to bark beetle outbreaks, particularly high-value trees in the urban-interface, recreation areas, and high elevation ecosystems.

Semiochemical-based bark beetle control has been the subject of a substantial research effort (summarized by Borden 1997, Skillen et al. 1997, and Wood et al. 1985) since the identification of the first bark beetle pheromones (Silverstein et al. 1966, 1968). Land managers have had high expectations for the development of pheromones and other behavioral chemicals for bark beetle control because of limitations encountered with other pest control methods. For example, it is widely accepted that maintenance of stand health and vigor through vegetation management is the most durable approach to “beetle-proofing” stands (Amman et al. 1991; Amman and Logan 1998; Fettig et al. 2006c, 2007; Negrón et al. 2001; Whitehead and Russo 2005), but management objectives sometimes require maintenance of high basal area (Andrews et al. 2005) and/or the creation of down woody material that increases stand susceptibility to bark beetle attack (Ross et al. 2006). Treatments to reduce stand density are also time-consuming and can incur regulatory obstacles that may delay the implementation of treatments until stands have already been compromised by bark beetle attacks. Sanitation and salvage may help mitigate the effect of bark beetles, particularly in small, isolated infestations (Bentz and Munson 2000), but these methods are often insufficient and/or of unproven efficacy for landscape-altering outbreaks. Biological control, while generally a desirable approach to pest management, is of limited use against native bark beetle pests using their native natural enemies. While biological control manipulations such as augmentation of native natural enemies or inundative release of parasitoids and predators are theoretically possible, it is unlikely that they would be implemented over large scales because of logistical constraints. Insecticides have been

tested for decades for bark beetle control (DeGomez et al. 2006; Fettig et al. 2006a, 2006b, Haverty et al. 1998; Naumann and Rankin 1999), but they are generally too toxic, time-consuming, expensive, and difficult to deploy in remote areas for widespread use on public lands, with the exception of high-value trees in the wildland-urban interface, campgrounds, ski resorts, and administrative sites. The development of semiochemicals, therefore, is an appealing alternative to other integrated pest management (IPM) methods for mitigation of damage by bark beetles. IPM is a systematic approach to pest control that incorporates monitoring to assess the need for treatments, then initiates treatments as needed, beginning with the most environmentally benign methods. Typically, cultural or mechanical control methods are attempted first, followed by biological control and/or semiochemicals, then use of insecticidal control only if other methods fail (Kogan 1998, Smith 1962).

Early attempts to control damage by bark beetles using semiochemicals were handicapped by insufficient information about the components of the semiochemical blends and by inadequate release devices. That is, the release devices either did not release sufficient quantities of semiochemicals or did not release the semiochemicals long enough to protect stands during the entire flight periods of the targeted pest species (Holsten et al. 2000). Because of the limitations of other pest control strategies and the urgent need to protect conifers from bark beetle attack, recent research has focused on the development of more effective active ingredients such as aggregation pheromones, synergists, and anti-attractants and on more effective release devices for dispersal of these semiochemicals. New information about behaviorally active semiochemical blends, newer release devices, and the integration of semiochemicals with silvicultural pest management methods have led to more effective strategies to minimize damage by these pests.

In describing case histories of semiochemical methods for controlling western bark beetles, we have organized the discussion by pest species. Although we discussed southern pine beetle (*Dendroctonus frontalis*) applications in our symposium presentation (Clarke et al. 1999, Salom et al. 1995), in keeping with the overall symposium theme, this article will be restricted to the major western bark beetle species. Likewise, we have not included discussions of the use of semiochemicals for monitoring invasive bark beetle species (see Seybold and Downing, this Proceedings) or for the control of ambrosia beetles or forest Lepidoptera, although the use of sex pheromones in mating disruption has been quite successful for reducing damage by forest moths. The resources described below are not intended as an exhaustive list; this is an active field of research and development, with new active ingredients and release systems being constantly developed and tested for efficacy.

Semiochemicals and Applied Chemical Ecology

Semiochemicals are chemicals emitted by one organism that can affect the behavior of another organism; the term “semiochemical” is derived from the Greek “semeion,” meaning signal. The terminology for describing semiochemicals has changed over time, with multiple terms for the same phenomena (Nordlund and Lewis 1981). Terms used in the past, with some overlap in meaning, include

- Infochemicals
- Signalling chemicals
- Behavioral chemicals
- Behavior modifying chemicals
- Pheromones
- Semiochemicals

The term “semiochemical” has been widely accepted as an umbrella term for these chemicals. Semiochemicals that act within a species are called pheromones, and those that act between species are referred to as allelochemicals (fig. 1). 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.

For example:

- Bark beetles use aggregation pheromones to concentrate enough adult beetles of the same species to overcome tree defenses (acts within a species to enhance progeny survival).
- Humans infected with malaria exhale volatile allelochemicals that attract the Anopheline mosquito vectors of malaria (acts between species to the detriment of the human host but to the benefit of both the mosquito and the malaria parasite).
- Skunks use a noxious spray to repel predators (benefits the sender, thus an allomone).
- Ambrosia beetles use ethanol emanating from fermenting tree tissues as a cue in host location (benefits the receiver, thus a kairomone).

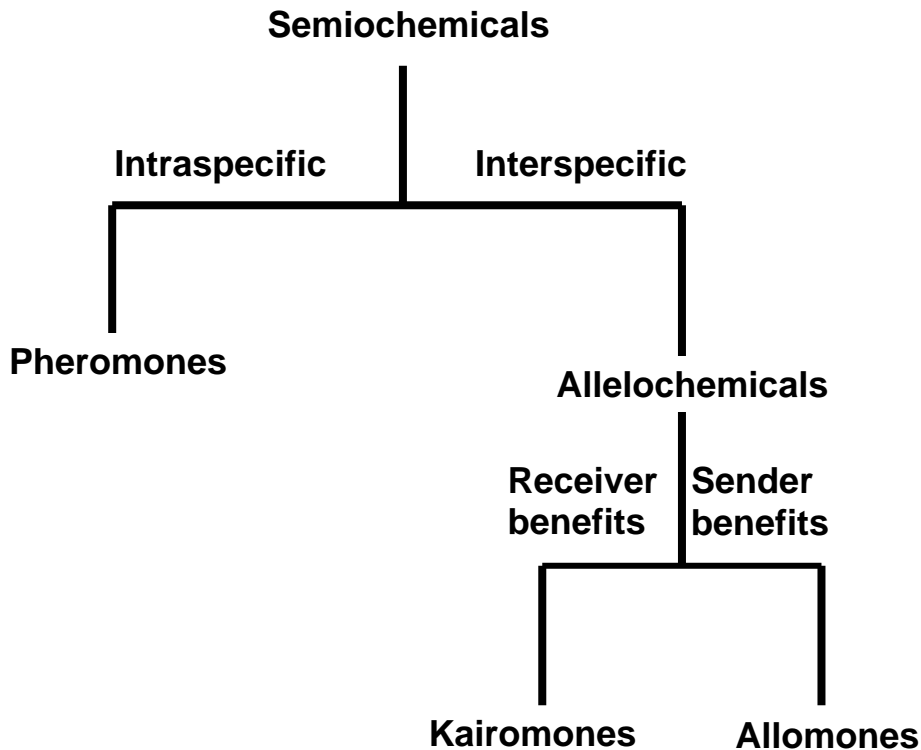


Figure 1—Diagram of semiochemical activity.

In practice, most semiochemicals used operationally in pest control are either pheromones or kairomones. There are several other issues that are important to keep in mind when using semiochemicals:

- Most semiochemicals are multifunctional
 - Their release rate can affect the behavior elicited
 - They can be attractive at low rates, repellent at high rates
- Most semiochemicals are multicomponent blends
 - The components of the blend may be inactive by themselves
 - Many aggregation pheromone blends include host volatile compounds with the beetle-produced pheromones, often as synergists
- Chiral pheromones and kairomones
 - Many semiochemicals are optically active and can exist in “mirror image” forms (enantiomers, “plus” vs. “minus,” “*R*” vs. “*S*,” or “*L*” vs. “*D*”), which have nearly identical physical properties but can result in different behavioral responses by the receiving insect
 - The “antipode” or opposite enantiomer of a semiochemical, for example, may be inactive or may even interrupt the response to the other enantiomer
- Insects can use different semiochemical “dialects” in different parts of their range
 - Therefore it is important to use semiochemicals that are regionally appropriate
 -

It is therefore crucial to have certain information before implementing a semiochemical-based strategy for bark beetle control. In other words, we must know

- All of the major semiochemical components, including synergists
- The most effective release rate
- The correct enantiomeric composition
- Whether there is variation in insect response across its geographic range (i.e., we need the right “dialect”)

Semiochemicals can influence insect behavior in myriad ways, but for the sake of simplicity we will treat just two generalized types: attraction (e.g., host attractants and aggregation and sex pheromones) and anti-attraction (e.g., interruptants, inhibitors, anti-aggregants, non-host volatiles (NHVs), “marking” pheromones, and repellants). All of the widely used semiochemical strategies employ attractants (“pull,” “attract-and-kill,” and “containment-and-concentration” strategies), anti-attractants (“push” strategy), or both (“push-pull”). Aggregation and sex pheromones typically provide a very strong cue, and they are hence effective at extremely low release rates (1 to 10 mg/day). Other attractants (e.g., host volatiles) and anti-attractants generally require much higher release rates and/or application rates (100 to 1000 mg/day) to affect beetle behavior. These traits have influenced the types of release devices that have been developed for the dispersal of semiochemicals in forest stands.

Commonly Used Semiochemical-Based Strategies

- *Monitoring* is not intended to control bark beetle populations, but to detect and measure population levels of bark beetles using attractants (usually aggregation pheromones) in release devices such as bubblecaps, vials, or solid polymer tubing
- *Trap-out* removes bark beetles from the population by luring them with attractants released from bubblecaps, vials, or solid polymer tubing. These techniques include traps, trap-trees and attract-and-kill
- *Repellency* (interruption or inhibition of aggregation or host location) causes dispersal away from stands using repellents in release devices such as bubblecaps, pouches, puffers, or flakes
- *Push-pull* involves the use of an attractive pheromone at the perimeter of stands coupled with a repellent pheromone in the center of treated stands. This technique, combining both trap-out and repellency (Cook et al. 2007), has been shown to improve efficacy of repellents in some cases

Terminology and techniques

Trap “lures” normally consist of aggregation pheromones combined with attractant or synergistic host volatiles (Seybold et al. 2006), and are meant to be attached to multiple-funnel, panel, or vane traps (fig. 2). Tree “baits,” on the other hand, consist of aggregation pheromones formulated without the host volatiles and are intended to be stapled or nailed to the host tree trunk. The host tree is presumed to release the monoterpene synergists. In some cases, host monoterpenes synergize the attraction of aggregation pheromones and are thus considered part of the pheromone blend.

A.



B.



Figure 2—A, multiple funnel trap (reprinted with permission from Pherotech International (now Contech International)); B, panel trap (reprinted with permission from Aptive, Inc.).

Non-host volatiles (NHVs), which include green leaf volatiles (GLVs) and angiosperm volatiles (i.e., non-conifer volatiles, collectively), have shown promise in increasing the efficacy of one of the two primary anti-attractants, verbenone, for some beetle species. The effective blend is often quite species-specific, so a single blend will probably not serve all needs.

Release devices such as bubblecaps, pouches, puffers, and vials range in size from about 2.5–10.2 cm and are meant to be manually attached to the substrate (e.g., traps or trees) (fig. 3A–C). Bubblecaps, pouches, vials, and flakes are “passive” releasers, so their release rate varies with changes in temperature and humidity. In practice these variations may not be important, because temperature changes also affect insect emergence and flight, often in ways that parallel the need for semiochemical emission. Puffers are small battery-activated reservoirs that emit frequent, measured puffs of semiochemical, thus overcoming the problem of depletion of the release device and variable release rates under fluctuating temperatures. Flakes are much smaller, usually 3–6 mm² in size, and are intended for aerial application over large areas. 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 forest canopy. Flakes can also be applied using a hand-held

fertilizer spreader to cover smaller acreages. Flakes, like other passive releasers, are temperature-dependent in their release profiles.

A.



B.



C.



Figure 3A, DFB two-part lure; 3B, MCH bubblecap; 3C, verbenone pouch (all with permission of Synergy Semiochemicals).

Baited traps

Baited traps are typically used to determine flight periodicity in order to time the implementation of suppression projects. Baited traps can also be used as a suppression tactic, in which sufficient numbers of insects are trapped to reduce local infestation levels. This tactic is often combined with other suppression treatments to enhance treatment success. When used for suppression, baited traps should be placed at least 25 meters from susceptible hosts, and generally in an elevated and/or shaded position. Multiple-funnel traps (with varying numbers of funnels) or panel traps (fig. 2 A-B) are both effective for monitoring bark beetles.

Trap trees for concentration or trap-and-kill

When used as a suppression tactic (concentration or trap-and-kill), baited trees should be of fairly large diameter and in shaded sites. Adjacent hosts may also be attacked, so it is important to place baits carefully to avoid undesired tree mortality. All attacked trees are intended to be sacrificed, and once they are infested they should be removed, burned, or debarked.

Aerially applied flakes

Semiochemical-releasing flakes have been used for decades in the Gypsy Moth Slow-the-Spread program (Sharov et al. 2002), but have been only recently developed for bark beetle pheromones (Gillette et al. 2006, 2009a, 2009b). Recent tests have demonstrated the promise of this technology for control of Douglas-fir beetle and MPB, and testing continues for other bark beetle species.

Semiochemicals for Major Western Bark Beetle Pests

Mountain pine beetle (MPB)

Effective techniques have been developed for most of the major hosts of MPB, including lodgepole pine, whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*Pinus flexilis* James), and ponderosa pine. The primary anti-attractant for MPB, verbenone, has also shown behavioral activity for several other bark beetle species and is produced by a wide variety of organisms including bacteria, fungi, gymnosperms and angiosperms (Gillette et al. 2006). Combining verbenone with nonhost volatiles may provide better protection than verbenone alone (Huber and Borden 2001).

Monitoring and Trapping (Pull)

A blend of *trans*-verbenol, *exo*-brevicomin, myrcene, and terpinolene is highly effective for attracting MPB when used as a trap lure. Earlier research suggested that the first three components comprised the aggregation attractant blend (Borden and Lacey 1985, Conn et al. 1983), but more recent work has shown that the addition of terpinolene greatly increases trap catch (Pureswaran and Borden 2005). If reduced attraction is desirable, for example where there is a risk of inducing attack on adjacent healthy trees, the two-component tree bait (*trans*-verbenol and *exo*-brevicomin) can be deployed instead (Borden et al. 1993). Attract-and-kill or concentration techniques have been tested for decades and were shown to be effective in reducing rate of attack on adjacent trees (Gray and Borden 1989, Smith 1986). The four-component aggregation semiochemical blend described above is presumably optimal for trapping-based methods. The earliest trap-based control methods utilized insecticide-treated trees that were baited with the aggregation pheromone (Smith 1986). Vandygriff et al. (2000) successfully used aggregation pheromones to focus beetle attacks in areas designated for fuelwood harvest, potentially improving stand health in baited sites. More recent studies have shown good control of adjacent stands by baiting “sacrificial trees” that are intended for immediate harvest as soon as they are attacked and fully colonized (Borden et al. 2003, 2006, 2007).

Push

The interruptant verbenone has been widely tested for repellency of MPB. Early tests using lower-release rate bubblecapsules did not provide sufficiently high release (Holsten et al. 2000, Lister et al. 1990), but subsequent higher-release devices called pouches (Contech International, formerly Pherotech International, Delta, BC, Canada; Synergy Semiochemicals, Burnaby, BC, Canada; ChemTica USA, Durant, OK, USA; Aptiv, Portland, OR, USA; Alpha Scents, Bridgeport, NY, USA) generally have provided significant protection (Bentz et al. 2005; Borden et al. 2004, 2007; Gibson and Kegley 2004; Kegley et al. 2003; Kegley and Gibson 2004; Progar 2003). In some cases of extreme beetle pressure and/or stand susceptibility, efficacy appears less certain (Progar 2005), but newer formulations are registered to allow higher application rates, which may improve efficacy (Gillette et al. 2009a). The verbenone pouches contain 7.1–7.4 g verbenone (Pherotech International, Synergy Semiochemicals). The addition of NHVs to verbenone often improves efficacy of the repellent (Borden et al. 2003, 2006, Huber and Borden 2001), but in many cases sufficient efficacy is achieved with verbenone alone (Kegley and Gibson 2004, Kegley et al. 2003). Pouches are typically applied 3–4 m above the ground and are applied to the north sides of trees in a grid with roughly 50–100 pouches per hectare, with higher rates recommended for more challenging situations. Some verbenone treatments are applied at the rate of 50 pouches/hectare with replacement at mid-season. This approach is especially desirable where weather conditions indicate that pouches may become depleted before the end of the season. Area protection treatments using verbenone are significantly more effective if all the infested trees within the treatment area are removed before beetle flight. Increasing the verbenone grid to include a 25–30 m treated buffer may also enhance efficacy. Where individual trees, rather than stands, are intended to be protected, pouches are applied at the rate of two per tree on the northeast and northwest sides of the trees. In the case of whitebark pines, which often occur as mixed stands with other pine species, adequate protection can be achieved by placing pouches on both the whitebark pines and surrounding trees, to create an area effect that ensures that the pheromone plume encompasses the trees to be protected regardless of wind direction. Additional studies are underway to test ways of increasing the efficacy of this technique, particularly by adding NHVs to the anti-attractant verbenone.

Verbenone-releasing flakes, which can be applied to individual trees using hydroseeders or to stands using aircraft or broadcast spreaders, have recently been shown to provide good protection when applied at the rate of 15 g/tree (individual tree tests, described in Gillette et al. 2006) or 370 g/hectare (aerial application tests, described in Gillette et al. 2009a).

Push-pull

Combining anti-attractants along with aggregation pheromones deployed in trap trees has been shown to provide increased protection of lodgepole pine trees from attack by MPB, with the caveats that the density of lodgepole pines should be greater than 400 stems/hectare, the mean diameter at breast height (dbh) should be equal to or less than 25 cm, the current attack rate should be less than 15%, and the tactic should be

combined with sanitation harvesting to remove infested trees (Borden et al. 2006, Lindgren and Borden 1993). One study, however, questioned the need for use of the anti-attractant (Vandygriff et al. 2000), and this hypothesis warrants further examination considering the costs of deploying the anti-attractants. Vandygriff et al. (2000) showed that baiting with the attractant was highly effective in removing sufficient numbers of beetles to reduce rate of attack in treated stands as compared to controls. They also demonstrated the utility of using the tree-baiting technique as a simultaneous sanitation effort, where mistletoe-infested stands were targeted for baiting and subsequent harvest, in order to remove both the bark beetles and mistletoe inoculum.

Douglas-fir Beetle (DFB)

The DFB often builds up high populations in wind- and avalanche-thrown Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees or in fire-damaged stands (Furniss and Carolin 1977). It can be desirable to treat such areas to prevent population build-up and infestation of healthy adjacent stands (Furniss et al. 1981, 1982). The development of semiochemical methods for control of DFB has been one of the signal success stories in the history of semiochemical research and development, perhaps because DFB is reputed to be such an olfactory specialist (Campbell and Borden 2006), i.e., it relies more on olfactory cues than do some bark beetle species, and thus be more readily manipulated with semiochemicals.

Monitoring and trapping (Pull)

Seudenol (3-methylcyclohex-2-en-1-ol) or MCOL (1-methylcyclohex-2-en-1-ol), with or without frontalin and ethanol, provides excellent efficacy for trapping DFB when used with multiple funnel traps, which are reported to work better than panel traps for this beetle species (Ross and Daterman 1998). Frequent lure replacement (every 4-6 weeks) may be necessary to maintain constant levels of release.

Push

The anti-aggregation pheromone methylcyclohexenone (3-methylcyclohex-2-en-1-one or MCH) is extremely effective with several different release devices. Bubblecap release devices deployed at the rate of about 75–100/hectare 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 (Ross and Daterman 1994, 1998; Ross et al. 1996, 2002). Individual high-value trees can be effectively protected with the application of two bubblecaps per tree. The primary limitations to the use of bubblecaps or verbenone pouches are the cost of labor for hand application and the inability to treat remote or steep terrain by hand. For these reasons, there have been several attempts to develop aerially applied products for treatment of large, remote, and/or steep areas. In the past, aerially applied granular controlled-release formulations were successful in area-wide tests (Furniss et al. 1981, 1982), and newer flake formulations (Hercon Environmental, Emigsville, PA) are showing similar promise for treatment of large areas using fixed wing aircraft or helicopters (Gillette et al. 2009b). Initial tests provided good results with 370 g of MCH/hectare, and preliminary results from ongoing tests suggest that lower application rates may provide equivalent

protection (Constance Mehmehl, USDA Forest Service, Wenatchee, WA, personal communication).

Push-pull

When beetle populations are very high, stands are extremely stressed, or windstorms, avalanches, or fire have resulted in many dead or damaged trees for beetle population build-up, it is probably advisable to combine the repellent technique with a trap-out technique (Ross et al. 1994, Blackford, 2007). In this scenario, the healthy stands are treated with MCH-releasing bubblecaps or flakes, while the perimeter, especially near fallen or damaged trees, is treated with 12-funnel traps baited with the three-component lure [Seudenol (or MCOL), frontalinal, and ethanol]. Care must be taken, however, to place baited traps far enough from healthy trees to avoid spill-over attack from beetles attracted to the baited traps.

Spruce Beetle (SB)

The SB normally attacks only weakened or windthrown spruce trees. Occasionally, however, large outbreaks develop in which healthy trees of all ages and diameters are attacked and killed (Furniss and Carolin 1977). The principal hosts are *Picea engelmannii* Parry, *P. glauca* (Moench) Voss, and *P. sitchensis* (Bong.) Carr.

Monitoring and trapping (Pull)

The SB is effectively attracted by either a two-component (frontalinal + α -pinene) or three-component (frontalinal + α -pinene + MCOL) lure, with substantial increases obtained with the addition of MCOL (Ross et al. 2005). Werner et al. (1988) used baited trap trees that were treated with a silvicide and removed from the forest to reduce populations of SB and achieve a measure of damage control for experimental purposes. However, available silvicides are not registered in the United States for this use.

Push

MCH and green leaf volatiles have been tested with some success for interruption of host location by SB (Poland et al. 1998, Werner et al. 1988), but the use of semiochemicals in a “push” strategy has only recently been shown to be successful for tree protection, probably because of the difficulty in achieving sufficient and/or sustained release in the cooler high elevation and sub-boreal regions where spruce beetle occurs (Borden et al. 1996, Holsten et al. 2000, Ross et al. 2004). Recently a type of puffer known as the Med-E-Cell, which is an active, battery-operated, timed-release device, was shown to provide significant protection for Lutz and Sitka spruce in Alaska (Holsten et al. 2003). However, other studies in Utah using MCH in the same releaser were not effective because the devices leaked and were not capable of retaining enough MCH to ensure efficacy throughout the beetle's flight period. Further studies and product development are therefore required to achieve consistent repellency of SB with this technology.

Western Pine Beetle (WPB)

The aggregation pheromone blend for WPB has been known for nearly four decades (Bedard et al. 1969, Browne et al. 1979, Silverstein 1968, Wood 1972, Wood et al. 1970) and an early trap-out study showed significant success in reducing beetle populations in ponderosa pine (*Pinus ponderosa* Laws.) stands (Bedard and Wood 1981, DeMars et al. 1980). Efforts to develop a fully operational methodology for semiochemical control of WPB has been somewhat stalled, however, probably for lack of a sufficiently effective anti-attractant semiochemical blend to deploy as a repellent strategy. Although verbenone showed some early promise as an anti-attractant for WPB (Bedard et al. 1980, Tilden et al. 1985), when used alone for tree protection its efficacy has been equivocal (Bedard and Wood 1981, Gillette et al. 2009a, 2009b). More recently, Erbilgin et al. (2007b, 2008) and Fettig et al. (2005, 2008a, 2008b) have demonstrated efficacy of adjuvants to verbenone and other active ingredients to enhance efficacy of a “push” or “push-pull” technique for WPB. The adjuvants (NHVs), which are largely those that have shown efficacy for MPB, are still being tested for area-wide use but have shown substantial efficacy in individual tree tests (Fettig et al. 2008a, 2008b).

Monitoring and trapping (Pull)

The three component blend of *exo-brevicomin*, *frontalin*, and *myrcene* is an extremely effective lure used in multiple funnel or panel traps for monitoring WPB populations (Bedard et al. 1980, Wood 1972). While a large trap-out study using this pheromone blend suggested that the technique may have promise for control of WPB, further wide-scale testing has not been conducted. The recent advances made in finding effective anti-aggregation semiochemicals (Erbilgin et al. 2008, Fettig et al. 2008a, 2008b), however, may reinvigorate this line of investigation as part of a push-pull strategy.

Push

An operational anti-aggregation method for the WPB is not presently available except for single-tree treatments (Fettig et al. 2008a), but research is active in this area and includes developmental testing of alternative active ingredients and tests of acetophenone and ipsdienol in broadcast dispenser applications for stand-level treatments (Gillette et al. 2009a, 2009b). Active ingredients such as those identified by Fettig et al. (2008b) warrant testing for area-wide stand protection as well as individual tree protection.

Red Turpentine Beetle (RTB)

RTB is normally considered a secondary pest of all pine species (Furniss and Carolin 1977), but recent outbreaks have been reported where RTB acts as a primary tree killer (Rappaport et al. 2001). The introduction of RTB into China has raised concerns about its spread across the entire Holarctic region from Asia into Europe and North Africa, since it appears to attack all species within the genus *Pinus* L., and there is a corridor of pines westward from Asia to Europe (Erbilgin et al. 2007a). In Asia, consequently, there has been a concerted effort to control RTB populations and minimize the spread of this

invasive species (Yan et al. 2005). In North America there has been less emphasis on control of RTB than in China, but drought stress is known to exacerbate RTB damage (Smith 1961), leading to concerns that warming climates will result in increased damage and a need for control measures.

Monitoring and trapping (Pull)

The standard commercial lure for RTB has been the three-component blend of α - and β -pinene, and Δ^3 -carene in a 1:1:1 ratio (Contech International, formerly Pherotech International) (Hobson et al. 1993). Recently, however, it was shown that Δ^3 -carene is the most attractive of these monoterpenes over the range of RTB in both North America and Asia (Erbilgin et al. 2007a), and Δ^3 -carene alone is a more effective lure for RTB than the blend in most cases. Although trap-out programs have not been conducted in North America, a regional trap-out program conducted in China, where RTB was accidentally introduced in the mid-1980s, was credited in part with a large reduction in RTB populations (J.H. Sun, Chinese Academy of Sciences, personal communication). RTB is widely polyphagous, so trapping programs are underway at ports in many pine-growing regions where accidental introduction of RTB is a concern.

Push

Verbenone pouches (along with NHVs) (Fettig et al. 2005, 2008a, 2008b) and verbenone flakes (Gillette et al. 2006) have been shown to provide significant protection of individual pines from attack by RTB. The application of verbenone-releasing flakes at the rate of 3.57 oz (15 g) of flakes/tree reduced attack rate by RTB on individual trees to nearly zero compared to control trees (Gillette et al. 2006), so this method gives very good individual tree protection. The application of verbenone-releasing flakes may be warranted in campgrounds, ski resorts, and administrative sites to protect individual trees from attack by red turpentine beetle.

Conclusions

Research and development of semiochemicals for bark beetle control has yielded many products and strategies that have recently come to fruition and are now being used to protect high-value stands on public and private lands. Recent developments with products for aerial application have provided tools that are appropriate over larger areas and sites that are inaccessible for hand-applied release devices. This is an active area of research, and new products—both active ingredients and new release devices—are constantly emerging for reducing bark beetle-caused tree mortality. It is therefore important to stay current with new developments and to contact extension entomologists and pheromone company representatives for the latest available information, as the field is rapidly and constantly changing. We wish to emphasize, however, that the use of semiochemicals to protect forest stands from bark beetle attack is really only a short-term solution to a long-term problem. While semiochemicals can provide significant protection over the short term, long-term vegetation management strategies are required to reduce susceptibility to bark beetle damage (Negrón et al. 2008). The need for semiochemical strategies can be significantly diminished by manipulating age class structure, encouraging species diversity and maintaining lower

tree densities. In the face of possible climate shifts, however, there may well be increasing need for semiochemicals to protect high-value areas until vegetation management can be implemented to reduce bark beetle risk. These methods may furthermore be helpful in protecting stands or individual trees during periods of temporary vulnerability such as the periods following wildfire, avalanches, and windstorms. They can also be used as part of an intensive management program that incorporates baited sacrificial trees to temporarily reduce bark beetle risk in climate-stressed stands.

Acknowledgments

We thank John Lundquist (USDA Forest Service, Anchorage, AK) for organizing the symposium where this report was first presented, and Jane Hayes (USDA Forest Service, La Grande, OR) and John Lundquist for preparing this proceedings report. We also thank C.J. Fettig (USDA Forest Service, Davis, CA), K. Gibson (USDA Forest Service, Missoula, MT), R. Kelsey (USDA Forest Service, Corvallis, OR), J. Lundquist, and S. Seybold (USDA Forest Service, Davis, CA), for constructive reviews of the manuscript.

Note: Mention of a product does not constitute recommendation for its use by the USDA Forest Service or the authors.

Literature Cited

- Amman, G.D.; Logan, J.A. 1998.** Silvicultural control of mountain pine beetle: prescriptions and the influence of microclimate. *American Entomologist*. 44: 166–177.
- Amman, G.D.; Thier, R.W.; Weatherby, J.C.; Rasmussen, L.A.; Munson, A.S. 1991.** Optimum dosage of verbenone to reduce infestation of mountain pine beetle [*Dendroctonus ponderosae*] in lodgepole pine [*Pinus contorta* var. *latifolia*] stands of central Idaho. Res. Pap. INT-RP-446. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 6 p.
- Andrews, S.L.; Perkins, J.P.; Thraillkill, J.A.; Poage, N.J.; Tappeiner, J.C., II. 2005.** Silvicultural approaches to develop northern spotted owl nesting sites, central Coast ranges, Oregon. *Western Journal of Applied Forestry*. 20: 13–27.
- Bedard, W.D.; Tilden, P.E.; Wood, D.L.; Silverstein, R.M.; Brownlee, R.G.; Rodin, J.O. 1969.** Western pine beetle: response to its sex pheromone and a synergistic host terpene, myrcene. *Science*. 164: 1284–1285.
- Bedard, W.D.; Silverstein, R.M.; Wood, D.L. 1970.** Bark beetle pheromones. *Science*. 167(3925): 1638–1639.

- Bedard, W.D.; Tilden, P.E.; Lindahl, K.Q.J.; Wood, D.L.; Rauch, P.A. 1980.** Effects of verbenone and *trans*-verbenol on the response of *Dendroctonus brevicomis* to natural and synthetic attractant in the field. *Journal of Chemical Ecology*. 6: 997–1014.
- Bedard, W.D.; Wood, D. L. 1981.** Suppression of *Dendroctonus brevicomis* by using a mass-trapping tactic. In: Mitchell, E. R., ed. *Management of insect pests with semiochemicals*. New York: Plenum Press:103–114.
- Bentz, B.J.; Kegley, S.; Gibson, K.; Thier, R. 2005.** A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) attacks. *Journal of Economic Entomology*. 98: 1614–1621.
- Bentz, B.J.; Munson, A.S. 2000.** Spruce beetle population suppression in northern Utah. *Western Journal of Applied Forestry*. 15(3):122–128.
- Blackford, D.C. 2007.** Aspen Grove Trailhead Area, Pleasant Grove, Ranger District, Uinta National Forest. Functional Assistance Report. OFO-TR-07-02. Ogden, UT: US Department of Agriculture, Forest Service, Forest Health Protection. 7 p.
- Borden, J.H. 1997.** Disruption of semiochemical-mediated aggregation in bark beetles. In: Cardé, R.T.; Minks, A.K., eds. *Insect pheromone research: new directions*. New York: Chapman and Hall: 421–438.
- Borden, J.H.; Birmingham, A.L.; Burleigh, J.S. 2006.** Evaluation of the push-pull tactic against the mountain pine beetle using verbenone and non-host volatiles in combination with pheromone-baited trees. *Forestry Chronicles*. 82: 579–590.
- Borden, J.H.; Chong, L.J.; Earle, T.J.; Huber, D.P.W. 2003.** Protection of lodgepole pine from attack by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using high doses of verbenone in combination with nonhost bark volatiles. *Forestry Chronicles*. 79: 685–691.
- Borden, J.H.; Chong, L.J.; Lindgren, B.S.; Begin, E.J.; Ebata, T.M.; MacLauchlan, L.E.; Hodgkinson, R.S. 1993.** A simplified tree bait for the mountain pine beetle. *Canadian Journal of Forest Research*. 23(6): 1108–1113.
- Borden, J.H.; Gries, G.; Chong, L.J.; Werner, R.A.; Holsten, E.H.; Wieser, H.; Dixon, E.A.; Cerezke, H.F. 1996.** Regionally-specific bioactivity of two new pheromones for *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae). *Journal of Applied Entomology*. 120: 321–326.

- Borden, J.H.; Lacey, T.E. 1985.** Semiochemical-based manipulation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins: a component of lodgepole pine silviculture in the Merritt Timber Supply area of British Columbia. *Zeitschrift für Angewandte Entomologie*. 99(2): 139–145.
- Borden, J.H.; Pureswaran, D.S.; Poirier, L.M. 2004.** Evaluation of two repellent semiochemicals for disruption of attack by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia*. 101: 117–123.
- Borden, J.H.; Sparrow, G.R.; Gervan, N.L. 2007.** Operational success of verbenone against the mountain pine beetle in a rural community. *Arboriculture and Urban Forestry* 33(5): 318–324.
- Browne, L.E.; Wood, D.L.; Bedard, W.D.; Silverstein, R.M.; West, J.R. 1979.** Quantitative estimates of the western pine beetle attractive pheromone components, *exo-brevicomin*, *frontalin*, and *myrcene* in nature. *Journal of Chemical Ecology*. 5(3): 397–414.
- Campbell, S.A.; Borden, J.H. 2006.** Integration of visual and olfactory cues of hosts and nonhosts by three bark beetle species (Coleoptera: Scolytidae). *Ecological Entomology*. 31(5): 437–449.
- Carroll, A.L.; Taylor, S.W.; Régnière J.; Safranyik, L. 2003.** Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore; T.L.; Brooks, J.E.; Stone, J.E., eds. *Mountain pine beetle symposium, challenges and solutions*. October 30–31, Kelowna, BC. Victoria, BC: Natural Resources Canada, Information Report BC-X-399. Canadian Forest Service, Pacific Forestry Centre: 223–232.
- Clarke, S.R.; Salom, S.M.; Billings, R.F.; Berisford, C.W.; Upton, W.W.; McClellan, Q.C.; Dalusky, M.J. 1999.** A scentsible approach to controlling southern pine beetles: two new tactics using verbenone. *Journal of Forestry*. 97: 26–31.
- Conn, J.E.; Borden, J.H.; Scott, B.E.; Friskie, L.M.; Pierce, H.D. Jr.; Oehlschlager, A.C. 1983.** Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in British Columbia: field trapping studies. *Canadian Journal of Forest Research*. 13(2): 320–324.
- Cook, S.M.; Khan, Z.R.; Pickett, J.A. 2007.** The use of push-pull strategies in integrated pest management. *Annual Review of Entomology*. 52: 375–400.
- DeGomez, T.E.; Hayes, C.J.; Anhold, J.A.; McMillin J.D.; Clancy, K.M.; Bosu, P.P. 2006.** Evaluation of insecticides for protecting southwestern ponderosa pines from attack by engraver beetles (Coleoptera: Curculionidae: Scolytinae). *Journal of Economic Entomology*. 99: 393–400.

- DeMars, C.J.; Slaughter, G.W.; Bedard, W.D.; Norick, N.X.; Roettgering, B. 1980.** Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. *Journal of Chemical Ecology*. 6(5): 853–866.
- Ebata, T. 2004.** Current status of mountain pine beetle in British Columbia. Information Report BC-X-399. Victoria, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre: 52–56.
- Erbilgin, N.; Mori, S.R.; Sun, J.H.; Stein, J.D.; Owen, D.R.; Campos Bolaños, R.; Merrill, L.D.; Raffa, K.F.; Méndez Montiel, T.; Wood, D.L.; Gillette, N.E. 2007a.** Response to host volatiles by native and introduced populations of *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae) in North America and China. *Journal of Chemical Ecology*. 33: 131–146.
- Erbilgin, N.; Gillette, N.E.; Mori, S.R.; Stein, J.D.; Owen, D.R.; Wood, D.L. 2007b.** Acetophenone as an anti-attractant for the western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae). *Journal of Chemical Ecology*. 33: 817–823.
- Erbilgin, N.; Gillette, N.E.; Owen, D.R.; Mori, S.R.; Nelson, A.S.; Uzoh, F.; Wood, D.L. 2008.** Acetophenone superior to verbenone for reducing attraction of western pine beetle *Dendroctonus brevicomis* to its aggregation pheromone. *Agricultural and Forest Entomology*. 10(4): 433–441.
- Fettig, C.J.; McKelvey, S.R.; Huber, D.P.W. 2005.** Nonhost angiosperm volatiles and verbenone disrupt response of western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to attractant-baited traps. *Journal of Economic Entomology*. 98: 2041–2048.
- Fettig, C.J.; Allen, K.K.; Borys, R.R.; Christopherson, J.; Dabney, C.P.; Eager, T.J.; Gibson, K.E.; Hebertson, E.G.; Long, D.F.; Munson, A.S.; Shea, P.J.; Smith, S.L.; Haverty, M.I. 2006a.** Effectiveness of bifenthrin (Onyx) and carbaryl (Sevin SL) for protecting individual, high-value conifers from bark beetle attack (Coleoptera: Curculionidae: Scolytinae) in the Western United States. *Journal of Economic Entomology*. 99: 1691–1698.
- Fettig, C.J.; DeGomez, T.; Gibson, K.E.; Dabney, C.P.; Borys, R.R. 2006b.** Effectiveness of permethrin plus-C (MasterlineReg.) and carbaryl (Sevin SLReg.) for protecting individual, high-value pines (*Pinus*) from bark beetle attack. *Arboriculture and Urban Forestry*. 32: 247–252.
- Fettig, C.J.; McMillin, J.D.; Anhold, J.A.; Hamud, S.M.; Borys, R.R.; Dabney, C.P.; Seybold, S.J. 2006c.** The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *Forest Ecology and Management*. 230: 55–68.

- Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negron, J.F.; Nowak, J.T. 2007.** The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*. 238: 24–53.
- Fettig, C.J.; Dabney, C.P.; McKelvey, S.R.; Huber, D.P.W. 2008a.** Nonhost angiosperm volatiles and verbenone protect individual ponderosa pines from attack by western pine beetle and red turpentine beetle (Coleoptera: Curculionidae, Scolytinae). *Western Journal of Applied Forestry*. 23(1): 40–45.
- Fettig, C.J.; McKelvey, S.R.; Dabney, C.P.; Borys, R.R.; Huber, D.P.W. 2008b.** Response of *Dendroctonus brevicornis* to different release rates of nonhost angiosperm volatiles and verbenone in trapping and tree protection studies. *Journal of Applied Entomology*. doi:10.1111/j.1439-0418.2008.01317.x
- Furniss, M.M.; Clausen, R.W.; Markin, G.P.; McGregor, M.D.; Livingston, R.L. 1981.** Effectiveness of Douglas-fir beetle antiaggregative pheromone applied by helicopter. Gen.Tech. Rep. INT-GTR-10. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 7 p.
- Furniss, M.M.; Markin, G.P.; Hager, V.J. 1982.** Aerial application of Douglas-fir beetle antiaggregative pheromone: equipment and evaluation. Gen. Tech. Rep. INT-137. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 9 p.
- Furniss, R.L.; Carolin, V.M. 1977.** Western Forest Insects. Miscellaneous Publication 273. Washington DC: US Department of Agriculture, Forest Service 654 p.
- Gibson, K.; Kegley, S. 2004.** Testing the efficacy of verbenone in reducing mountain pine beetle attacks in second-growth ponderosa pine. Forest Health Protection Report, Report 04-7. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region: 8 p. http://www.fs.fed.us/r1-r4/spf/fhp/publications/bystate/R1Pub04-7_verbenone_mpb.pdf
- Gillette, N.E.; Erbilgin, N.; Webster, J.N.; Pederson, L.; Mori, S.R.; Stein, J.D.; Owen, D.R.; Bischel, K.M.; Wood, D.L. 2009a.** Aerially applied verbenone-releasing flakes protect *Pinus contorta* stands from attack by *Dendroctonus ponderosae* in California and Idaho. *Forest Ecology and Management*. 257: 1405–1412
- Gillette, N.E.; Mehmehl, C.J.; Erbilgin, N.; Mori, S.R.; Webster, J.N.; Wood, D.L.; Stein, J.D. 2009b.** Aerially applied methylcyclohexenone-releasing flakes protect *Pseudotsuga menziesii* stands from attack by *Dendroctonus pseudotsugae*. *Forest Ecology and Management*. 257(4): 1231–1236

- Gillette, N.E.; Stein, J.D.; Owen, D.R.; Webster, J.N.; Fiddler, G.O.; Mori, S.R.; Wood, D.L. 2006.** Verbenone-releasing flakes protect individual *Pinus contorta* trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). *Agricultural and Forest Entomology*. 8: 243–251.
- Graves, A.D.; Holsten, E.H.; Ascerno, M.E.; Zogas, K.P.; Hard, J.S.; Huber, D.P.W.; Blanchette, R.A.; Seybold, S.J. 2008.** Protection of spruce from colonization by the bark beetle, *Ips perturbatus*, in Alaska. *Forest Ecology and Management*. 256(11): 1825–1839.
- Gray, D.R.; Borden, J.H. 1989.** Containment and concentration of mountain pine beetle (Coleoptera: Scolytidae) infestations with semiochemicals: validation by sampling of baited and surrounding zones. *Journal of Economic Entomology*. 82: 1399–1495.
- Haverty, M.I.; Shea, P.J.; Hoffman, J.T.; Wenz, J.M.; Gibson, K.E. 1998.** Effectiveness of esfenvalerate, cyfluthrin, and carbaryl in protecting individual lodgepole pines and ponderosa pines from attack by *Dendroctonus* spp. Res. Pap. PSW-RP-237. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 12 p.
- Hicke, J.A.; Jenkins, J.C. 2008.** Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. *Forest Ecology and Management*. 255: 1536–1547.
- Hicke, J.A.; Logan, J.A.; Powell, J.; Ojima, D.S. 2006.** Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research*. 111: [Not paged] G02019, doi:10.29/2005JG000101.
- Hobson, K.R.; Wood, D.L.; Cool, L.G.; White, P.R.; Ohtsuka, T.; Kubo, I.; Zavarin, E. 1993.** Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. *Journal of Chemical Ecology*. 19: 1837–1847.
- Holsten, E.H.; Shea, P.J.; Borys, R.R. 2003.** MCH released in a novel pheromone dispenser prevents spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Scolytidae) attacks in south-central Alaska. *Journal of Economic Entomology*. 96: 31–34.
- Holsten, E.H.; Webb, W.; Shea, P.J.; Werner, W.A. 2000.** Release rates of methylcyclohexenone and verbenone from bubblecap and bead releasers under field conditions suitable for the management of bark beetles in California, Oregon, and Alaska. Res. Pap. PNW-RP-544. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 28 p.

- Huber, D.P.W.; Borden, J.H. 2001.** Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. *Entomologia Experimentalis et Applicata*. 99: 131–141.
- Kegley, S.; Gibson, K. 2004.** Protecting whitebark pine trees from mountain pine beetle attack using verbenone. Forest Health Protection Report 04-8. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region. 4 p.
- Kegley, S.; Gibson, K.; Schwandt, J.; Marsden, M. 2003.** A test of verbenone to protect individual whitebark pine from mountain pine beetle attack. Forest Health Protection Report. Report 03-9. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region. 6 p.
- Kogan, M. 1998.** Integrated pest management: historical perspectives and contemporary developments. *Annual Review of Entomology*. 43: 243–270.
- Krist, F.J.; Jr., Sapio, F.J.; Tkacz, B.M. 2007.** Mapping risk from forest insects and diseases. FHTET-2007-6. Morgantown, WV: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Forest Health Technology Enterprise Team. 125 p.
- Kurz, W.A.; Dymond, C.C.; Stinson, G.; Rampley, G.J.; Neilson, E.T.; Carroll, A.L.; Ebata, T.; Safranyik, L. 2008a.** Mountain pine beetle and forest carbon feedback to climate change. *Nature*. 452: 987–990.
- Kurz, W.A.; Stinson, G.; Rampley, G.J.; Dymond, C.C.; Neilson, E.T. 2008b.** Risk of natural disturbance makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences*. 105(5): 1551–1555.
- Lindgren, B.S.; Borden, J.H. 1993.** Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to their antiaggregation and aggregation pheromones. *Canadian Journal of Forest Research*. 23(2): 286–290.
- Lister, C.K.; Schmid, J.M.; Mata, S.A.; Haneman, D.; O'Neil, C.; Pasek, J.; Sower, L. 1990.** Verbenone bubble caps ineffective as a preventive strategy against mountain pine beetle attacks in ponderosa pine. Res. Note RM-501. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 3 p.
- Logan, J.A.; Powell, J.A. 2001.** Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*. 47: 160–173.

- Naumann, K.; Rankin, L.J. 1999.** Pre-attack systemic applications of a neem-based insecticide for control of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Journal of the Entomological Society of British Columbia. 96: 13–19.
- Negrón, J.F.; Bentz, B.J.; Fettig, C.J.; Gillette, N.E.; Hansen, E.M.; Hayes, J.L.; Kelsey, R.G.; Lundquist, J.E.; Lynch, A.M.; Progar, R.A.; Seybold, S.J. 2008.** US Forest Service bark beetle research in the western United States: Looking toward the future. Journal of Forestry. 106: 325–331.
- Negrón, J.F.; Anhold, J.A.; Munson, A.S. 2001.** Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). Environmental Entomology. 30: 215–224.
- Nordlund, D.A.; Lewis, W.J. 1981.** Semiochemicals: A review of the terminology. In: Nordlund, D.A.; Jones, R.L.; Lewis, W.J., eds. Semiochemicals: their role in pest control. New York: John Wiley & Sons: 13–28.
- Ono, H. 2004.** The mountain pine beetle: scope of the problem and key issues in Alberta. Information Report BC-X-399. Victoria, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre: 62-66.
- Poland, T.M.; Borden, J.H.; Stock, A.J.; Chong, L.J. 1998.** Green leaf volatiles disrupt responses by the spruce beetle, *Dendroctonus rufipennis*, and the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae) to attractant-baited traps. Journal of the Entomological Society of British Columbia. 95: 17-24.
- Progar, R.A. 2003.** Verbenone reduces mountain pine beetle attack in lodgepole pine. Western Journal of Applied Forestry. 18: 229–232.
- Progar, R.A. 2005.** Five-year operational trial of verbenone to deter mountain pine beetle (*Dendroctonus ponderosae*; Coleoptera: Scolytidae) attack of lodgepole pine (*Pinus contorta*). Environmental Entomology. 34: 1402–1407.
- Pureswaran D.S.; Borden, J.H. 2005.** Primary attraction and kairomonal host discrimination in three species of *Dendroctonus* (Coleoptera: Scolytidae). Agricultural and Forest Entomology. 7(3): 219-230.
- Rappaport, N.G.; Owen, D.R.; Stein, J.D. 2001.** Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. Environmental Entomology. 30: 837–841.

- Ross, D.W.; Daterman, G.E. 1994.** Reduction of Douglas-fir beetle infestation of high-risk stands by antiaggregation and aggregation pheromones. *Canadian Journal of Forest Research*. 24: 2184–2190.
- Ross, D.W.; Daterman, G.E. 1998.** Pheromone-baited traps for *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae): influence of selected release rates and trap designs. *Journal of Economic Entomology*. 91: 500–506.
- Ross, D.W.; Daterman, G.E.; Munson, A.S. 1996.** Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology*. 89: 1204–1207.
- Ross, D.W.; Daterman, G.E.; Munson, A.S. 2002.** Elution rate and spacing of antiaggregation pheromone dispensers for protecting live trees from *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology*. 95: 778–781.
- Ross, D.W.; Daterman, G.E.; Munson, A.S. 2004.** Evaluation of the antiaggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), to protect live spruce from spruce beetle (Coleoptera: Scolytidae) infestation in southern Utah. *Journal of the Entomological Society of British Columbia*. 101: 145–146.
- Ross, D.W.; Daterman, G.E.; Munson, A.S. 2005.** Spruce beetle (Coleoptera: Scolytidae) response to traps baited with selected semiochemicals in Utah. *Western North American Naturalist*. 65: 123–126.
- Ross, D.W.; Hostetler, B.B.; Johansen, J. 2006.** Douglas-fir beetle response to artificial creation of down wood in the Oregon Coast Range. *Western Journal of Applied Forestry*. 21: 117–122.
- Salom, S.M.; Grosman, D.M.; McClellan, Q.C.; Payne, T.L. 1995.** Effect of an inhibitor-based suppression tactic on abundance and distribution of the southern pine beetle (Coleoptera: Scolytidae) and its natural enemies. *Journal of Economic Entomology*. 88: 1703–1716.
- Seybold, S.J.; Downing, M. 2009.** What risk do invasive bark beetles and woodborers pose to forests of the western U.S? A case study of the Mediterranean pine engraver, *Orthotomicus erosus*. In: Hayes, J.L.; Lundquist, J.E., comps. *Western Bark Beetle Research Group—a unique collaboration with Forest Health Protection symposium, Society of American Foresters Conference*, 23–28 October 2007, Portland, OR. Gen. Tech. Rep. PNW-GTR-784, Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 111–134.

- Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. 2006.** Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochemistry Reviews*. 5: 143–178.
- Sharov, A.A.; Leonard, D.; Liebhold, A.M.; Roberts, E.A.; Dickerson, W. 2002.** “Slow the spread:” a national program to contain the gypsy moth. *Journal of Forestry*. 100: 30–35.
- Shore, T.L.; Safranyik, L.; Lemieux, J.P. 2000.** Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. *Canadian Journal of Forest Research*. 30: 44–49.
- Silverstein, R.M.; Brownlee, R.G.; Bellas, T.E.; Wood, D.L.; Browne, L.E. 1968.** Brevicomins: principal sex attractant in the frass of the female western pine beetle. *Science*. 158(3817): 889–891.
- Silverstein, R.M.; Rodin, J.O.; Wood, D.L. 1966.** Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science*. 154: 509–510.
- Skillen, E.L.; Berisford, C.W.; Camann, M.A.; Reardon, R.C. 1997.** Semiochemicals of forest and shade tree insects in North America, and management implications. FHTET-96-15. Morgantown, WV: U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team. 189 p.
- Smith, R.F. 1962.** Principles of integrated pest control. Proceedings of the North Central Branch, Entomological Society of America. Lanham, MD, 17, 7 p.
- Smith, R.H. 1961.** Red turpentine beetle. Forest Pest Leaflet 55. Washington, DC: U.S. Department of Agriculture, Forest Service. 8 p.
- Smith, R.H. 1986.** Trapping western pine beetles with baited toxic trees. Res. Note. PSW-RN-382. Berkeley, CA: US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 9 p.
- Tilden, P.E.; Bedard, W.D.; Wood, D.L.; Stubbs, H.A. 1981.** Interruption of response of *Dendroctonus brevicomis* to its attractive pheromone by components of the pheromone. *Journal of Chemical Ecology*. 7: 183–196.
- Vandygriff, J.C.; Rasmussen, L.A.; Rineholt, J.F. 2000.** A novel approach to managing fuelwood harvest using bark beetle pheromones. *Western Journal of Applied Forestry*. 15(4): 183–188.
- Werner, R.A.; Hard, J.; Holsten, E.H. 1988.** The development of management strategies to reduce the impact of the spruce beetle in south-central Alaska. *Northwest Environmental Journal*. 4(2): 319–358.

- Westfall, J. 2007.** 2006 Summary of forest health conditions in British Columbia. Pest Management Report Number 15, Victoria, BC: British Columbia Ministry of Forests and Range. 73 p.
- Whitehead, R.J.; Russo, G.L. 2005.** 'Beetle-proofed' lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle. Information Report BC-X-402. Victoria, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. 17 p.
- Wilent, S. 2005.** Mountain pine beetles threaten Canadian, US forests. The Forestry Source. http://www.safnet.org/archive/0505_beetle.cfm (28 February 2006).
- Wood, D.L. 1972.** Selection and colonization of ponderosa pine by bark beetles. In: van Emden, H.F., ed. Insect/plant relationships. Oxford: Blackwell Science Publications: 101–117.
- Wood, D.L.; Browne, L.E.; Ewing, B.; Lindahl, K.; Bedard, W.D.; Tilden, P.E.; Mori, K.; Pitman, G.B.; Hughes, P.R. 1976.** Western pine beetle: specificity among enantiomers of male and female components of an attractant pheromone. Science. 192: 896–898.
- Wood, D.L.; Stark, R.W.; Waters, W. W.; Bedard, W.D.; Cobb, F.W., Jr. 1985.** Treatment tactics and strategies. In: Waters, W.W; Stark, R.W.; Wood, D.L., eds. Integrated pest management in pine-bark beetle ecosystems. New York, New York: John Wiley and Sons:121–140.
- Yan, Z.L.; Sun, J.H.; Owen, D.R.; Zhang, Z.N. 2005.** The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodiversity and Conservation. 14(7): 1735–1760.