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Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a primary agent of forest disturbance in western North America. Episodic outbreaks occur at the convergence of favorable forest age and size class structure and climate patterns. Recent outbreaks have exceeded the historic range of variability of *D. ponderosae*-caused tree mortality affecting ecosystem goods and services at broad spatial scales. At the same time, significant advances have occurred in our understanding of the chemical ecology of *D. ponderosae* and in the development of semiochemical-based tools and tactics to protect trees from mortality attributed to *D. ponderosae*. We synthesize related information relevant to the ecology and management of *D. ponderosae* and identify factors limiting the effectiveness and utility of semiochemical treatments, areas of continuing research and fields for which further work is needed.

Keywords: attractant, *Dendroctonus ponderosae*, *exo*-brevicomin, inhibitor, kairomone, pheromone, *cis*-verbenol, *trans*-verbenol, verbenone

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are commonly recognized as important tree mortality agents in conifer forests of the western United States (Furniss and Carolin 1977). Recent outbreaks of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, have been especially severe, long-lasting, and well documented (Bentz et al. 2009). This species is considered a major cause of disturbance in the forests of western Canada and throughout much of the western United States. *D. ponderosae* colonizes several pine species, most notably lodgepole pine, *Pinus contorta* Dougl. ex Loud.; ponderosa pine, *Pinus ponderosa* Dougl. ex Laws.; sugar pine, *Pinus lambertiana* Dougl.; limber pine, *Pinus flexilis* E. James; western white pine, *Pinus monticola* Dougl. ex D. Don; and whitebark pine, *Pinus albicaulis* Engelm. (Gibson et al. 2009). Although often considered univoltine, the life cycle of *D. ponderosae* varies throughout its range. More than one generation may occur annually in *P. ponderosa* forests of the southwestern United States, whereas it may take several years to complete a generation in subalpine forests (Amman 1973, Furniss and Carolin 1977).

The extent of tree mortality resulting from *D. ponderosae* outbreaks may be limited to small spatial scales (e.g., individual trees or small groups of trees at endemic population levels) or may affect entire landscapes. Episodic outbreaks are common, particularly in mature forests of *P. contorta* where tree mortality often occurs contiguously across extensive areas. Recent outbreaks have exceeded the range of historic variability in magnitude and extent and have oc-

curred in areas where *D. ponderosae* outbreaks were once rare (e.g., *P. albicaulis* forests) (Bentz et al. 2009, 2010). Extensive levels of tree mortality associated with *D. ponderosae* outbreaks may result in replacement of *D. ponderosae* hosts by other tree species and plant associations, with subsequent impacts on timber and fiber production, fuels and fire behavior, water quality and quantity, fish and wildlife populations, esthetics, recreation, grazing capacity, real estate values, biodiversity, carbon storage, threatened and endangered species, and cultural resources, among others.

Tactics to manage *D. ponderosae* include silvicultural treatments that reduce stand density (thinning) and presumably host susceptibility (Fettig et al. 2014), sanitation harvests that remove infested trees (McMullen et al. 1986), applications of insecticides to protect individual trees (Fettig et al. 2013), and applications of semiochemicals (i.e., chemicals produced by one organism that elicit a behavioral response in another organism), including aggregation pheromones deployed in trap out, trap tree, or concentration approaches (e.g., Gray and Borden 1989, Gibson and Weber 2004, Borden et al. 2006) and inhibitors used to disrupt colonization of individual trees (e.g., Borden et al. 2004, Kegley and Gibson 2004, Gillette et al. 2006, Kegley and Gibson 2009) or typically small-scale (e.g., <4 ha) stands (e.g., Wilson et al. 1996, Amman et al. 1989, 1991, Bentz et al. 1989, 2005, Lindgren et al. 1989, Lister et al. 1990, Gibson et al. 1991, Shea et al. 1992, Shore et al. 1992, Lindgren and Borden 1993, Huber and Borden 2001, Borden et al. 2003, 2004, 2006, Progar 2003, 2005, Kegley and Gibson 2004, Negrón et al. 2006,

Gillette et al. 2009a, 2009b, 2012a, Fettig et al. 2012a, Progar et al. 2013). In recent years, significant advances have occurred in our understanding of bark beetle chemical ecology and semiochemical synthesis and in the development of semiochemical-based tools and tactics to protect trees from bark beetle infestation (Gillette and Munson 2009). Our primary objective is to synthesize information relevant to the ecology and management of *D. ponderosae*, which remains a top research priority of forest health specialists in the western United States (Negrón et al. 2008).

Chemical Ecology

The primary pheromones and other semiochemicals associated with *D. ponderosae* have been known for decades (Borden 1982, Wood 1982, Lindgren and Borden 1989). *D. ponderosae* uses a complex system of semiochemical communication in host location, selection and colonization, and mating behaviors (Wood 1982, Borden et al. 1987) (Table 1). In short, *D. ponderosae* infests the lower tree bole in a behavioral sequence facilitated by aggregation pheromones (Pitman et al. 1968, Pitman and Vité 1969, Ryker and Libbey 1982) and host kairomones (Pitman et al. 1968, Renwick and Vité 1970, Borden et al. 1987, Miller and Lafontaine 1991). When searching for new hosts, adult bark beetles maintain very limited energy reserves (Atkins 1966) and are highly susceptible to predation, starvation, and adverse abiotic conditions (McMullen and Atkins 1962). Therefore, beetles must efficiently detect and locate the correct habitat, correct tree species, and the most susceptible trees within those species (Byers 1995, Borden 1997, Schlyter and Birgersson 1999). Research has demonstrated that many bark beetles use host volatiles (kairomones) to locate suitable habitats and hosts. Host finding is followed by host acceptance or selection, which is indicated by gallery initiation. Gallery initiation is followed by release of aggregation pheromones to concentrate conspecifics to the target tree attracting high numbers of beetles that "mass attack" the tree (Borden 1985, Byers 1995, Zhang and Schlyter 2004). Recruiting a critical minimum number of beetles to "mass attack" an individual tree (Pitman and Vité 1969, Wood 1982) enables *D. ponderosae* to overcome tree defenses (Franceschi et al. 2005).

In more detail, aggregation of females (i.e., the sex that initiates host colonization) occurs in response to semiochemicals released by the first pioneering females in contact with new host material (Vité and Gara 1962). *trans*-Verbenol and *cis*-verbenol are the primary volatile compounds produced in the insect's hindgut (Vité and Pitman 1967, Miller and Lafontaine 1991) and are secreted through the alimentary system (Vité and Pitman 1967). *cis*-Verbenol, produced by female *D. ponderosae,* has been shown to increase the attraction of conspecific females to *exo*-brevicomin, but its effect is less than that of *trans*-verbenol (Miller and Lafontaine 1991). Attraction is enhanced by the presence of host volatiles α-pinene (Pitman et al. 1968), myrcene, and terpinolene (Borden et al. 1987, 2008, Seybold 2002). *exo*-Brevicomin is produced by both sexes and appears to be attractive at low concentrations and inhibitory at higher concentrations (Rudinsky et al. 1974, Pureswaran et al. 2000). Males attracted to the target tree release *exo*-brevicomin, which is a primary attractant of females, further augmenting mass attack (Amman and Lindgren 1995). As the abundance of colonizing male *D. ponderosae* increases, the attractiveness of the tree (as defined by the release of pheromones) is reduced by increasing levels of male-secreted *exo*-brevicomin and frontalin (Ryker and Libbey 1982, Ryker and Rudinsky 1982, Raffa and Berryman 1983, Chatelain and Schenk 1984, Borden et al. 1987, 1990). At the same time,

concentrations of the aggregation pheromones *trans*- and *cis*-verbenol and host monoterpenes decline (Renwick and Vité 1970) (Table 1).

During the latter stages of tree colonization, increasing amounts of verbenone are produced by autoxidation of α-pinene to *trans*- and *cis*-verbenol and then to verbenone (Hunt et al. 1989), primarily by intestinal and gallery-inhabiting microbes within both beetle sexes (Hunt and Borden 1989, 1990) (*see* Inhibitors) (Table 1). The secretion of 2-phenylethanol by males (Pureswaran et al. 2000) and the release of 1-octen-3-ol by females (Pureswaran and Borden 2004) may further reduce attraction (Table 1). Increasing release of verbenone inhibits additional *D. ponderosae* from infesting the target tree, thus limiting the number of infesting beetles to a density that increases the likelihood of brood survival (Amman and Lindgren 1995). Newly arriving beetles then reorient to adjacent trees where the cycle of colonization is repeated (Geiszler and Gara 1978).

Host Finding and Selection

The first step in host finding is location of habitats containing host trees (Figure 1). The dominant theory of host selection proposes that pioneering females use a combination of random landings and visual orientations followed by direct assessment based on olfactory and/or gustatory cues (Hynum and Berryman 1980, Raffa and Berryman 1982, 1983, Wood 1982, Moeck and Simmons 1991, Pureswaran and Borden 2003). There is also some evidence that *D. ponderosae* orients to *P. contorta* trees suffering from injury or disease (Gara et al. 1984), particularly at endemic population levels. Similarly, Eckberg et al. (1994) proposed that factors associated with the physiological condition of *P. ponderosa* influence host selection, supporting other findings of a relationship between low tree vigor and *D. ponderosae* infestation in this tree species (Larsson et al. 1983). Low tree vigor has been linked to decreased monoterpene production upon fungal inoculation by *D. ponderosae* symbionts, a condition that may reduce the ability of the host tree to defend against beetle infestation (Raffa and Berryman 1982).

Shepherd (1966) and Rasmussen (1972) found evidence that *D. ponderosae* selects trees with large silhouettes, implying that visual cues are used during the initial phase of host selection. Burnell (1977) suggested that *D. ponderosae* randomly selects trees to infest, but that large trees are infested more frequently simply because they represent targets with a larger surface area. Mitchell and Preisler (1991) found that rates of infestation were positively correlated with tree diameter. Small trees were not infested unless they were near infested large trees, and large trees (>23 cm dbh, diameter at 1.37 m in height) were infested with greater frequency than could be accounted for by a random attack model. In addition, among trees of similar diameter, *D. ponderosae* appears to select trees with the thickest phloem, suggesting that chemical cues may be used in host selection because terpenes occur at higher levels in thicker phloem (Cole et al. 1981) (Table 1).

Several investigators observed that the pattern of tree selection changes over the course of a *D. ponderosae* outbreak in *P. contorta* forests with large trees infested initially and progressively smaller trees colonized as the reservoir of large trees declines over time (Klein et al. 1978, Cole and Amman 1980, Amman and Cole 1983, but see Geiszler et al. 1980a). Large trees have thick phloem (Berryman 1982) that affords the offspring of *D. ponderosae* a higher reproductive potential and a higher probability of survival (Amman 1969, 1975, Klein et al. 1978), factors shown to influence overall reproductive success. For example, Graf et al. (2012) found that the

Table 1. Primary semiochemicals associated with *Dendroctonus ponderosae* and their applications in management.

Class	Emmiters	Receivers	Function	Potential utility
Attractants				
Host volatiles				
α–Pinene, Myrcene, Terpinolene	*Pinus* spp.	Male and female *D. ponderosae*	Enhance attraction to suitable hosts	Increase the attraction of aggregation pheromone components to *D. ponderosae* in traps and on trees; useful in detection surveys, for monitoring, and for reducing levels of tree mortality (e.g., during push-pull tactics)
Aggregation pheromones				
trans-Verbenol, *cis*-Verbenol	Female *D. ponderosae*	Male and female *D. ponderosae*	Attracts *D. ponderosae* during initial colonization	Oxidized to produce verbenone; useful in detection surveys, for monitoring, and for reducing levels of tree mortality
exo-Brevicomin	Male and female *D. ponderosae*	Female *D. ponderosae*	Attracts female *D. ponderosae* at low concentrations; repels at high rates	Useful in detection surveys, for monitoring, and for reducing levels of tree mortality
Frontalin	Male *D. ponderosae*	Female *D. ponderosae*	Attracts female *D. ponderosae* at low concentrations	Limited, as quaternary blend of *trans*-verbenol, *exo*-brevicomin, myrcene, and terpinolene are shown to be most effective for detection surveys and other trapping applications
Inhibitors				
Nonhost volatiles				
Green leaf volatiles, Angiosperm bark volatiles	Angiosperm and monocotyledonous plants	Male and female *D. ponderosae*	Provide cues that indicate host tree is unsuitable for colonization	Useful for protecting individual trees and stands from infestations, especially when combined with verbenone
Antiaggregation pheromones				
exo-Brevicomin	Male and female *D. ponderosae*	Female *D. ponderosae*	Reduces attraction of females at high concentrations	Variable and inconsistent results in the inhibitory response result in limited utility
Frontalin	Male *D. ponderosae*			
Verbenone	Female *D. ponderosae* and multiple pathways of oxidation of precursors	Male and female *D. ponderosae*	Inhibits *D. ponderosae* colonization; thus partitioning the resource to enhance brood survival	Useful for protecting individual trees and stands from infestations, but with mixed results in some applications; verbenone is the principle antiaggregative pheromone of *D. ponderosae*
2-Phenylethanol, 1-Octen-3-ol	Male *D. ponderosae*, Female *D. ponderosae*	Male and female *D. ponderosae*	May inhibit aggregation and induce dispersal after emergence under some circumstances	Limited. May be used in compounds containing blends of nonhost volatiles and verbenone to reduce attraction

Figure 1.   Decision nodes (shaded boxes) that a bark beetle encounters during host selection and colonization. Several of these nodes may be exploited by application of semiochemicals to mitigate levels of tree mortality attributed to bark beetles. (Based on Borden 1997, Schlyter and Birgersson 1999, Zhang and Schlyter 2004, and Shepherd et al. 2007.)

diameter of *P. contorta* was positively correlated with beetle body size (i.e., width of the pronotum), which in turn was positively correlated with absolute lipid content in both sexes and relative lipid content in males. Safranyik et al. (1974) reported that *P. contorta* trees ≤25 cm dbh serve as sinks for *D. ponderosae* reproduction, because the abundance of brood produced is less than the number of infesting beetles, whereas trees >25 cm dbh produce more brood beetles than infesting beetles. This relationship is commonly observed in *P. contorta* (Safranyik and Carroll 2006, Björklund et al. 2009) and is one reason why stands with an average dbh >20.5 cm are considered highly susceptible to infestation by *D. ponderosae* (Safranyik et al. 1975, Cole and Amman 1980). Progar et al. (2013) defined hosts as "susceptible" (13–23 cm dbh), "suitable" (23–33 cm dbh), and "preferred" (>33 cm dbh) based on work in the Intermountain West. In general, *P. contorta* <13 cm dbh are rarely colonized. Although *P. ponderosa* as small as 2.54 cm dbh may be colonized during outbreaks, most are >12.7 cm dbh, but no clear preference for larger trees is evident in this host species (McCambridge et al. 1982, Fettig et al. 2014). However, stands with an average dbh ≥20.3 cm typically support most outbreaks (Sartwell and Stevens 1975). High tree density appears to be even more important than average tree diameter in *P. ponderosa*, presumably because of the negative effects of increased competition on tree susceptibility (Olsen et al. 1996, Fettig et al. 2007).

Host Colonization

After landing on a suitable host tree, female pioneering beetles move upward at an oblique angle (Rasmussen 1974), examining bark crevices and scales before entering the tree and initiating egg gallery construction. The beetles avoid smooth areas and burrow under bark scales 60% of the time and into crevices 40% of the time (Rasmussen 1974). It is thought that bark scales and crevices provide a point against which *D. ponderosae* braces when starting a gallery (Shepherd 1965). If the host is accepted, the female begins to construct a gallery and in the process initiates a mass attack (Borden 1982) as described above. Gallery construction occurs most frequently on the northern aspect of trees (Reid 1963, Shepherd 1965, Rasmussen 1974), where bark surface temperatures tend to be cooler (Powell 1967). Bark and phloem thickness decreases with increasing bole height; therefore, the density of infesting beetles also decreases with bole height. Rasmussen (1974) indicated that nearly 80% of gallery initiations occurred between 1.2 and 2.1 m above ground level, with a mean height of 1.4 m.

Reciprocal adaptation has resulted in a complex relationship between *D. ponderosae* and its host trees (Seybold et al. 2006). The larger, more vigorous trees that *D. ponderosae* prefer to colonize are also the trees that are typically best able to defend against infestation (Shrimpton 1973, Boone et al. 2011). Tree defenses include the release of resins from constitutive resin ducts severed by boring beetles (Smith 1963, Shrimpton and Whitney 1968, Berryman 1972) in addition to secondary induced resinosus (Smith 1963, Berryman 1972, Raffa and Berryman 1982, 1983) that can slow boring beetles or even expel them from the tree. As previously mentioned, host colonization requires overcoming tree defenses by recruiting a critical minimum number of beetles to mass attack individual trees. At low levels of colonization, trees respond by confining beetles and their associated fungi within necrotic lesions containing toxic or inhibitory compounds. However, above some critical

threshold value, for example ~40 galleries/m² of bole surface area in *P. contorta* (Raffa and Berryman 1983), the defensive capacity of the tree is compromised, and mortality often occurs. Therefore, host colonization and thus reproductive success are directly related to the depletion of host defenses.

D. ponderosae exhibits two responses to host defenses. First, aggregation pheromones (Table 1) focus infesting beetles on select trees, exhausting the tree's defensive resources by causing it to expend resin supplies in defense against large numbers of infesting beetles (Safranyik et al. 1975, Raffa and Berryman 1983, Berryman et al. 1989). Second, as the beetles bore through the bark and phloem, they inoculate the host with blue-stain fungal spores stored in specialized circular adaptations called mycangia that are present in both male and female adult beetles (Whitney and Farris 1970). These fungi rapidly spread throughout the phloem and sapwood, reducing tree resin production and transpiration, and increasing the rate of tree desiccation (Mathre 1964, Safranyik et al. 1975, Ballard et al. 1982, Solheim 1995). Developing larvae and new adults also obtain vital nutrients by feeding on associated fungal structures (Six and Paine 1998), but the contribution of blue-stain fungi in the death of trees infested by *D. ponderosae* is still under debate (Six and Wingfield 2011).

Outbreak Dynamics

D. ponderosae has long been considered a major pest in western forests with some notable outbreaks resulting in mortality of 70–90% of *P. contorta* ≥23 cm dbh over vast areas (Safranyik et al. 1974, Amman 1977, Klein et al. 1978, Progar 2003, 2005, Klutsch et al. 2009, Westfall and Ebata 2011, Kashian et al. 2011, Progar et al. 2013). *P. ponderosa* also experiences outbreaks of *D. ponderosae* across its range (Parker and Stevens 1979, McCambridge et al. 1982), most significantly in the Black Hills of South Dakota and Wyoming (Hopkins 1902, Blackman 1931).

Two general requirements are necessary for an outbreak to develop: (1) there must be several years of favorable weather (Safranyik 1978), including summer heat accumulations and winter temperatures conducive to beetle survival and brood development (Safranyik et al. 1975, Carroll et al. 2004); and (2) there must be an abundance of suitable host trees (Safranyik 1978, Fettig et al. 2014). In areas of suitable climate, forest species composition and age and size class structure will be the dominant factors influencing host susceptibility and outbreak severity (Taylor and Carroll 2004). As discussed, at endemic levels *D. ponderosae* primarily invades individual weakened trees, but during outbreaks, healthy trees are also infested (Rudinsky 1962). At the start of an outbreak, large trees are targeted by pioneering female *D. ponderosae*, and then adjacent trees are quickly and heavily colonized (Geiszler and Gara 1978), often resulting in tree mortality over large areas (McCambridge 1967, Reid et al. 1967, Billings 1974, Rasmussen 1974). The killing of trees in groups is a fundamental characteristic of *D. ponderosae* infestations (Geiszler et al. 1980b). The process of switching from heavily colonized to adjacent trees continues as long as sufficient numbers of beetles continue to arrive, and as long as acceptable hosts are available and the climate remains suitable, resulting in a chain reaction that expands the infested area for the duration of an outbreak (Mitchell and Preisler 1991).

Geiszler et al. (1980b) described three conceptual models of the host switching process of *D. ponderosae*. The first model was proposed by Renwick and Vité (1970) and is labeled the "Passive Model" because the signal for incoming beetles to switch host trees is identified as the lack of resin exudation that occurs when a tree's defenses have been successfully defeated by *D. ponderosae*. This model is partially supported by evidence that beetles produce more attractant pheromone when infesting trees with substantial quantities of oleoresin (Vité and Pitman 1968). The second model is termed the "Threshold Model" because it assumes that a threshold level or concentration of *trans*-verbenol is required to stimulate landing and gallery initiation. When the pheromone concentration surrounding adjacent trees reaches a sufficient threshold, incoming beetles are thought to be stimulated to land on and infest a nearby (recipient) tree, creating a new focus tree. According to Geiszler et al. (1980b), the recipient tree competes with the focus tree for incoming beetles. Thus, the rate of infestation of the initial focus tree declines and the recipient tree assumes the role of the focus tree, and the process is repeated.

A third model termed the "Repelling Model" suggested that *trans*-verbenol and a "repelling pheromone" cause switching (Geiszler et al. 1980b). Large quantities of *trans*-verbenol are secreted during mass attack, attracting large numbers of *D. ponderosae*. However, at high densities of infestation, the beetles emit a repelling pheromone (*see* Inhibitors) that deters further infestation. Although *trans*-verbenol is still secreted, the attracted beetles are repelled from the focus tree by the repelling pheromone and instead infest neighboring trees. This model was supported by the identification of inhibitory pheromones in other *Dendroctonus* spp. (Renwick and Vité 1970, Furniss et al. 1973). Rudinsky et al. (1974) reported that *exo*-brevicomin is an antiaggregation pheromone of *D. ponderosae*. Later studies showed that verbenone exhibited a strong inhibitory effect on *D. ponderosae* (Ryker and Yandell 1983, Schmitz 1988, Amman et al. 1989, Lindgren et al. 1989, Miller et al. 1995) (Table 1).

The Repelling Model best fits observations made in the field and has become the most widely accepted (Geiszler et al. 1980b). The Passive Model was discounted because the reduction of resin exudation that was proposed as the switching signal did not reduce the numbers of *D. ponderosae* that remain attracted during the process of switching to a new focus tree (Geiszler and Gara 1978, Geiszler 1979). The Threshold Model was discounted because it forecasts that switching occurs during peak *trans*-verbenol production and release; however, switching from a focus tree to a recipient tree generally occurs after the peak in *trans*-verbenol emission, not before (Geiszler and Gara 1978).

Attractants

Person (1931) was first to suggest that bark beetle aggregation resulted from chemical-mediated attraction after initial tree infestation, leading to decades of active study in search of behaviorally active principles. Silverstein et al. (1966) isolated and identified the first known bark beetle aggregation pheromone and demonstrated its behavioral activity for *Ips confusus* LeConte (= *I. paraconfusus*). Shortly afterward, Renwick (1967) isolated and identified *trans*-verbenol, the first known aggregation pheromone for the genus *Dendroctonus*, from southern pine beetle, *Dendroctonus frontalis* Zimmerman, and western pine beetle, *Dendroctonus brevicomis* LeConte. Since the demonstration of its behavioral activity as an aggregation pheromone for *D. ponderosae* (Pitman et al. 1968, 1969, Pitman and Vité 1969), considerable research has been conducted to identify other attractants and synergists to optimize levels of attractant for detection, monitoring and manipulation purposes; and to develop effective methods for reducing tree losses to *D. ponderosae*.

Figure 2. Lindgren multiple-funnel traps deployed in a *Pinus contorta* forest to determine the response of *Dendroctonus ponderosae* to novel inhibitors (Uinta-Wasatch-Cache National Forest, Utah).

Early research indicated that the attraction of *D. ponderosae* to *trans*-verbenol required one or more synergists (Pitman et al. 1968, Pitman 1971). Many potential synergists were tested, including *exo*-brevicomin and frontalin in addition to the host volatiles α-pinene, β-pinene, 3-carene, limonene, myrcene, β-phellandrene, and terpinolene, with somewhat variable results (Pitman 1971, Billings et al. 1976, Ryker and Rudinsky 1982, Borden et al. 1983, Conn et al. 1983). The consensus of these studies was that the most consistently attractive blend included *trans*-verbenol, *exo*-brevicomin, myrcene, and possibly terpinolene. More recent studies confirmed that the quaternary blend of *trans*-verbenol, *exo*-brevicomin, myrcene, and terpinolene was more effective for attracting *D. ponderosae* when used as a trap lure (Miller and Lindgren 2000, Pureswaran et al. 2000, Pureswaran and Borden 2005, Borden et al. 2008, Strom et al. 2008). Host volatiles produced naturally by the tree may serve as synergists when lures are used to induce colonization of live trees, and, therefore, the two-component blend of *trans*-verbenol and *exo*-brevicomin is often sufficient for this use (Borden et al. 1983).

Utilization of Attractants

Detection and Monitoring

In addition to advances in the identification of behaviorally active chemicals, improvements in trap design were essential to facilitate the detection, monitoring, and manipulation of beetle populations. Early trap designs included screened cages (Chapman and Kinghorn 1955), cardboard tubes coated with sticky material (Pitman 1971), drainpipe traps (Pitman 1971), bucket traps (Moser and Browne 1978), and sticky-coated vane traps (Browne 1978). Lindgren (1983) developed a much more effective and portable multiple-funnel trap that is still widely used today (Figure 2). More recently, a lightweight, foldable-vane or panel trap has shown considerable promise for detection and monitoring purposes (Czokajlo et al. 2001).

The effectiveness of multiple-funnel and foldable-vane or panel traps for collecting *D. ponderosae* has not been compared, but evidence from studies of related bark beetles suggests that both designs work well for detection and monitoring purposes, with foldable-vane traps capturing slightly more individuals than multiple-funnel traps (Czokajlo et al. 2001, 2003, Dodds et al. 2010, Miller and Crowe 2011, Miller et al. 2013). When multiple-funnel traps are used, it is important to place the attractant lures inside the funnels rather than to suspend them from the trap exterior because internal lure placement yields significantly higher trap catches (Miller et al. 2013). The use of baited traps to detect *D. ponderosae* populations is well supported; however, baited traps have been shown to disproportionately collect (sample) *D. ponderosae,* even when most of the beetle population has not yet emerged from subcortical overwintering sites (Bentz 2006). This anomaly may occur because beetles are attracted from long distances or because natural sources of aggregation pheromones and host kairomones compete with the synthetic lures in traps (Bentz 2006). Caution should therefore be used in interpreting trap catches for monitoring purposes.

Trap Out, Trap Trees, Concentration, and Containment

Shortly after the discovery of effective attractants for *D. ponderosae*, Pitman (1971) explored several methods for using synthetic lures to reduce beetle populations and mitigate levels of tree mortality. Pitman (1971) developed the use of baited traps to remove beetles from the ecosystem or "trap out," the use of insecticide-treated "toxic trap trees," and the use of baited sacrificial trees intended to induce lethal levels of intraspecific competition among developing brood. The latter method was quickly abandoned because researchers were unable to overcome the innate capacity of *D. ponderosae* to avoid overcrowding, which was later determined to result from release of verbenone (Ryker and Yandell 1983). A primary disadvantage of the use of attractants is the risk of inducing infestation of nearby trees (Pitman 1971). The ability of synthetic baits to lure *D. ponderosae* from great distances rather than simply removing beetles from the immediate area remains a serious limitation of employing trapping strategies to reduce levels of tree mortality. Another concern is the logistical issue of treating a large enough area.

Nevertheless, attract-and-kill or beetle concentration-and-containment techniques (accomplished by removal of baited, infested trees) have continued to be tested for decades and have been shown to be effective in reducing the amount of infestation in adjacent stands in some studies (Smith 1986, Gray and Borden 1989, Lindgren and Borden 1993). Strategies may vary, depending on population density, size of the infested area, stand susceptibility, and the infestation status of surrounding untreated sites. Vandygriff et al. (2000) successfully used attractants to focus *D. ponderosae* infestation in areas designated for future fuelwood harvests, potentially improving the health of stands adjacent to baited sites. Other recent studies have shown protection of adjacent stands by baiting sacrificial trees that are immediately harvested after they are fully colonized (Borden et al. 2003, 2006, 2007), but this tactic is limited to use in stands where management practices permit the deliberate sacrifice of living trees for the greater good of the larger stand.

Push-Pull

An alternative approach, known as "push-pull," combines the use of trap out or trap tree methods with inhibitors to divert beetles from high-value stands to baited traps or trees. The potential advantages of this method are reduced levels of tree mortality compared with those for singular methods, and, if traps are used instead of trap trees, push-pull is compatible with forest management policies that prohibit harvest or destruction of healthy trees. However, as with

any technique using attractants, there is a risk of attracting beetles to adjacent areas, which may result in undesirable levels of tree mortality.

Lindgren and Borden (1993) were the first to systematically examine push-pull for *D. ponderosae* and reported that the addition of a "pull" component marginally improved stand protection over that achieved by inhibitors alone. Shea and Neustein (1995) tested push-pull on the California five-spined ips, *Ips paraconfusus* Lanier, and while their treatments were successful, that study was not replicated or controlled, and was complicated by the sudden end of drought conditions that had precipitated the initial outbreak (Littrell 1992). Gillette et al. (2012b) conducted a two-phase study to determine whether adding perimeter traps to verbenone-treated stands further reduced levels of tree mortality attributed to *D. ponderosae*. They reported that at two different levels of spacing, adding a pull component had no effect. It is possible that effectiveness might be improved using larger plots or different trap spacing, but current evidence suggests that neither tactic is cost-effective for the management of *D. ponderosae* in *P. albicaulis* or *P. contorta* forests. The installation of large numbers of traps in a push-pull tactic is considerably more expensive than use of inhibitors alone, so it is important to verify that further decreases in levels of tree mortality occur using this approach. Not surprising, push-pull tactics are currently under scrutiny to assess whether the added effort and cost of an attractive component is merited. The scale at which effectiveness can be balanced with efficiency has yet to be defined (Gillette et al. 2012b) and dose-range tests (Miller et al. 1995) may need to be incorporated in related studies to aid in decisions about which combinations of semiochemical treatments best meet management objectives and desired levels of tree protection.

A disadvantage of push-pull, as discussed earlier (*see* Trap Out, Trap Trees, Concentration, and Containment), is that some beetles may infest or "spill over" onto adjacent trees, resulting in undesirable levels of tree mortality. This behavior is exhibited in many *Dendroctonus* species, including *D. ponderosae*. When baited traps are used, placement of traps in areas of nonhost trees or in forest openings should be considered to reduce spillover (Progar et al. 2010). Similarly, baiting trees that are widely separated from other hosts (e.g., by >10 m) should reduce the probability of spill over.

Inhibitors

In recent years, research has focused on the use of antiaggregation semiochemicals, primarily verbenone, and other inhibitory compounds to disrupt the responses of *D. ponderosae* to attractants and to reduce levels of tree mortality. Trace amounts of verbenone were first identified from the hindgut of emergent and feeding *D. ponderosae* females (Pitman et al. 1969) and from the air surrounding male-female mating pairs (Rudinsky et al. 1974). The first evidence of inhibitory properties of verbenone against *D. ponderosae* resulted when laboratory and field bioassays of (−)-verbenone inhibited the *D. ponderosae* response to selected host- and beetle-produced attractants (Ryker and Yandell 1983). Today, verbenone is regarded as the principle antiaggregation semiochemical of *D. ponderosae*.

Verbenone originates from at least three sources: female beetles (Pitman et al. 1969); autoxidation of α-pinene to *cis-* and *trans-*verbenol and then to verbenone (Hunt and Borden 1989, Lindgren and Borden 1989); and oxidation of *cis-* and *trans-*verbenol by microorganisms (primarily yeasts) associated with *D. ponderosae* (Hunt and Borden 1989, Lindgren and Borden 1989). In nature, verbenone is produced in small amounts by autoxidation of the mono-

terpene α-pinene (Hunt et al. 1989), but the primary route of production is through metabolic conversion by bark beetles of inhaled and ingested α-pinene to the terpene alcohols *cis-* and *trans-*verbenol, which are metabolized by yeasts in the beetles' alimentary system and in their galleries to verbenone (Leufvén et al. 1984, Hunt and Borden 1990). Verbenone is now known to be produced by females alone in new galleries, in reduced amounts by females that have been joined by males in galleries, and in large amounts by the newly paired males (Pureswaran et al. 2000).

Early experiments in stands of *P. contorta* showed that there was significantly less *D. ponderosae*-caused tree mortality on verbenone-treated plots than on untreated plots, with a trend of reducing tree mortality with increasing dose (Lindgren et al. 1989, Amman et al. 1991, Gibson et al. 1991, Safranyik et al. 1992, Amman and Lindgren 1995). Subsequent studies yielded inconsistent or ambiguous results over time (Shea et al. 1992, Amman 1994), geographical area (Gibson et al. 1991, Amman 1994), outbreak intensity (Progar 2003, 2005, Progar et al. 2013), dose (Borden and Lindgren 1988, Gibson et al. 1991), or tree species, with other studies indicating that verbenone is ineffective for reducing levels of tree mortality in *P. ponderosa* (Bentz et al. 1989, Lister et al. 1990, Gibson et al. 1991, Negrón et al. 2006, Fettig et al. 2009). Recent research has focused on combining verbenone with other inhibitors, specifically nonhost volatiles (*see* Utilization for Protection of Individual Trees and Utilization for Protection of Small-Scale Stands).

There is evidence that *exo*-brevicomin has a multifunctional role in the chemical ecology of *D. ponderosae*, at low concentrations inducing attraction and at high concentrations causing inhibition (Rudinsky et al. 1974). Experiments evaluating various release rates of *exo*-brevicomin as a pheromone for *D. ponderosae* on traps and trees with and without other attractants may be summarized as follows: at release rates of ≤0.04 mg/24 hours there is no observable effect (Libbey et al. 1985); at release rates of 0.05 mg/24 hours an aggregative response is found (Conn et al. 1983, Borden et al. 1987); and at release rates ≥4.0 mg/24 hours an inhibitory response occurs (Ryker and Rudinsky 1982, Libbey et al. 1985, Borden et al. 1987). However, the response of *D. ponderosae* to rates between 0.05 and 4.0 mg/24 hours are inconsistent (Shore et al. 1992). As a result of the risk associated with aggregation at low release rates, research on *exo*-brevicomin for reducing levels of tree mortality attributed to *D. ponderosae* has paled in comparison to that focusing on verbenone.

Methods of Application

Several methods for applying verbenone and, to a lesser extent, other inhibitors, have been evaluated for protecting individual trees and forest stands from mortality attributed to *D. ponderosae*. The most common method involves rudimentary bubble cap and pouch release devices applied by hand (Figure 3), primarily because of cost limitations. Bubble caps and pouches are typically stapled at maximum reach (~2 m in height) to individual trees prior to *D. ponderosae* flight in spring and applied in a gridded pattern of distribution to achieve uniform coverage when stand protection is the objective. Bead, flake, and sprayable formulations may be applied by ground- or aerial-based methods (Figure 4). The release rates of passive releasers vary with changes in temperature and humidity and, because they dispense semiochemicals through a membrane, are strongly influenced by meteorological conditions, making the amount of semiochemical released somewhat unpredictable (*see* Barriers to the Development of Effective Semiochemical-Based Tools).
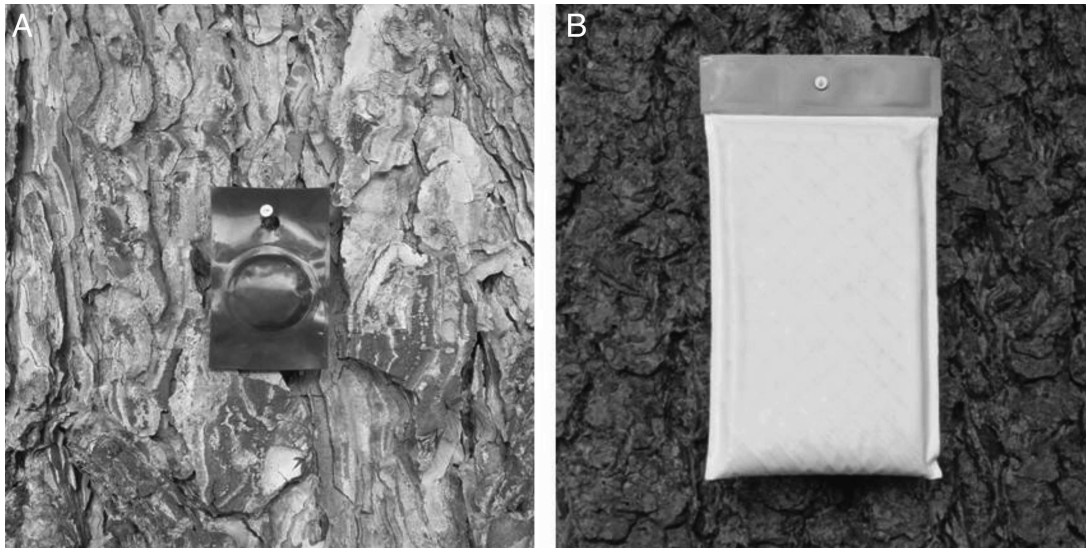
Figure 3. Common passive-release devices include bubble caps (A) and pouches (B).

Figure 4. Biodegradable flakes ($\sim$3 mm^2) containing verbenone suitable for aerial applications.

Initial experiments were conducted in the mid-1980s using 0.5-g bubble caps containing verbenone (Amman and Lindgren 1995). Through the mid-1990s, *D. ponderosae* populations were relatively low, so research concerning the development of novel application methods diminished. However, during the 1990s, *D. frontalis* populations were epidemic in many areas of the southern United States, and research there resulted in the development of a novel 5-g pouch for dispensing verbenone that was registered by the US Environmental Protection Agency (EPA) in 1999 (Clarke et al. 1999). Subsequently, the 5-g verbenone pouch and, later, larger capacity pouches (7-g) were evaluated and registered for management of *D. ponderosae* in western forests. The pouch remains popular for individual tree (*see* Utilization for Protection of Individual Trees) and small-scale stand protection (*see* Utilization for Protection of Small-Scale Stands).

Shea et al. (1992) were first to aerially apply verbenone formu-

lated in cylindrical 5- $\times$ 5-mm plastic beads released by helicopter, but results were inconsistent as no treatment effect (on levels of tree mortality) was observed, but the mean ratio of infested trees between subsequent years (1988 treated/1987 untreated) was significantly lower with the verbenone treatment. Gillette et al. (2006, 2009a, 2012a, 2012b, 2013) demonstrated that verbenone could be deployed as verbenone-impregnated plastic flakes by ground and/or aerial application. Flakes are smaller ($\sim$3–6 mm^2) than beads 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 or tree bole when applied with ground-based equipment. Development of the flake formulation is ongoing, but results to date are promising, and a newer biodegradable flake has been developed and registered.

Puffers are small battery-activated reservoirs that emit frequent, measured releases of aerosolized liquid, thus overcoming some of the problems associated with passive releasers (*see* Barriers to the Development of Effective Semiochemical-Based Tools; see also Holsten et al. 2002, 2003) but are prohibitively expensive for most forestry applications. Med-e-Cell has developed prototypes that actively push fluid to the outside, potentially offering more control over release rates. However, once the fluid is dispensed, evaporative properties and thus volatile release rates within stands are heavily influenced by meteorological conditions. Most recently, Fettig et al. (2012d) demonstrated the effectiveness of a novel wax emulsion matrix impregnated with verbenone deployed by hand for reducing levels of tree mortality (*see* Utilization for Protection of Individual Trees). Formulations of verbenone currently registered by the EPA and commercially available for use in the western United States include pouches (several registrants), the Disrupt Micro-Flake VBN and Disrupt Bio-Flake VBN formulations (Hercon Environmental, Emigsville, PA), and SPLATVerb (ISCA Technologies, Inc., Riverside, CA).

Utilization for Protection of Individual Trees
Verbenone Pouches

Much of the research conducted on protection of individual trees with verbenone pouches has been on *P. albicaulis,* for which they have been shown to be very effective (Kegley et al. 2003, Kegley and

Gibson 2004, 2007). Statistically significant reductions in levels of tree mortality between treated and untreated trees have also been demonstrated for *P. contorta* (e.g., Kegley and Gibson 2009, Kegley et al. 2010). Kegley and Gibson (2009) reported that applying two verbenone pouches to individual *P. ponderosa* reduced levels of tree mortality compared with that for the untreated control in Montana, although verbenone is generally regarded as ineffective for protecting stands of *P. ponderosa* (Negrón et al. 2006, Fettig et al. 2009).

Verbenone Beads and Flakes

The inconsistent effectiveness of verbenone bubble caps and pouches to provide stand-level protection (*see* Utilization for Protection of Small-Scale Stands, Verbenone Pouches) has induced the development of other formulations of verbenone (Shea et al. 1992, Rappaport et al. 2001, Gillette et al. 2006, 2013) that could be used to protect individual trees by applying the material around the circumference of the tree, assuming that a circumferential release from numerous small point sources would provide better protection than fewer or an individual point source per tree (i.e., as provided by bubble caps or pouches). Microencapsulated verbenone applied as an aerosol spray showed promise for protecting pines from colonization by the related red turpentine beetle, *Dendroctonus valens* LeConte (Rappaport et al. 2001), but this formulation was not developed commercially. Gillette et al. (2006) reported near complete protection of *P. contorta* from *D. ponderosae* infestation in California using a newer plastic flake formulation consisting of 3-mm^2 laminated polyvinyl chloride layers surrounding a plastisol middle layer that released verbenone. Kegley et al. (2010) compared flakes to a widely used pouch release device in Montana and concluded that levels of *P. contorta* protection were similar, but that flakes were more costly and laborious to apply. In that study, however, the targeted application of 15 g of verbenone per tree was not always reached because of limitations imposed by the method of application. Despite this, fewer mass-attacked trees and more unsuccessful attacks (pitchouts and strip attacks) were observed with verbenone flakes than with pouches. These observations suggest that the more uniform circumferential release of verbenone provided by flakes may increase levels of tree protection, a relationship that warrants further investigation with this and other semiochemicals. A newer formulation of biodegradable flakes has recently been developed, and initial studies demonstrated substantial reductions in tree mortality in areawide applications conducted in *P. albicaulis, P. contorta,* and *P. flexilis* forests (Gillette et al. 2012b, 2013). Further research to evaluate similar formulations for protection of individual trees should be considered.

The flake formulation released ~25% of its verbenone in the first 4 weeks of field deployment and another 15% in the second 4 weeks (Norris Starner, Hercon Environmental, pers. comm., Jan. 15, 2013). Therefore, if 15 g of verbenone were applied to the trunk of a tree, it would release on average ~125 mg/day for the first 4 weeks. Studies indicate that behaviorally active levels of verbenone (e.g., sufficient to reduce baited trap catches) remain in forested areas treated with verbenone flakes for more than 1 month (Gillette et al. 2013).

Combining Verbenone with Nonhost Volatiles

As discussed previously, *D. ponderosae* must successfully locate suitable hosts to reproduce. When the decision nodes that a bark beetle encounters during host selection and colonization are considered (Figure 1, shaded boxes), three of these might be exploited as points for active management by combining verbenone with nonhost volatiles, including habitat suitability (e.g., green leaf volatiles and angiosperm bark volatiles), host presence (e.g., green leaf volatiles and angiosperm bark volatiles), and host suitability and susceptibility (e.g., antiaggregation and aggregation pheromone components of con- and heterospecifics and host volatiles that signal changes in host vigor and/or tissue quality) (Borden 1997, Schlyter and Birgersson 1999, Zhang and Schlyter 2004, Shepherd et al. 2007). In recent years, nonhost volatiles have been the focus of numerous studies, which demonstrated that these compounds, especially acetophenone and some of the green leaf volatiles, are capable of reducing aggregation in some *Dendroctonus* spp. (Zhang and Schlyter 2004, Zhang et al. 2007, Erbilgin et al. 2007, 2008). Although there are exceptions (Huber et al. 1999, 2000), this approach usually requires combinations of two or more compounds, which led to research evaluating combinations of verbenone with nonhost volatiles for tree protection. Wilson et al. (1996), Borden et al. (1998), and Huber and Borden (2001) reported that combinations of green leaf volatiles and angiosperm bark volatiles significantly reduced mass attack infestation densities of attractant-baited *P. contorta* in British Columbia. Kegley and Gibson (2009) reported significant reductions in levels of tree mortality when *P. albicaulis, P. contorta,* and *P. ponderosa* were treated with a combination of verbenone and green leaf volatiles in Montana. Kegley et al. (2010) reported that verbenone flakes, verbenone pouches, and a combination of verbenone and two green leaf volatiles were equally effective for protecting individual *P. contorta* from *D. ponderosae* in Montana.

Verbenone Plus

A semiochemical-based tool was recently developed to protect trees from *D. brevicomis* infestation (Fettig et al. 2008a, 2008b). However, initial semiochemical blends were complex and probably not feasible for operational use. As a result, Fettig et al. (2012b) examined the response of *D. brevicomis* to modified blends, as informed by gas chromatographic-electroantennographic detection analyses (Shepherd et al. 2007), which resulted in a novel four-component blend [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (−)-verbenone] (Verbenone Plus) that was demonstrated to inhibit the response of *D. brevicomis* to attractant-baited traps and trees (Fettig et al. 2012b, 2012c). As a result, researchers compared verbenone (7-g pouch) and Verbenone Plus for protecting individual *P. contorta* from mortality attributed to *D. ponderosae* in Utah. Both treatments were effective, but no significant difference in levels of tree mortality was observed between treatments (C.J. Fettig and A.S. Munson, unpub. data, Jan. 15, 2013). At present, the use of Verbenone Plus rather than verbenone alone for protecting individual *P. contorta* from *D. ponderosae* is not justified.

SPLATVerb

In recent years, a SPLAT (Specialized Pheromone & Lure Application Technology; ISCA Technologies, Inc.) has been developed using a wax emulsion matrix that can be applied by hand (e.g., using a caulking gun) or by mechanical means (e.g., using aircraft in some systems) and provides a long-lasting, controlled-release formulation to dispense semiochemicals (Figure 5). SPLAT has many desirable characteristics for use as a tree protection tool (Holsten et al. 2002, 2003; *see also* Barriers to the Development of Effective

Figure 5. A dollop (~5 cm wide) of SPLAT impregnated with verbenone (SPLATVerb).

Semiochemical-Based Tools). For example, Fettig et al. (2012d) began evaluating SPLAT formulated with verbenone ("SPLAT-Verb") for protecting individual *P. contorta* from mortality attributed to *D. ponderosae* in Wyoming in 2011. After being deployed in the field for 23 days, dollops of SPLATVerb (Figure 5) still contained ~40% of their original concentration of verbenone, and it was not until ~12 months in the field that trace amounts of chrysanthenone, a compound with no known effects on bark beetle behavior (*see* Chemical Stability in the Forest Environment for related issues), were detected (C.J. Fettig, A. Mafra-Neto, and A.S. Munson, unpubl. data, Jan. 15, 2013). Although this research is in the early stages of development, SPLATVerb appears promising for individual tree protection as 100% tree protection was observed, whereas 93.3% tree mortality occurred in the untreated control (C.J. Fettig, A. Mafra-Neto, and A.S. Munson, unpubl. data, Jan. 15, 2013).

Utilization for Protection of Small-Scale Stands
Verbenone Pouches
Numerous studies have evaluated verbenone bubble caps and pouches for protecting small stands from *D. ponderosae* infestation. Both releasers have been shown to reduce the incidence of *D. ponderosae* infestation in *P. contorta* stands (e.g., Schmitz 1988, Amman et al. 1989, 1991, Lindgren et al. 1989, Gibson et al. 1991, Shore et al. 1992, Lindgren and Borden 1993, Amman and Ryan 1994, Miller et al. 1995, Progar 2003, 2005, Bentz et al. 2005, Borden et al. 2007) and in *P. albicaulis* stands (Bentz et al. 2005), but results have been inconsistent in other studies as discussed previously. Borden et al. (2007) compared infestation levels on verbenone-treated plots where trees containing current *D. ponderosae* brood were removed (sanitation) with infestation levels on verbenone-treated plots where trees with brood were not removed and found infestation levels to be 5 times lower on plots where the combined treatment of verbenone and sanitation occurred. On the other hand, the verbenone pouch is ineffective for protecting *P. ponderosa* from *D. ponderosae* infestations (Bentz et al. 1989, Lister et al. 1990, Negrón

et al. 2006), and further research is needed to develop an effective semiochemical treatment for use in *P. ponderosa*.

Verbenone Beads and Flakes
The recent listing of *P. albicaulis* as a candidate for threatened or endangered species status (Federal Register 2011), coupled with escalating *D. ponderosae* outbreaks in high-elevation forests (Tomback and Achuff 2010), has led to a renewed focus on the development of semiochemical-based methods to protect *P. albicaulis* and other high-elevation "sky-island" pine species from *D. ponderosae*. However, these forests are often difficult to access, making aerial applications especially desirable for logistical reasons (Gillette et al. 2012a, 2013). Two flake formulations of verbenone, based on the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), mating disruption product used in the Slow-the-Spread Program (Sharov et al. 2002) have been evaluated for aerial application in *P. contorta*. These formulations exhibited promising release properties in laboratory tests and were effective in field tests for tree protection (Gillette et al. 2012a, 2012b). The first of these, Hercon Disrupt Micro-Flake VBN, was applied to *P. albicaulis* stands at the rate of 370 g/ha to 4.0-ha plots in both Washington and Wyoming (Gillette et al. 2012a). At both sites, tree protection exceeded 50%. The same formulation applied at 1,101 g/ha to 4.0-ha plots in *P. contorta* stands in California reduced the portion of infested trees by 37% (Gillette et al. 2012b). In response to concerns regarding applications of nondegrading plastic flakes, biodegradable flakes have been developed and tested in applications combining verbenone with green leaf volatiles (Gillette et al. 2012a).

Combining Verbenone with Nonhost Volatiles
As discussed earlier, most of the research combining verbenone with nonhost volatiles has focused on protecting individual trees, primarily *P. contorta*, from *D. ponderosae*. In contrast, Borden et al. (2003) deployed high release rates of verbenone and nonhost angiosperm volatiles on a 10-m grid in 40 × 40-m plots in *P. contorta* forests in British Columbia. No significant difference in the number of trees colonized per plot (infestation density) was observed, but the proportion of mass-attacked trees (>17.5 cm dbh) was significantly lower on plots treated with verbenone and nonhost angiosperm volatiles than for the untreated control. The authors concluded that the tactic was operationally feasible for short-term protection of small, high-value stands.

Verbenone Plus
Fettig et al. (2012a) evaluated Verbenone Plus for protecting stands of *P. albicaulis* from *D. ponderosae* in California. Significantly fewer trees were killed by *D. ponderosae* on Verbenone Plus-treated plots than for the untreated control. A 78% reduction in tree mortality was observed. Similar studies are ongoing in *P. contorta* in Idaho.

SPLATVerb
Researchers are comparing verbenone and SPLATVerb for protection of *P. contorta* stands in Idaho, but studies are still ongoing (Fettig et al. 2012d).

Utilization for Protection of Larger Areas (≥10 ha)
It is assumed that inhibitors are more effective when applied at larger spatial scales because large areas have smaller edge/area ratios

Table 2. Barriers to the development of effective semiochemical-based tools for protecting trees from mortality attributed to *Dendroctonus ponderosae*.

Barrier	Explanation
Complexity of the semiochemical signals used in the host selection process	Bark beetles use a variety of contextual cues during host selection. Insufficient reductions in tree mortality may be due, in part, to inadequate chemical signaling. For example, synthetic verbenone deployed alone without other beetle-derived or nonhost cues may not provide sufficient inhibition for adequate tree protection under some situations.
Variation in stand composition and structure, especially tree density	Concentrations of semiochemicals rapidly decrease with increasing distance from a point source, and in low-density forests (e.g., *Pinus ponderosa*) unstable layers and multidirectional traces (eddies) may dilute concentrations and have a negative impact on effectiveness. Stands of trees with larger diameters have been shown to be more susceptible to infestation and produce more progeny, potentially reducing the effectiveness of semiochemical treatments.
Chemical stability of the formulation in the forest environment	Concerns regarding the degradation of verbenone to chrysanthenone in modern release devices appear unimportant. However, little is known about chemical stability once verbenone is released into the active airspace.
Inconsistent release	Several authors have speculated that failures have resulted from problems associated with passive release, which is largely controlled by ambient temperature. However, with notable exceptions, most studies have found that conventional release devices (e.g., bubble caps, pouches, and plastic flakes) maintain target release rates for sufficient periods of time under field conditions.
Levels of inhibition	Verbenone significantly reduces the response of *D. ponderosae* to attractant-baited traps, and substantial reductions (>95%) in trap catches are commonly observed. However, sensitivity likely varies among populations and among individuals within a population, thus influencing effectiveness.
Range of inhibition	Studies show that the maximum range of inhibition of verbenone released from conventional devices is limited (<4 m). Higher densities of small, point-source releasers may provide for better dispersal patterns and greater reductions in tree mortality.
Population size	Effectiveness declines with increasing population density. Higher levels of tree mortality are expected during severe outbreaks and with a declining proportion of preferred hosts when populations still exist at epidemic levels.
Ratio of inhibitors to attractants	The response of *D. ponderosae* to inhibitors in the presence of aggregation pheromones and host kairomones often depends on the ratio of inhibitors to attractants.
Costs and small market conditions	These factors are significant barriers to investment in research and development.

and therefore experience fewer edge effects associated with semiochemical loss caused by downwind dispersal from treated areas. Despite the intuitive advantage of treating large areas, few studies have examined inhibitors on areas ≥10 ha (Gillette et al. 2009a, 2009b), and only one of them studied *D. ponderosae* (Gillette et al. 2009a). Gillette et al. (2009a) examined the ability of aerially applied verbenone-releasing plastic flakes (370 g/ha of Hercon Disrupt Micro-Flake VBN) to protect *P. contorta* from colonization by *P. ponderosae* in California and Idaho. They found significant reductions in the infestation of *P. contorta* by *D. ponderosae*, suggesting that this approach is effective for the rapid treatment of large areas. Newer formulations with more effective and/or less expensive active ingredients are on the horizon and warrant further testing.

Barriers to the Development of Effective Semiochemical-Based Tools

As discussed earlier, the effectiveness of semiochemical-based tools varies by semiochemical, tactic, geographic location, host species, and population density (e.g., Bentz et al. 1989, Lister et al. 1990, Gibson et al. 1991, Shea et al. 1992, Amman and Lindgren 1995, Progar 2003, 2005, Negrón et al. 2006, Fettig et al. 2009, Progar et al. 2013). In an operational context, inhibitors such as verbenone have been shown to be effective for protecting *P. contorta,* whether applied as individual passive release devices (bubble caps or pouches) or in bead, flake, and sprayable formulations. Yet, failures are not uncommon (e.g., Gibson et al. 1991, Shea et al. 1992, Progar 2003, 2005, Bentz et al. 2005), and significant reductions in levels of tree mortality have not been demonstrated in *P. ponderosa* at the stand level (e.g., Bentz et al. 1989, Lister et al. 1990, Negrón et al. 2006). Negative results are linked to a variety of factors (Table 2). We discuss several of these largely in the context of developing verbenone as a tool for tree and stand protection.

Complexity of the Host Selection Process

Failures of verbenone to reduce levels of tree mortality may be due, in part, to lack of a realistic foraging context (Seybold et al.

2000, Shepherd et al. 2007). That is, synthetic verbenone deployed in the absence of other beetle-derived or nonhost cues may deliver an incomplete or insufficient signal to beetles to confer the desired levels of inhibition. Zhang and Schlyter (2004) introduced the semiochemical-diversity hypothesis as one factor, among others, explaining why homogeneous stands (i.e., a monoculture being the extreme) experience outbreaks of forest insects more often than heterogeneous stands. In the context of pest management, a diverse array of chemical cues and signals may disrupt bark beetle host searching more than high doses of a single semiochemical (e.g., verbenone) or even mixtures of semiochemicals intended to mimic one type of signal (e.g., antiaggregation pheromones) based on the semiochemical-diversity hypothesis because they represent heterogeneous stand conditions to searching insects. It is well documented that higher levels of inhibition occur when verbenone is combined with nonhost volatiles than with verbenone alone (Zhang and Schlyter 2004). The addition of nonhost volatiles is an attempt to shift the foraging context toward one in which a searching beetle would be reluctant to land on potential hosts for any appreciable amount of time, rather than simply attempting to overwhelm it with what is presumed to be a particular type of signal (Figure 1).

During outbreaks, *D. ponderosae* releases large quantities of verbenone into the airspace beneath the forest canopy over extended periods as trees are colonized at different times (dates) within the same year. Despite this, *D. ponderosae* is still successful in colonizing trees, which suggests that selection might have favored behaviors that help beetles circumvent the gross effect of verbenone during outbreaks. This behavior infers a hierarchical ordering of the behavioral mechanisms affecting the process of host selection. If this assumption is valid, then reliance on verbenone alone will probably yield unsatisfactory results during high population densities (*see* Population Size).

Variation in Stand Composition and Structure, Specifically Tree Density

Thinning stands prevents bark beetle infestations by reducing the ability of beetles to locate and successfully colonize host trees

(Fettig et al. 2014). This concept may help explain the lack of success in using verbenone and other inhibitors in stands of lower tree density such as in *P. ponderosa* forests. Semiochemicals released from an individual point source passively diffuse into three-dimensional airspace and concentrations rapidly decrease with increasing distance from that point source. Some authors reported that inversions occur in the stem zone immediately beneath the canopy, which creates a chamber of more stable air (Chapman 1967, Fares et al. 1980), thus influencing semiochemical plumes. These inversions tend to be stronger and last longer in dense stands (Fares et al. 1980). Thistle et al. (2004) examined near-field canopy dispersion of a tracer gas (SF_6), as a surrogate for bark beetle pheromones below the tree canopy. They showed that when surface layers of air are stable (e.g., during low wind velocities) the tracer plume remained concentrated and showed directional consistency because of the suppression of turbulent mixing by the canopy overhead. Lower stand density results in unstable layers of air and multidirectional traces (eddies) that dilute pheromone concentrations and may reduce beetle aggregation, thus influencing host finding and subsequent tree colonization. In the case of verbenone and other inhibitors, these effects would have a negative impact on the performance of semiochemical plumes created by multiple release devices. Strand et al. (2009, 2012) also modeled surrogate pheromone dispersion under different forest canopy conditions. Their work provides useful guidelines for more effective deployment of semiochemical releasers in varied forest canopy conditions.

Chemical Stability in the Forest Environment

In areas of direct sunlight, verbenone may be photoisomerized to chrysanthenone (Kostyk et al. 1993), a compound with no known effects on bark beetle behavior. This was considered enough of a concern that a CYASORB UV stabilizer that scavenges UV-generated radicals was added to verbenone pouches. Fettig et al. (2009) reported that chrysanthenone was not detected in any of the volatile extracts obtained from verbenone pouches that were deployed in *P. ponderosa* forests in California; however, trace amounts of filifolone, a thermal or photo rearrangement product of (+)-chrysanthenone (Asfaw et al. 2001), was present in both unexposed and field-exposed pouches. It appears that even in the Mediterranean climate of California (i.e., warm and sunny), only minor and indirect evidence of isomerization of verbenone to chrysanthenone occurs and therefore probably does not represent a substantial concern in areas (e.g., the northern Rockies) where verbenone is most frequently used to protect trees from *D. ponderosae* in the western United States. It is important to note that these and similar analyses do not address changes in the chemical stability of verbenone once released into the active airspace, which may influence levels of inhibition and consequently tree protection.

Inconsistent and/or Inadequate Release

Several authors have speculated that previous failures in effectiveness resulted from problems associated with the passive release of verbenone from bubble caps and pouches, which is controlled by ambient temperatures in conjunction with membrane composition and internal vapor pressure (Amman and Lindgren 1995, Holsten et al. 2002). Holsten et al. (2003) detailed the characteristics of an ideal pheromone release system: (1) release of consistent amounts of pheromone per unit time; (2) ability to release different pheromones; (3) ability to provide different release rates; (4) protection from environmental degradation; (5) release of all pheromones; and (6) time-specified release. They described beads, bubble caps, and pouches as first-order emitters whose release rates generally decline over time, which is commonly observed in laboratory studies. This may be undesirable because concentrations must be maintained at biologically active levels during the entire treatment interval.

Gibson and Kegley (2004) evaluated the release rate of verbenone pouches in *P. ponderosa* forests in Montana. During the first 53 days, release rates ranged from ∼38 to 80 mg/day, but at 63 days verbenone was no longer being released despite ∼1.9 g of verbenone remaining in the pouch (Gibson and Kegley 2004). Fettig et al. (2009) reported few meaningful differences in the release rates of unexposed and field-exposed pouches in *P. ponderosa* forests in California. During field exposure, temperatures ranged from −3.0 to 42° C, but pouches that were field-exposed for 4 weeks still maintained a target release rate of >50 mg/day for an additional 16 days in the laboratory at 30° C. Similarly, Fettig et al. (2012c) analyzed each component of Verbenone Plus [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (−)-verbenone] and reported that unexposed and field-exposed devices showed little decline in release rate, with the exception of the pouch containing green leaf volatiles [(*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] that had been deployed in the field for 8 weeks. In that case, release rates started to decline after 24 days at 25° C in the laboratory, and two of the three pouches ceased releasing material after a total of 87 days (8 weeks in the field plus 31 days in the laboratory). Laboratory tests have shown that verbenone flakes release for a longer period than earlier bead-type formulations (Holsten et al. 2002, Gillette et al. 2012a), perhaps because each laminated flake is essentially a reservoir with a relatively small surface area for release (i.e., along the edges of flakes), unlike the beads that had a coating of active ingredient that released from the surface (Gillette et al. 2012a). Studies concerning the release rate of SPLATVerb are ongoing (Fettig et al. 2012d).

Release rate data for select semiochemicals and release devices are available (USDA Forest Service 2010). Given the relatively short period (e.g., ∼2 months) in which the majority of *D. ponderosae* flight occurs in *P. contorta* forests, concerns regarding passive release do not appear to be well substantiated. Of course, distribution and concentration in the active airspace are mediated by meteorological conditions, microclimatic influences, and interaction with surfaces and aerosols in forests, which are heavily affected by stand structure and composition as noted above.

Levels of Inhibition

It is well established that verbenone inhibits the response of *D. ponderosae* to attractant-baited traps and that associated reductions in trap catch are substantial. For example, Lindgren and Miller (2002) reported that levels of verbenone >0.2 mg/day resulted in an almost complete shutdown of *D. ponderosae* attraction to its aggregation pheromone. Borden et al. (2004) reported that verbenone (1.8 mg/day) reduced catches of both male and female *D. ponderosae* by >97%. However, sensitivity to verbenone probably varies among populations and among individuals within a population, which is likely to influence levels of inhibition and thus tree protection (Borden et al. 1986).

Range of Inhibition

Miller (2002) found that verbenone bubble caps inhibited *D. ponderosae* attraction to baited multiple-funnel traps at a distance of <4 m in *P. contorta* forests in British Columbia. Fettig et al. (2009) reported similar results for *D. brevicomis* in *P. ponderosa* forests in

California, which is surprising, given the substantial differences among studies. In both cases, maximizing the effect of verbenone would require a substantial increase in the number of bubble caps or pouches typically deployed for stand protection (i.e., 4–5 times higher), which would probably be uneconomical under most scenarios. As discussed earlier, higher densities of small, point-source releasers (e.g., impregnated beads, flakes, or SPLAT) may provide for better dispersal patterns and higher reductions in levels of tree mortality than conventional release devices (Gillette et al. 2006).

Population Size

Lynch et al. (2006) noted that the population dynamics of *D. ponderosae* differed with the intensity of outbreaks. Similarly, it appears the effectiveness of verbenone for tree protection varies with population density. Progar (2003, 2005) examined the ability of verbenone pouches to protect stands of *P. contorta* in Idaho from infestation by *D. ponderosae* for the duration of an outbreak and reported that verbenone was very effective initially, but that the ability of the semiochemical to protect trees declined in subsequent years. The author hypothesized that the reduction in effectiveness over time was caused by the increase in beetle population size concurrent with the decrease in the abundance of preferred hosts. That is, in the early stages of a *D. ponderosae* outbreak, beetle populations increase partially because of the availability of large-diameter trees that afford a higher reproductive potential (*see* Host Finding and Selection), but as the outbreak progresses, the numbers of these trees decline, limiting selection to smaller-diameter trees and increasing the probability of attack on remaining large-diameter trees in adjacent areas treated with verbenone. *D. ponderosae* infestation of these trees indicates that a shift occurred in the mechanism of host selection in which the influence of verbenone as an inhibitor was reduced or ignored or possibly the beetles became habituated to verbenone, after which they may not respond to the semiochemical signal (Progar 2005). Bentz et al. (2005) reported reductions in the effectiveness of verbenone pouches when >140 *P. contorta* trees were infested per hectare the previous year. Similarly, Progar et al. (2013) found that in areas where *D. ponderosae* killed >20% of the available trees in a single year, verbenone pouches failed to provide adequate levels of tree protection.

The rapid expansion of *D. ponderosae* populations, either through growth or immigration, appears to be an important factor influencing the effectiveness of verbenone as a tree protectant (Progar et al. 2013). In addition, Amman and Lindgren (1995) indicated that large populations of beetles at the peak of an outbreak may not respond to verbenone (*see* Complexity of the Host Selection Process). This finding agrees with recent studies documenting an increase in effectiveness when brood tree removal (i.e., before the initiation of flight activity) was combined with the use of verbenone pouches (*see* Utilization for Protection of Small-Scale Stands) (Borden et al. 2007, Progar et al. 2013). Some authors have suggested that if >15% of trees are currently infested with *D. ponderosae*; verbenone treatments may not be effective without brood tree removal (Gibson 2009).

Most studies that evaluated the performance of inhibitors to protect trees from infestation by *D. ponderosae* were conducted for only a single season and therefore do not account for variations in beetle populations over time nor changes in beetle behavior that may be associated with the diminishing abundance of preferred host trees that occurs over the course of an outbreak. Studies are usually conducted during the early stages of an outbreak when populations are low, but increasing, and there are plenty of host trees available. More studies should be conducted for multiple years (or for the duration of an outbreak) to assess the performance of verbenone and other inhibitors under these conditions.

Ratio of Inhibitors to Attractants

Research has shown that the response of *D. ponderosae* to verbenone in the presence of aggregation pheromones and host kairomones often depends on the ratio of verbenone to attractants (Miller et al. 1995, Pureswaran et al. 2000) and varies among individuals within a population (Borden et al. 1986). Furthermore, the use of synthetic baits in experimental designs, which would be absent under natural conditions, probably provides a rigorous evaluation at the expense of detecting any subtle treatment effects (Borden et al. 2003, Fettig et al. 2009).

Development Costs and Small Market Conditions

Development of novel semiochemical-based tools and tactics involves risk and substantial investments in research and development. These are significant barriers to success for minor use crops, such as pines, where returns on investments are generally limited (e.g., compared with returns for agricultural systems).

Future Work
Applied Chemical Ecology

Significant advances have been made regarding the molecular biology and biochemistry of pheromone production in bark beetles, the synthesis of semiochemicals in the laboratory, the deployment of semiochemicals in the field, and the fate of semiochemicals once released into the active airspace of forests. However, significant research related to the applied chemical ecology of *D. ponderosae* remains to be addressed, including (1) improving the effectiveness and cost effectiveness of inhibitory blends, (2) determining the maximum range of inhibition, (3) redefining selection criteria for target areas where semiochemical-based treatments are likely to be most effective to achieve desired results, (4) improving the efficiency and cost-effectiveness of delivery systems, (5) examining the effects of forest structure and climate on semiochemical plumes, (6) expanding related research into understudied forest types, and (7) assessing semiochemical performance at varied levels of beetle population and host availability during the course of an outbreak. Further research in these areas is essential to the full development of semiochemical-based tools to reliably protect high-value forest resources. The results of a recent meta-analysis demonstrating the effectiveness of semiochemicals to reduce levels of tree mortality attributed to *D. ponderosae* and other bark beetles (Schlyter 2012) are encouraging and should spur additional research and development.

Development of Attractants

In recent years, researchers have concentrated on the development of inhibitors largely to the exclusion of attractants. Improvements in our understanding of the functioning and utility of attractants are important to develop our knowledge base and to assess tools and tactics for tree protection and are an important focus for future research. For example, the known attractants for *D. ponderosae* are generally assumed to be less attractive to beetles when deployed in traps than on trees that are being actively colonized by conspecifics. The reasons for this phenomenon are not entirely understood but warrant further study. Furthermore, the attractive blend may vary across the range of *D. ponderosae*, the release rates and ratios of

components may not be optimal, or the effect of synergistic host volatiles may vary among stands because of differences in host constitutive resins, host physiological status, or stand structure. There may also be important attractants relevant to the chemical ecology of *D. ponderosae* that remain to be discovered.

Combining Semiochemicals with Other Methods to Enhance Effectiveness

Integrated pest management (IPM) strategies that combine semiochemicals with other tactics may be more effective in reducing undesirable levels of tree mortality attributed to *D. ponderosae*. Promising results to date include the use of silvicultural and insecticidal methods (*see* Utilization of Attractants). For example, removal of competing attractants by harvesting trees containing live brood or beetles (sanitation) in addition to treatment with verbenone is the current IPM practice recommended for mitigating *D. ponderosae* infestations in *P. contorta* forests in the western United States.

Reducing the Cost of Synthetic Semiochemicals

Within the last 30 years, advances in the genetic engineering of microbes for the production of inexpensive, high-purity hydrocarbons has raised the possibility that enantiomerically pure and affordable bark beetle pheromones, notably verbenone but also other promising semiochemicals, will become widely available (Bernardt 2006, Keasling 2010). Cytochrome P-450 genes are a large and ubiquitous family of genes that code for proteins that can process a wide variety of chemical reactions, enabling the microbial redirection of metabolic pathways dubbed "metabolic engineering" that is used in commercial applications (Keasling 2010). Enzymatic processes derived from yeast and bacterial metabolic pathways have been developed to produce biofuels, pharmaceuticals, fragrances, and pheromones, including verbenone (Bell et al. 2003). In nature, the conversion of α-pinene to verbenone is accomplished via a two-step oxidation process yielding first either *trans-* or *cis-*verbenol, depending on the enantiomeric composition of the starting material, and then either (+)- or (−)-verbenone.

Cytochrome P-450 genes that code for the stepwise oxidation of α-pinene to verbenone have been cloned into the *Pseudomonas putida* Trevisan genome, a soil bacterium widely used in biotechnology for potential commercial production of specialty chemicals using inexpensive, available (+)- or (−)-α-pinene precursors (Bell et al. 2003). This development raises the possibility that very pure (+)- and (−)-verbenone may be economically produced. Recent advances in biotechnology describe microbial enzymatic production of 5-carbon alcohols that suggest the possibility of using even more readily available carbon sources in the future (Chou and Keasling 2012). Finally, research and development of bark beetle pheromones has long been constrained by issues surrounding the cost of active ingredients, but as more enzymatic processes become commercially viable, it is possible that even very costly semiochemicals may see further development for field applications.

Managing Expectations

Applications of insecticides to protect individual *P. contorta* from mortality attributed to *D. ponderosae* involve ground-based sprays of bifenthrin, carbaryl, or permethrin that often provide 100% tree protection if properly applied (Fettig et al. 2013). However, many sites (e.g., campgrounds) where bole sprays are frequently applied occur near intermittent or ephemeral streams, which limits insecticide applications owing to restrictions concerning the use of no-spray buffers to protect nontarget aquatic organisms (Fettig et al. 2013). Because of these and other restrictions, we feel it is inappropriate to compare the utility and effectiveness of insecticides for tree protection with that of semiochemicals as is commonly done. We should not expect semiochemical tactics to provide the same or similar levels of tree protection as insecticidal sprays; however, inhibitors nearly always yield reductions in levels of tree mortality in *P. contorta* (*see* Inhibitors) and may be applied more widely and with less restriction than insecticides. To appropriately manage expectations, further research is warranted to determine under what conditions inhibitors are likely to be most effective.

Conclusions

D. ponderosae is considered a major disturbance agent in forests throughout much of the western United States. Research on the development of semiochemical-based tools and tactics for management of *D. ponderosae* has progressed steadily since the late 1960s, resulting in development of treatments for monitoring and reducing levels of *D. ponderosae*-caused tree mortality at spatial scales ranging from individual trees to large-scale forest stands. The basic science that deciphered the olfactory cues *D. ponderosae* uses to locate and colonize hosts and also to regulate population density within individual hosts served as a sound and useful foundation to advance semiochemical research. This remains an active area of forest research with dynamic developments of new strategies, methods, products, and tactics spurred by the recent significance of *D. ponderosae* outbreaks. Recent developments with products for aerial application have provided tools that are appropriate for use over larger areas and sites that are inaccessible for hand-applied release devices. Other research directions include the development of new formulations for ground-based applications in the form of SPLAT-Verb and Verbenone Plus. An obstruction to acceptance of semiochemical-based management is the relatively high cost of semiochemical materials. Recent advances in microbial production of semiochemicals will enable production of less expensive, but purer semiochemicals.

Evaluation of possible tactics combining semiochemical strategies with IPM is a recent area of research. The behavioral response of *D. ponderosae* at differing population levels to semiochemical signals, whether aggregative or inhibitory, and to stand manipulation has been observed to vary in aggressiveness and is an area of research that has yet to be fully investigated. Attention should be directed toward integration of strategies and tactics that evaluate mitigation of *D. ponderosae*-caused tree mortality across all population levels and intensities. Continuing studies in this field will lead to the refinement of semiochemical-based tools and tactics for mitigating *D. ponderosae*-caused tree mortality, particularly in high-value areas.

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