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Review

Applied Chemical Ecology of the Western Pine Beetle, an Important Pest of Ponderosa Pine in Western North America

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Abstract: Western pine beetle (*Dendroctonus brevicomis* LeConte) is a major cause of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) mortality in western North America. Twenty-first century epidemics are among the largest in history and have affected hundreds of thousands of hectares. We synthesize literature on the chemical ecology of western pine beetle and on efforts to exploit our understanding of the western pine beetle-ponderosa pine system to reduce host tree losses. This literature dates back to the early 20th century and focuses on populations in California and Oregon, U.S., where western pine beetle exerts its largest impacts. Research in the 1960s–1970s yielded an effective semiochemical attractant (*exo*-brevicomin, frontalin, and myrcene) that helped inform understanding of the biology, ecology, and management of this species. Later, research focused on isolation and identification of semiochemical repellents. To date, Verbenone Plus (acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and verbenone) is the only semiochemical repellent demonstrated effective for protecting ponderosa pines from mortality attributed to western pine beetle in multiple studies in Canada and the U.S.

Keywords: attractant; *Dendroctonus brevicomis*; *Pinus ponderosa*; pheromone; repellent; semiochemical; verbenone; Verbenone Plus

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1. Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae) represent a large and diverse group of insects consisting of ~550 species in North America [1]. However, only ~20 species are important disturbance agents in conifer forests [2]. Trees of all species, ages, and sizes may be colonized and killed by bark beetles, but each species exhibits unique host preferences, life history traits, and impacts. Some species, such as California fivespined ips (*Ips paraconfusus* Lanier), primarily colonize stressed, dead, or dying host trees at small spatial scales (<100 ha). Other species, such as western pine beetle (*Dendroctonus brevicomis* LeConte), can kill large numbers of host trees over extensive areas (>100,000 ha) [2]. At endemic population levels, bark beetles create small gaps in the forest canopy by killing trees stressed by age, drought, defoliation, or other factors. This differs from epidemic population levels wherein timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, carbon storage, cultural resources, and endangered species, among other resources, may be affected [3].

Bark beetle epidemics develop when weather conducive to beetle survival and population growth (i.e., typically warm and dry weather) co-occurs with an abundance of susceptible host trees [4]. In recent years, this was demonstrated for several species, including western pine beetle, when large epidemics occurred in the central and southern Sierra Nevada, California, U.S. In the most heavily affected areas, ~49% of trees died

during 2014–2017 [5] (Figure 1). Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Pinales: Pinaceae) had the highest levels of mortality (~90%), which was concentrated in larger-diameter trees (>32 cm dbh, and a diameter of 1.37 m) and attributed primarily to western pine beetle [5]. Levels of tree mortality observed are considered by some experts to be unprecedented [6]. A decade earlier a notable western pine beetle epidemic occurred in the Transverse and Peninsula Ranges in southern California [7] where the majority of ponderosa and Coulter pines (*Pinus coulteri* D. Don), the two primary hosts, were killed. Tree mortality was >80% in some areas [8]. Western pine beetle occurs from British Columbia, Canada southward through parts of Washington, Oregon, Idaho, Nevada, Montana, and California, U.S. [9]. *Dendroctonus barberi* Hopkins occurs in eastern Nevada, Utah, Colorado, Arizona, New Mexico, and Texas, U.S., and Mexico. We caution the reader that *D. barberi* was synonymized with *D. brevicomis* in 1963 but was reinstated as a separate species in 2019 based on differences in morphological characteristics, chemical ecology, and other factors [10–13].

Figure 1. Tree mortality in the Sequoia National Forest, California, 2017. Most of the faded trees were colonized and killed by western pine beetle (*Dendroctonus brevicomis*) in 2016. Photo credit: C.J. Fettig, USDA Forest Service.

2. Host Finding, Host Selection, and Host Colonization

Bark beetles maintain limited energy reserves and are susceptible to adverse weather, starvation, and predation when searching for host trees. As such, it is important that bark beetles efficiently locate the correct habitat, correct tree species, and the most susceptible trees within these species [14,15]. During host finding and host selection, western pine beetle uses a combination of random landings, visual orientations, and direct assessments of hosts (and nonhosts) via olfactory and gustatory cues [16,17]. If the host is selected, pioneering (female) western pine beetles bore through the outer bark and initiate gallery construction in the phloem. Successful colonization of host trees may require overcoming formidable constitutive and induced physical and chemical defenses [18]. Healthy pines are capable of mobilizing large amounts of resin upon wounding of the tree by beetles. Pioneers are often killed by drowning or immobilization in resin that fills portions of the gallery and collects at the entrance hole (Figure 2). Smith [19] proposed that resistance of

ponderosa pine to western pine beetle could be calculated as a function of resin quantity and resin quality/attack density and beetle quality. At the time, he indicated that there were "no known reliable measures of beetle quality" but suggested that the prevalence of nematodes and/or variations in fecundity might serve as useful measures [19]. Resin terpenes are highly toxic to beetles at high vapor concentrations [20,21].

Figure 2. A western pine beetle (*Dendroctonus brevicomis*) killed in resin accumulated at the entrance hole, California. Photo credit: C.J. Fettig, USDA Forest Service.

Like most major tree-killing bark beetle species, western pine beetle uses a complex system of semiochemical communication in host location, host selection, host colonization, and mating behaviors (Table 1). Acoustic communication may also play a role [22] but has not been adequately studied. During the early stages of colonization, female western pine beetle release *exo*-brevicomin synthesized de novo, which in combination with host terpenes is attractive to conspecifics [23]. Frontalin, synthesized de novo by males [24], enhances attraction and facilitates mass attack (i.e., an adequate number of beetles to overcome host tree defenses) [25,26]. Both sexes orient upwind to these stimuli [27]. Verbenone, *trans*-verbenol, and ipsdienol are also produced by western pine beetle (Table 1) and inhibit the response of western pine beetle to aggregation pheromones thus reducing attraction to the host tree [28,29]. The relative abundance of these and other semiochemicals fluctuates during the colonization sequence (Table 1), with ratios influencing behavioral responses. There are one to four generations per year throughout most of the range. Voltinism may be increasing in some populations of western pine beetle due to warming attributed to climate change [30].

Table 1. Major semiochemicals associated with western pine beetle (*Dendroctonus brevicomis*) used in management and/or research.

Compound	Emitter	Response and Common Use (If Applicable)
Aggregation pheromones		
exo-Brevicomin	Female *D. brevicomis*	Signal [1] drawing in conspecifics of both sexes of *D. brevicomis*. Used in commercial trap lures and tree baits.
Frontalin	Male *D. brevicomis*	Signal that synergizes with the female-produced aggregation pheromone component drawing in conspecifics of both sexes of *D. brevicomis.* Used in commercial trap lures and tree baits.
Host volatiles		
Myrcene	*Pinus ponderosa*, *P. coulteri*, other pines	Cue [1] received by both sexes of *D. brevicomis*. Enhances attraction to aggregation pheromone components and likely involved in host recognition and confirmation. Used in commercial trap lures and tree baits.
Aggregation pheromones + host volatile		
exo-Brevicomin + frontalin + myrcene	Above	Highly effective attractant for both sexes of *D. brevicomis.* Useful as trapping lure and tree bait.
Antiaggregation pheromones		
Verbenone	Primarily male *D. brevicomis*, autoxidation of α-pinene, microbial sources	Signal and cue received by both sexes of *D. brevicomis* that inhibit aggregation behavior. Inhibits responses of male and female *D. brevicomis* to baited traps. Used in combination with other repellents for tree protection (experimental use only).
Ipsdienol	Male *Ips paraconfusus*, male *D. brevicomis*	Signal and cue received by both sexes of *D. brevicomis* that inhibits aggregation behavior. Inhibits responses of male and female *D. brevicomis* to baited traps.
trans-Verbenol	Primarily female *D. brevicomis*	Signal received by both sexes of *D. brevicomis* that inhibits aggregation behavior. Inhibits responses of male and female *D. brevicomis* to baited traps at high doses.
Nonhost volatiles		
Acetophenone	Common plant volatile, several *Dendroctonus* spp.	Cue (also potential signal) received by both sexes of *D. brevicomis* that inhibits aggregation behavior. Inhibits responses of male and female *D. brevicomis* to baited traps. Used in combination with other repellents for tree protection (experimental use only).
(*E*)-2-Hexenal	Angiosperm green leaf volatile	Cue received by both sexes of *D. brevicomis* that inhibits host-searching and aggregation behaviors.
(*E*)-2-Hexen-1-ol (*Z*)-2-Hexen-1-ol	Angiosperm green leaf volatile	Cues received by both sexes of *D. brevicomis* that inhibit host-searching and aggregation behaviors. Used in combination with other repellents for tree protection (experimental use only).
Benzaldehyde + benzyl alcohol + conophthorin + guaiacol + nonanal + salicylaldehyde	Angiosperm bark volatiles	Cues received by both sexes of *D. brevicomis* that inhibit host-searching and aggregation behaviors.
Verbenone Plus		
Verbenone + acetophenone + *E*-2-hexen-1-ol + *Z*-2-hexen-1-ol	Above	Signal and cues received by both sexes of *D. brevicomis* that inhibit host-searching and aggregation behaviors. Inhibits responses of male and female *D. brevicomis* to baited traps and baited trees. Used as tree protectant (experimental use only).

[1] Signal = produced by *D. brevicomis*; Cue = produced by other sources.

3. Management Tools and Tactics

Substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of tree mortality attributed to western pine beetle. Most of this work has focused on western pine beetle populations in California and Oregon where the beetle causes substantial host tree losses [9,31]. Much of the early knowledge gained was published in a seminal book, "Biology and Control of the Western Pine Beetle", by noted USDA Forest Service scientists J.M. Miller and F.P. Keen [31]. Direct control (suppression) involves short-term tactics designed to address current infestations and includes the use of insecticides (bole sprays and systemic injections), semiochemicals (attractants and repellents, as shown below), sanitation harvests, or a combination of these and other treatments. Indirect control (prevention) reduces the probability and severity of future infestations by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts, primarily through thinning and prescribed burning [32]. It is important to note that killing weakened trees is an important ecosystem function fulfilled by western pine beetle during endemic populations [9].

3.1. Semiochemical Attractants

In 1931, Person [33] suggested that aggregation of western pine beetle resulted from chemically mediated attraction. This was informed by his studies in California and Oregon on the beetle's preference for colonizing medium-large diameter ponderosa pines (~51–76 cm dbh) with small crowns [34]. He concluded that " . . . an initial weak attraction is due to the formation of volatile oils, such as aldehydes or esters, which are by-products of a respiratory fermentation or abnormal enzyme activity in subnormal trees. This attracts beetles from the immediate vicinity, these in turn introduce a yeast into the inner bark which produces a fermentation strong enough to attract other beetles from a wider radius." Substantial advances in understanding of bark beetle attraction have been made since the work of Person [34]. However, it was not until the mid-1960s that the first bark beetle pheromones were isolated and identified [35,36]. Today, commercial lures and baits containing the aggregation pheromones *exo*-brevicomin and frontalin and the host volatile myrcene are readily available and effective attractants for surveying and detecting western pine beetle populations and for inducing mass attacks [37] (Table 1). Semiochemical attractants are not registered with the U.S. Environmental Protection Agency or the Health Canada Pest Management Regulatory Agency.

3.1.1. Baited Traps for Survey, Detection, and Experimental Purposes

Baited traps are used for surveying and detecting western pine beetle and for monitoring of diurnal and seasonal flight for a variety of purposes [38], including timing of control tactics. Unbaited traps catch very few beetles (e.g., <1/d) even during severe epidemics. Baited traps are also commonly used in assays evaluating the effectiveness of semiochemical repellents for use as tree protectants (e.g., [39,40]). Baited traps should be placed >20 m from susceptible host trees to avoid spillover (i.e., a situation in which beetles are attracted to baited traps (or baited trees) but colonize adjacent host trees) (Figure 3), which may confound trap catches and result in undesirable tree mortality. It is important to note that studies in California have shown that the use of baited multiple-funnel traps is not effective for predicting future levels of tree mortality attributed to western pine beetle [41]. Higher doses of attractants generally result in higher trap catches [42] but increase the risk of spillover.

Predatory beetles such as *Temnoscheila chlorodia* (Mannerheim) (Coleoptera: Trogossitidae) and *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) are among the first insects to respond to ponderosa pines colonized by western pine beetle [43]. These and other natural enemies are likely important in regulating western pine beetle populations at endemic levels but not at epidemic levels [44]. Some predatory beetles are attracted to western pine beetle pheromones and may be captured and killed in large numbers in baited traps [45].

For example, Fettig and Dabney [46] described the abundance of bark beetle predators collected in 40 multiple-funnel traps baited with *exo*-brevicomin, frontalin, and myrcene in California over two years. A total of 32,903 *T. chlorodia*, 79 *E. lecontei*, and 12 *E. sphegeus* (F.) were collected. Caution should be taken to limit the bycatch of these and other natural enemies as much as possible when using baited traps [47,48]. For example, screen filters may be used to prevent the passage of predators larger than western pine beetle (e.g., *T. chlorodia* and *Enoclerus* spp.) into the collection cup.

Figure 3. A multiple-funnel trap baited with *exo*-brevicomin, frontalin, and myrcene to collect western pine beetles (*Dendroctonus brevicomis*) for experimental purposes, California. Photo credit: L.A. Mortenson, USDA Forest Service.

3.1.2. Mass Trapping for Population Suppression

Evaluating the effectiveness of mass trapping is difficult and hindered by the inability to accurately estimate bark beetle populations and to determine the effects of mass trapping on local populations. The first extensive study of mass trapping for suppression of western pine beetle was conducted in California in the early 1970s [49,50]. An area of ~65 km^2 was divided into two plots treated with baited sticky traps [51] and two untreated plots. Over 400,000 western pine beetles were collected. Ponderosa pine losses were higher in treated plots than in untreated plots the year (1970) treatments were implemented. The following year there was some evidence of population suppression based on declines in levels of ponderosa pine mortality. Despite this, mass trapping is not viewed as an effective control tactic for western pine beetle [52]. However, the use of modern tools (traps, baits, etc.) and technologies for mass trapping of western pine beetle have not been adequately studied. In general, the use of intelligent traps (e.g., those that release attractants at optimal rates and times of day) and/or remotely sensed data have not been adequately explored for mass trapping of bark beetles [53].

3.1.3. Baited Trap Trees for Population Suppression

Limited research has focused on the use of baited trap trees whereby living host trees are treated with an insecticide and then baited to induce the mortality of attacking

beetles. In California, Smith [54] demonstrated that treating the boles of ponderosa pines with carbaryl, lindane, permethrin, or deltamethrin and then inducing attack resulted in mortality of large numbers of western pine beetles (i.e., ~1075–5914 beetles/m^2 of bark surface). However, spillover effects were observed on adjacent (unbaited) ponderosa pines [54]. In addition, there are concerns regarding the effects of insecticides on nontarget invertebrates, specifically natural enemies that may be attracted to baited trap trees. The use of baited trap trees is not viewed as a viable control tactic [52].

3.1.4. Baited Trees for Snag Creation

Snags are important components of forest ecosystems providing feeding substrates, nesting and roosting sites, and habitats for a variety of vertebrate and invertebrate species. In some situations, forests may be snag deficient. A common technique to create snags is mechanical girdling with a chainsaw which prevents the transport of water and nutrients within the tree resulting in mortality of the tree. However, this technique is costly, laborious, and requires substantial personal protective equipment (PPE). In many conifer forests, snags can be created by placing baits on individual trees to induce colonization by bark beetles (Figure 4). Research suggests that snags created by baiting for western pine beetles are more biologically rich than those created by mechanical girdling with a chainsaw. For example, in California the number of emergence holes from wood-boring insects was ~16–20X higher on baited than girdled snags [55]. Six years after baiting, 44% of baited snags had woodpecker cavities, while no cavities were found in girdled snags [55]. When baiting trees to create snags, caution should be taken to avoid spillover. This can be achieved by regular monitoring of baited and surrounding trees and removal of baits once the baited tree has been adequately colonized (e.g., >75 attacks/m^2).

Figure 4. A ponderosa pine (*Pinus ponderosa*) snag created by baiting several years earlier, California. The parental "S-shaped" galleries of western pine beetle (*Dendroctonus brevicomis*) are still partially visible on the bole. Photo credit: C.J. Fettig, USDA Forest Service.

3.1.5. Baited Trees for Experimental Purposes

Tree baits may be used for a variety of experimental purposes. The most common purpose is baiting of host trees to test the efficacy of semiochemical repellents (e.g., [56–59]) or insecticides (e.g., [60,61]) for tree protection. It is rare for a high proportion (>30%) of unbaited host trees to be attacked by western pine beetles in any given year, and if trees are not baited investigators run the risk of few experimental trees being challenged (attacked) by beetles. Typically, repellents or insecticides (and a control) are randomly assigned to 20–30 trees per treatment and later baited with the goal of inducing attack by western pine beetles. Efficacy is based on comparisons of attack densities (e.g., by counting numbers of successful attacks (i.e., oxidized phloem material present in pitch tubes or points of attack containing boring dust and/or dry frass) and unsuccessful attacks (i.e., pitch tubes without oxidized phloem material)) and/or levels of tree mortality among treatments.

3.2. Semiochemical Repellents

Since the 1980s, the bulk of research on the applied chemical ecology of western pine beetle has focused on development of semiochemical repellents for tree protection. Bedard et al. [62] showed that verbenone reduced the number of western pine beetles collected in baited traps in California. Trap catches were further reduced by higher releases of verbenone [62–65], and by combining verbenone with ipsdienol [66]. Ipsdienol is produced by the male western pine beetle [67,68] and sympatric *Ips* and *Dendroctonus* spp. [69] (Table 1). Shea and Wentz [70] evaluated the effect of chirality on response of western pine beetle to verbenone in California and found that racemic and 97%-(–) verbenone were most effective in reducing attraction. It is assumed that in nature verbenone reduces intraspecific competition, and in some cases interspecific competition, by altering adult beetle behavior to minimize overcrowding of brood within the host tree [28,29]. Lindgren et al. [71] proposed that verbenone is an indicator of host tissue quality and that its quantity is a function of microbial degradation.

Verbenone was the focus of early research evaluating semiochemicals for tree protection. Bertram and Paine [72] reported that verbenone and ipsdienol significantly reduced numbers of western pine beetles landing on ponderosa pines and attack densities on ponderosa pines in California. Unfortunately, levels of tree mortality were not determined [72]. Verbenone applied to the stem of individual ponderosa pines in a flake formulation was ineffective at preventing western pine beetle colonization in California [73]. In Oregon, the effectiveness of 5 g and 7 g verbenone pouches, within an integrated approach that included infested tree removals (sanitation) and mass trapping, for protecting old-growth stands of ponderosa pine were inconclusive (J.L. Hayes, USFS, pers. comm. in [59]). Research in California also showed that 5 g verbenone pouches were ineffective [57]. No significant differences in the levels of western pine beetle-caused tree mortality or in the percentage of unsuccessfully attacked host trees were found between verbenone-treated and untreated plots (Figure 5). As such, verbenone (alone) is not considered effective for protecting individual ponderosa pines or stands of ponderosa pine from western pine beetle [52] (Table 1).

Zhang and Schlyter [74] introduced the semiochemical diversity hypothesis as one factor explaining why homogenous forest stands experience epidemics of insect pests more often than heterogeneous stands do. In the context of pest management, a diverse array of chemical cues and signals may disrupt bark beetles searching more than high doses of a single semiochemical (e.g., verbenone) or even mixtures of semiochemicals mimicking one type of signal (e.g., antiaggregation pheromones) because they represent heterogeneous stands. Poland et al. [39] examined the effects of nonhost angiosperm volatiles on western pine beetle attraction in British Columbia and reported that the green leaf aldehyde (*E*)-2-hexenal, and two green leaf alcohols (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol significantly reduced numbers of males caught in baited traps (Table 1). (*Z*)-2-Hexen-1-ol also reduced numbers of females (pioneers) caught in baited traps. Fettig et al. [40] reported that combinations of angiosperm bark volatiles (benzaldehyde, benzyl alcohol, (*E*)-

conophthorin, guaiacol, nonanal, and salicylaldehyde), green leaf volatiles ((*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol), or the nine compounds combined did not affect the response of western pine beetle to baited traps in California. However, when bark and green leaf volatiles were combined with verbenone trap catches were reduced to levels significantly below that of verbenone alone. No difference was observed between males and females [40]. A nine-component blend (benzyl alcohol, benzaldehyde, guaiacol, nonanal, salicylaldehyde, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol and verbenone) reduced trap catches by ~87% compared to the baited control (Figure 6). Based on this research, Fettig et al. [56] were first to demonstrate the successful application of semiochemical repellents for protecting ponderosa pine from mortality attributed to western pine beetle (Figure 7). Additional research confirmed the effect [58].

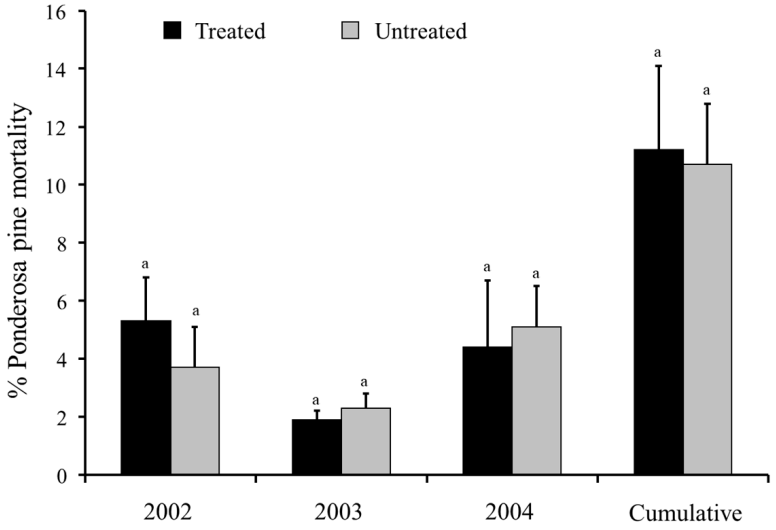

Figure 5. Mean percentages (+SEM) of ponderosa pines (*Pinus ponderosa*) killed by western pine beetle (*Dendroctonus brevicomis*) in verbenone-treated and untreated plots, California. Bars preceded by the same letter within year and cumulatively (2002–2004) are not significantly different ($p > 0.05$; Tukey's HSD). Adapted from Fettig et al. [57].

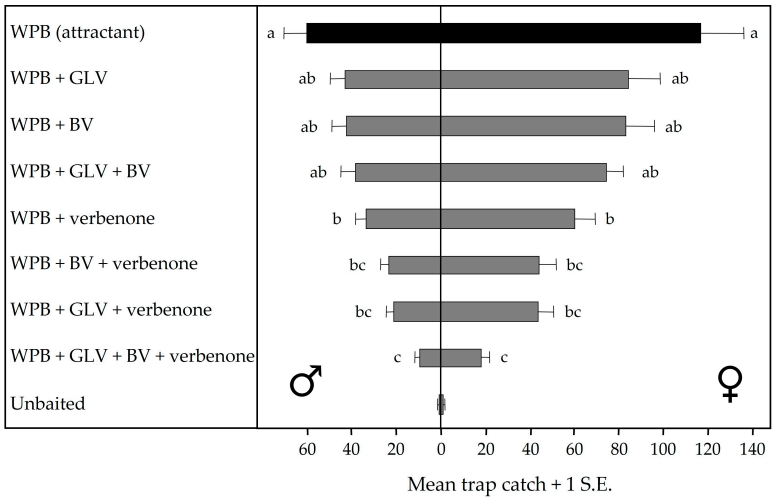

Figure 6. Daily captures of western pine beetle (*Dendroctonus brevicomis*) in multiple-funnel traps baited with an attractant (WPB), or with an attractant and green leaf volatile blend (GLV), bark volatile blend (BV), nonhost angiosperm volatile blend (GLV + BV), and verbenone, California. Bars preceded (for males) and followed (for females) by the same letter are not significantly different ($n = 30$; Tukey's HSD; $p > 0.05$). Adapted from Fettig et al. [40].

Figure 7. Fettig et al. [56] examined nonhost angiosperm volatiles and verbenone for protecting individual ponderosa pines (*Pinus ponderosa*) from western pine beetle (*Dendroctonus brevicomis*) in California. A combination of verbenone and nonhost angiosperm volatiles significantly reduced attack densities and mortality of baited trees. Components were formulated in four bubble-capsule bands based on similarity in chemical structure (i.e., alcohols, aldehydes, guaiacol (a phenol), and verbenone (a ketone)). This research informed development of Verbenone Plus in subsequent years [59]. Photo credit: C.J. Fettig, USDA Forest Service.

Fettig et al. [75] further examined the response of western pine beetle to several blends of nonhost angiosperm volatiles and verbenone in baited traps with the goal of improving the efficacy of their blend and reducing the number of components. They documented the inhibitory effect of a five-component blend (nonanal, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and verbenone), and later demonstrated that adding acetophenone [76,77] allowed the removal of the aldehydes (nonanal and (*E*)-2-hexenal) without compromising levels of inhibition. The resulting blend (acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and verbenone), "Verbenone Plus", has been demonstrated to inhibit the response of western pine beetle to baited traps and baited trees in multiple studies in California and British Columbia.

Related efforts to add acetophenone, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol to SPLAT® Verb (ISCA Technologies Inc., Riverside, CA, USA) (="SPLAT® Verbenone Plus") were ineffective for protecting stands of ponderosa pine from western pine beetle in California and Oregon (C.J.F. and R.A.P., unpubl. data) (Figure 8). SPLAT® Verb is a flowable, controlled-release emulsion [78] containing verbenone for management of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). It was registered by the U.S. Environmental Protection Agency for use on pines in 2013 [79]. An advantage of SPLAT® Verb is that, unlike other formulations that release semiochemicals through plastic membranes (i.e., requiring retrieval of release devices), SPLAT® Verb biodegrades in ~1–2 years under normal field conditions. A gas chromatograph with a flame ionization detector (GC-FID)

was used to quantify the amount of active ingredients (acetophenone, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and verbenone) remaining in samples of SPLAT® Verbenone Plus harvested from experimental plots after 60 d. (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol were nearly undetectable, indicating that sufficient releases of (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol were not maintained throughout the flight activity period of western pine beetle (C.J.F. et al., unpubl. data). Alternatives are being explored in the laboratory to increase the longevity of release of (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol within the SPLAT® matrix, but have not been evaluated in the field. The rheological properties of SPLAT® can be adjusted to create emulsions with a wide range of physical properties [78].

Figure 8. An early prototype of SPLAT® Verbenone Plus (acetophenone, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and verbenone; ISCA Technologies Inc., Riverside, CA, USA) applied to the bole of a ponderosa pine (*Pinus ponderosa*), California. Photo credit: C.J. Fettig, USDA Forest Service.

Several new semiochemical repellents were evaluated in trapping assays for western pine beetle in California and Idaho in 2022, but none appeared to be more effective than Verbenone Plus (C.S.H. et al., unpubl. data). Another tactic for managing bark beetles with semiochemicals is "push-pull," which causes beetles to disperse from a stand by combining semiochemical repellents within the stand (=push) with semiochemical attractants along the periphery of the stand (=pull) [37]. Push–pull has not been adequately studied for western pine beetle.

Verbenone Plus is the only semiochemical repellent that has been demonstrated to be effective for protecting ponderosa pines from mortality attributed to western pine beetle in multiple studies [80], but has yet to be commercialized. This is due, in part, to semiochemical repellents requiring registration with the U.S. Environmental Protection Agency and the Health Canada Pest Management Regulatory Agency. This takes time and is costly relative to the value of the marketplace (i.e., ponderosa pine is a minor-use crop with unpredictable fluctuations in western pine beetle populations). Efforts to develop Verbenone Plus for its use as a general bark beetle repellent, with the goal of increasing the marketplace, have been met with limited success. Verbenone Plus was only as effective as verbenone (alone) for protecting lodgepole pine (*Pinus contorta* Dougl. ex. Laws.) from mortality attributed to the mountain pine beetle in Idaho [81]. Furthermore, levels of inhibition were similar between Verbenone Plus and verbenone (alone) in trapping assays for pine engraver (*Ips pini* (Say)) in Arizona [82]. However, the addition of acetophenone, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol to MCH (3-methyl-2-cyclohexen-1-one), an antiaggregation pheromone of spruce beetle (*Dendroctonus rufipennis* Kirby), is promising for tree protection based on research in Wyoming, U.S. [83], with additional spruce beetle studies underway in Alaska, U.S., Colorado, and Utah (J.P.A. et al., unpubl. data).

4. Conclusions

Much progress has been made concerning the development of semiochemicals for management of bark beetles since discovery of the first bark beetle pheromone more than half a century ago. Some notable successes include effective repellents for Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins; MCH) and mountain pine beetle (verbenone) [37]. Since the early 2000s, MCH and verbenone have been applied to thousands of hectares of forest in western North America. Effective attractants for western pine beetle were identified in the 1960s–1970s, and their use in research has helped inform understanding of the biology, ecology, and management of western pine beetle. Unfortunately, development of an effective repellent for western pine beetle has been more challenging. It is our hope that with continued research, an effective semiochemical repellent will be commercialized as natural resource managers are increasingly challenged to limit host tree losses to western pine beetle and associated effects on a variety of resource objectives and ecosystem goods and services, a trend likely to continue in the future [4,84].

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References

1. Wood, S.L. *The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), A Taxonomic Monograph*; Brigham Young University: Provo, UT, USA, 1982.
2. Fettig, C.J.; Asaro, C.; Nowak, J.T.; Dodds, K.J.; Gandhi, K.J.K.; Moan, J.E.; Robert, J. Trends in bark beetle impacts in North America during a period (2000–2020) of rapid environmental change. *J. For.* **2022**, *120*, 693–713. [CrossRef]
3. Morris, J.L.; Cottrell, S.; Fettig, C.J.; DeRose, R.J.; Mattor, K.M.; Carter, V.A.; Clear, J.; Clement, J.; Hansen, W.D.; Hicke, J.A.; et al. Bark beetles as agents of change in social-ecological systems. *Front. Ecol. Environ.* **2018**, *16*, S34–S43. [CrossRef]
4. Bentz, B.J.; Régnière, J.; Fettig, C.J.; Hansen, E.M.; Hayes, J.L.; Hicke, J.A.; Kelsey, R.G.; Negrón, J.F.; Seybold, S.J. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* **2010**, *60*, 602–613. [CrossRef]
5. Fettig, C.J.; Mortenson, L.A.; Bulaon, B.M.; Foulk, P.B. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For. Ecol. Manag.* **2019**, *432*, 164–178. [CrossRef]
6. Stephens, S.L.; Collins, B.M.; Fettig, C.J.; Finney, M.A.; Hoffman, C.E.; Knapp, E.E.; North, M.E.; Safford, H. Drought, tree mortality, and wildfire in forests adapted to frequent fire. *Bioscience* **2018**, *68*, 77–88. [CrossRef]
7. Fettig, C.J. Socioecological impacts of the western pine beetle outbreak in southern California: Lessons for the future. *J. For.* **2019**, *117*, 138–143. [CrossRef]
8. Walker, R.; Rosenberg, M.; Warbington, R.; Schwind, B.; Beardsley, D.; Ramirez, C.; Fischer, L.; Frerich, B. Inventory of Tree Mortality in Southern California Mountains (2001–2004) Due to Bark Beetle Impacts. 2006. Available online: https://qcpages.qc.cuny.edu/~cyi/Michelle-Park-papers/Walker%20et%20al.,%202006.pdf (accessed on 9 March 2023).
9. Homicz, C.S.; Fettig, C.J.; Munson, A.S.; Cluck, D.R. *Western Pine Beetle*; FS-1192; U.S. Department of Agriculture, Forest Service: Portland, OR, USA, 2022.
10. Valerio-Mendoza, O.; Armendáriz-Toledano, F.; Cuéllar-Rodríguez, G.; Negrón, J.F.; Zúñiga, G. The current status of the distribution range of the western pine beetle, *Dendroctonus brevicomis* (Curculionidae: Scolytinae) in Northern Mexico. *J. Insect Sci.* **2017**, *17*, 92. [CrossRef]
11. Valerio-Mendoza, O.; García-Román, J.; Becerril, M.; Armendáriz-Toledano, F.; Cuéllar-Rodríguez, G.; Negrón, J.F.; Sullivan, B.T.; Zúñiga, G. Cryptic species discrimination in western pine beetle, *Dendroctonus brevicomis* LeConte (Curculionidae: Scolytinae), based on morphological characters and geometric morphometrics. *Insects* **2019**, *10*, 377. [CrossRef]
12. Sullivan, B.T.; Grady, A.M.; Hofstetter, R.W.; Pureswaran, D.S.; Brownie, C.; Cluck, D.R.; Coleman, T.W.; Graves, A.; Willhite, E.; Spiegel, L.; et al. Evidence for semiochemical divergence between sibling bark beetle species: *Dendroctonus brevicomis* and *Dendroctonus barberi*. *J. Chem. Ecol.* **2021**, *47*, 10–27. [CrossRef]

13. Armendáriz-Toledano, F.; Zúñiga, G. Illustrated key to species of genus *Dendroctonus* (Coleoptera: Curculionidae) occurring in Mexico and Central America. *J. Insect Sci.* **2017**, *17*, 34. [CrossRef]
14. Byers, J.A. Host-tree chemistry affecting colonization in bark beetles. In *Chemical Ecology of Insects 2*; Carde, R.T., Bell, W.J., Eds.; Springer: Boston, MA, USA, 1995; pp. 154–213.
15. Borden, J.H. Disruption of semiochemical-mediated aggregation in bark beetles. In *Insect Pheromone Research*; Carde, R.T., Minks, A.K., Eds.; Springer: Boston, MA, USA, 1997; pp. 421–438.
16. Strom, B.L.; Goyer, R.A.; Shea, P.J. Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. *Entomol. Exp. Appl.* **2001**, *100*, 63–67. [CrossRef]
17. Huber, D.P.W.; Fettig, C.J.; Borden, J.H. Disruption of coniferophagous bark beetle (Coleoptera: Curculionidae: Scolytinae) mass attack using angiosperm nonhost volatiles: From concept to operational use. *Can. Entomol.* **2021**, *153*, 19–35. [CrossRef]
18. Franceschi, V.R.; Krokene, P.; Christiansen, E.; Krekling, T. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* **2005**, *167*, 353–376. [CrossRef] [PubMed]
19. Smith, R.H. Formula for describing effect of insect and host tree factors on resistance to western pine beetle attack. *J. Econ. Entomol.* **1975**, *68*, 841–844. [CrossRef]
20. Smith, R.H. Effect of monoterpene vapors on the western pine beetle. *J. Econ. Entomol.* **1965**, *58*, 509–510. [CrossRef]
21. Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. Pine monoterpenes and pine bark beetles: A marriage of convenience for defense and chemical communication. *Phytochem. Rev.* **2006**, *5*, 143–178. [CrossRef]
22. Bedoya, C.L.; Hofstetter, R.W.; Nelson, X.J.; Hayes, M.; Miller, D.R.; Brockerhoff, E.G. Sound production in bark and ambrosia beetles. *Bioacoustics* **2021**, *30*, 58–73. [CrossRef]
23. Bedard, W.D.; Tilden, P.E.; Wood, D.L.; Silverstein, R.M.; Brownlee, R.G.; Rodin, J.O. Western pine beetle: Field response to its sex pheromone and a synergistic host terpene, myrcene. *Science* **1969**, *164*, 1284–1285. [CrossRef]
24. Kinzer, G.W.; Fentiman, A.F.; Page, T.F.; Foltz, R.L.; Vité, J.P.; Pitman, G.B. Bark beetle attractants: Identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. *Nature* **1969**, *221*, 477–478. [CrossRef]
25. Wood, D.L. Selection and colonization of ponderosa pine by bark beetles. In *Insect/Plant Relationships, Symposia of the Royal Entomological Society of London, Vol. 6*; Emden van, F., Ed.; Blackwell Scientific: Oxford, UK, 1972; pp. 101–117.
26. Bedard, W.D.; Lindahl, K.Q., Jr.; Tilden, P.E.; Wood, D.L. Behavior of the western pine beetle during host colonization. *J. Chem. Ecol.* **1985**, *11*, 1249–1261. [CrossRef]
27. Byers, J.A. Upwind flight orientation to pheromone in western pine beetle tested with rotating wind vane traps. *J. Chem. Ecol.* **1988**, *14*, 189–198. [CrossRef] [PubMed]
28. Byers, J.A.; Wood, D.L. Interspecific inhibition of the response of the bark beetles *Dendroctonus brevicomis* and *Ips paraconfusus* to their pheromones in the field. *J. Chem. Ecol.* **1980**, *6*, 149–164. [CrossRef]
29. Byers, J.A.; Wood, D.L.; Craig, J.; Hendry, L.B. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: Regulation of inter- and intraspecific competition. *J. Chem. Ecol.* **1984**, *10*, 861–877. [CrossRef]
30. Robbins, Z.J.; Xu, C.; Aukema, B.H.; Buotte, P.C.; Chitra-Tarak, R.; Fettig, C.J.; Goulden, M.L.; Goodsman, D.W.; Hall, A.D.; Koven, C.D.; et al. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. *Glob. Change Biol.* **2022**, *28*, 509–523. [CrossRef]
31. Miller, J.M.; Keen, P.P. *Biology and Control of the Western Pine Beetle*; Misc. Publ. 800; U.S. Department of Agriculture, Forest Service: Washington, DC, USA, 1960.
32. Fettig, C.J.; Hilszczański, J. Management strategies for bark beetles in conifer forests. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*; Vega, F.E., Hofstetter, R.W., Eds.; Academic Press: London, UK, 2015; pp. 555–584. [CrossRef]
33. Person, H.L. Theory in explanation of the selection of certain trees by the western pine beetle. *J. For.* **1931**, *29*, 696–699. [CrossRef]
34. Person, H.L. Tree selection by the western pine beetle. *J. For.* **1928**, *26*, 564–578. [CrossRef]
35. Silverstein, R.M.; Rodin, J.O.; Wood, D.L. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* **1966**, *154*, 509–510. [CrossRef]
36. Renwick, J.A. Identification of two oxygenated terpenes from the bark beetles, *Dendroctonus frontalis* and *Dendroctonus brevicomis*. *Contrib. Boyce Thompson Inst.* **1967**, *23*, 355–360.
37. Seybold, S.J.; Bentz, B.J.; Fettig, C.J.; Lundquist, J.E.; Progar, R.A.; Gillette, N.E. Management of western North American bark beetles with semiochemicals. *Annu. Rev. Entomol.* **2018**, *63*, 407–432. [CrossRef]
38. Fettig, C.J.; Shea, P.J.; Borys, R.R. Spatial and temporal distributions of four bark beetle species (Coleoptera: Scolytidae) along two elevational transects in the Sierra Nevada. *Pan-Pac. Entomol.* **2005**, *81*, 6–19.
39. Poland, T.M.; Borden, J.H.; Stock, A.J.; Chong, L.J. Green leaf volatiles disrupt responses by the spruce beetle, *Dendroctonus rufipennis*, and the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae) to attractant-baited traps. *J. Entomol. Soc. Brit. Columbia* **1998**, *95*, 17–24.
40. Fettig, C.J.; McKelvey, S.R.; Huber, D.P.W. Nonhost angiosperm volatiles and verbenone disrupt response of western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to attractant-baited traps. *J. Econ. Entomol.* **2005**, *98*, 2041–2048. [CrossRef] [PubMed]
41. Hayes, C.J.; Fettig, C.J.; Merrill, L.D. Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. *J. Econ. Entomol.* **2009**, *102*, 2170–2182. [CrossRef] [PubMed]

42. Tilden, P.E.; Bedard, W.D.; Lindahl, K.Q.; Wood, D.L. Trapping *Dendroctonus brevicomis*: Changes in attractant release rate, dispersion of attractant, and silhouette. *J. Chem. Ecol.* **1983**, *9*, 311–321. [CrossRef]
43. Stephen, F.M.; Dahlsten, D.L. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. *Can. Entomol.* **1976**, *108*, 283–304. [CrossRef]
44. Wegensteiner, R.; Wermelinger, B.; Herrmann, M. Natural enemies of bark beetles: Predators, parasitoids, pathogens, and nematodes. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*; Vega, F.E., Hofstetter, R.W., Eds.; Academic Press: London, UK, 2015; pp. 247–304. [CrossRef]
45. Pitman, G.B.; Vité, J.P. Predator-prey response to western pine beetle attractants. *J. Econ. Entomol.* **1971**, *64*, 402–404. [CrossRef]
46. Fettig, C.J.; Dabney, C.P. Seasonal abundance of Temnochila chlorodia (Mannerheim) (Coleoptera: Trogossitidae) collected in western pine beetle pheromone-baited traps in northern California. *J. Entomol. Sci.* **2006**, *41*, 75–83. [CrossRef]
47. Aukema, B.H.; Dahlsten, D.L.; Raffa, K.F. Improved population monitoring of bark beetles and predators by incorporating disparate behavioral responses to semiochemicals. *Environ. Entomol.* **2000**, *29*, 618–629. [CrossRef]
48. Ross, D.W.; Daterman, G.E. Pheromone-baited traps for *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae): Influence of selected release rates and trap designs. *J. Econ. Entomol.* **1998**, *91*, 500–506. [CrossRef]
49. DeMars, C.J.; Slaughter, G.W.; Bedard, W.D.; Norick, N.X.; Roettgering, B. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. *J. Chem. Ecol.* **1980**, *6*, 853–860. [CrossRef]
50. Smith, R.H. *Direct Control of Western Pine Beetle (Dendroctonus brevicomis LeConte): Review and Assessment*; PSW-GTR-121; U.S. Department of Agriculture, Forest Service: Berkeley, CA, USA, 1990. [CrossRef]
51. Browne, L.W. A trapping system for the western pine beetle using attractive pheromones. *J. Chem. Ecol.* **1978**, *4*, 261–275. [CrossRef]
52. Fettig, C.J. Native bark beetles and wood borers in Mediterranean forests of California. In *Insects and Diseases of Mediterranean Forest Systems*; Lieutier, F., Paine, T.D., Eds.; Springer International Publishing: Cham, Switzerland, 2016; pp. 499–528.
53. Hlásny, T.; König, L.; Krokene, P.; Lindner, M.; Montagné-Huck, C.; Müller, J.; Qin, H.; Raffa, K.F.; Schelhaas, M.J.; Svoboda, M.; et al. Bark beetle outbreaks in Europe: State of knowledge and ways forward for management. *Curr. Forestry Rep.* **2021**, *7*, 138–165. [CrossRef]
54. Smith, R.H. *Trapping Western Pine Beetles With Baited Toxic Trees*; PSW-RN-382; U.S. Department of Agriculture, Forest Service: Berkeley, CA, USA, 1986. [CrossRef]
55. Shea, P.J.; Laudenslayer, W.F., Jr.; Ferrell, G.; Borys, R. Girdled versus bark beetle-created ponderosa pine snags: Utilization by cavity-dependent species and differences in decay rate and insect diversity. In *Proceedings of the Symposium Ecology and Management of Dead Wood in Western Forests*; PSW-GTR-181; U.S. Department of Agriculture, Forest Service: Berkeley, CA, USA, 2002; pp. 145–153.
56. Fettig, C.J.; Dabney, C.P.; McKelvey, S.R.; Huber, D.P.W. Nonhost angiosperm volatiles and verbenone protect individual ponderosa pines from attack by western pine beetle and red turpentine beetle (Coleoptera: Curculionidae, Scolytinae). *W. J. Appl. For.* **2008**, *23*, 40–45. [CrossRef]
57. Fettig, C.J.; McKelvey, S.R.; Borys, R.R.; Dabney, C.P.; Hamud, S.M.; Nelson, L.J.; Seybold, S.J. Efficacy of verbenone for protecting ponderosa pine stands from western pine beetle (Coleoptera: Curculionidae: Scolytinae) attack in California. *J. Econ. Entomol.* **2009**, *102*, 1846–1858. [CrossRef]
58. Fettig, C.J.; McKelvey, S.R.; Dabney, C.P.; Borys, R.R.; Huber, D.P.W. Response of *Dendroctonus brevicomis* to different release rates of nonhost angiosperm volatiles and verbenone in trapping and tree protection studies. *J. Appl. Entomol.* **2009**, *133*, 143–154. [CrossRef]
59. Fettig, C.J.; McKelvey, S.R.; Dabney, C.P.; Huber, D.P.W.; Lait, C.G.; Fowler, D.L.; Borden, J.H. Efficacy of "Verbenone Plus" for protecting ponderosa pine trees and stands from *Dendroctonus brevicomis* (Coleoptera: Curculionidae) attack in British Columbia and California. *J. Econ. Entomol.* **2012**, *105*, 668–1680. [CrossRef] [PubMed]
60. 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.; et al. Effectiveness of bifenthrin (Onyx™) and carbaryl (Sevin® SL) for protecting individual, high-value trees from bark beetle attack (Coleoptera: Curculionidae: Scolytinae) in the western United States. *J. Econ. Entomol.* **2006**, *99*, 1691–1698. [CrossRef]
61. Grosman, D.M.; Fettig, C.J.; Jorgensen, C.L.; Munson, A.S. Effectiveness of two systemic insecticides for protecting western conifers from mortality due to bark beetle attack. *W. J. Appl. For.* **2010**, *25*, 181–185. [CrossRef]
62. Bedard, W.D.; Tilden, P.E.; Lindahl, K.Q., Jr.; Wood, D.L.; Rauch, P.A. Effects of verbenone and trans-verbenol on the response of *Dendroctonus brevicomis* to natural and synthetic attractant in the field. *J. Chem. Ecol.* **1980**, *6*, 997–1013. [CrossRef]
63. Bedard, W.D.; Wood, D.L.; Tilden, P.E.; Lindahl, K.Q., Jr.; Silverstein, R.M.; Rodin, J.O. Field response of the western pine beetle and one of its predators to host- and beetle-produced compounds. *J. Chem. Ecol.* **1980**, *6*, 625–641. [CrossRef]
64. Tilden, P.E.; Bedard, W.D. Effect of verbenone on response of *Dendroctonus brevicomis* to *exo*-brevicomin, frontalin, and myrcene. *J. Chem. Ecol.* **1988**, *14*, 113–122. [CrossRef] [PubMed]
65. Bertram, S.L.; Paine, T.D. Response of *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae) to different release rates and ratios of aggregation semiochemicals and the inhibitors verbenone and ipsdienol. *J. Chem. Ecol.* **1994**, *20*, 2931–2941. [CrossRef] [PubMed]

66. Paine, T.D.; Hanlon, C.C. Response of *Dendroctonus brevicomis* and *Ips paraconfusus* (Coleoptera: Scolytidae) to combinations of synthetic pheromone attractants and inhibitors verbenone and ipsdienol. *J. Chem. Ecol.* **1991**, *17*, 2163–2176. [CrossRef]
67. Byers, J.A. Male-specific conversion of the host plant compound, myrcene, to the pheromone, (+)-ipsdienol, in the bark beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* **1982**, *8*, 363–371. [CrossRef]
68. Seybold, S.J.; Teale, S.A.; Wood, D.L.; Zhang, A.; Webster, F.X.; Lindahl, K.Q.; Kubo, I. The role of lanierone in the chemical ecology of *Ips pini* (Coleoptera: Scolytidae) in California. *J. Chem. Ecol.* **1992**, *18*, 2305–2309. [CrossRef]
69. Borden, J.H. Aggregation pheromones. In *Comprehensive Insect Physiology, Biochemistry & Pharmacology, Vol. 9*; Kerkut, G.A., Gilbert, L.I., Eds.; Pergamon Press: Oxford, UK, 1985; pp. 257–285.
70. Shea, P.J.; Wenz, J.M. Bark beetle research in California. In *Proceedings of the Symposium on Management of Western Bark Beetles with Pheromones: Research and Development*; GTR-PSW-150; Shea, P.J., Ed.; U.S. Department of Agriculture, Forest Service: Berkeley, CA, USA, 2004; pp. 46–52.
71. Lindgren, B.S.; Nordlander, G.; Birgersson, G. Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). J. Appl. Entomol. 1996, 120, 397–403. [CrossRef]
72. Bertram, S.L.; Paine, T.D. Influence of aggregation inhibitors (verbenone and ipsdienol) on landing and attack behavior of *Dendroctonus brevicomis* (Coleoptera: Scolytidae). *J. Chem. Ecol.* **1994**, *20*, 1617–1629. [CrossRef] [PubMed]
73. Gillette, N.E.; Stein, J.D.; Owen, D.R.; Webster, J.N.; Fiddler, G.O.; Mori, S.R.; Wood, D.L. Verbenone-releasing flakes protect individual Pinus contorta trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). *Agric. For. Entomol.* **2006**, *8*, 243–251. [CrossRef]
74. Zhang, Q.-H.; Schlyter, F. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agric. For. Entomol.* **2004**, *6*, 1–20. [CrossRef]
75. Fettig, C.J.; McKelvey, S.R.; Dabney, C.P.; Huber, D.P.W. Responses of *Dendroctonus brevicomis* (Coleoptera: Curculionidae) in behavioral assays: Implications to development of a semiochemical-based tool for tree protection. *J. Econ. Entomol.* **2012**, *105*, 149–160. [CrossRef]
76. Erbilgin, N.; Gillette, N.E.; Mori, S.R.; Stein, J.D.; Owen, D.R.; Wood, D.L. Acetophenone as an anti-attractant for the western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae). *J. Chem. Ecol.* **2007**, *33*, 817–823. [CrossRef]
77. Erbilgin, N.; Gillette, N.E.; Owen, D.R.; Mori, S.R.; Nelson, A.S.; Uzoh, F.; Wood, D.L. Acetophenone superior to verbenone for reducing attraction of western pine beetle *Dendroctonus brevicomis* to its aggregation pheromone. *Agric. For. Entomol.* **2008**, *10*, 433–441. [CrossRef]
78. Mafra-Neto, A.; de Lame, F.M.; Fettig, C.J.; Munson, A.S.; Perring, T.M.; Stelinski, L.L.; Stoltman, L.; Mafra, L.E.J.; Borges, R.; Vargas, R.I. Manipulation of insect behavior with Specialized Pheromone & Lure Application Technology (SPLAT®). In *Pest Management with Natural Products*; Beck, J., Coats, J., Duke, S., Koivunen, M., Eds.; American Chemical Society: Washington, DC, USA, 2013; pp. 31–58.
79. Fettig, C.J.; Munson, A.S.; Reinke, M.; Mafra-Neto, A. A novel semiochemical tool for protecting lodgepole pine from mortality attributed to mountain pine beetle (Coleoptera: Curculionidae). *J. Econ. Entomol.* **2015**, *108*, 173–182. [CrossRef]
80. Borden, J.H. Management of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) with semiochemicals: Letter to a prospective graduate student. *Can. Entomol.* **2021**, *153*, 13–18. [CrossRef]
81. Fettig, C.J.; Munson, A.S. Efficacy of verbenone and a blend of verbenone and nonhost volatiles for protecting lodgepole pine from mountain pine beetle (Coleoptera: Curculionidae). *Agric. For. Entomol.* **2020**, *22*, 373–378. [CrossRef]
82. Gaylord, M.A.; Audley, J.P.; McMillin, J.D.; Fettig, C.J. Acetophenone and green leaf volatiles do not enhance the efficacy of verbenone for inhibiting attraction of *Ips pini* (Coleoptera: Curculionidae) to pheromone-baited traps in northern Arizona. *J. Econ. Entomol.* **2023**, *6*, toad016. [CrossRef]
83. Audley, J.P.; Fettig, C.J.; Munson, A.S.; Blackford, D.C.; Mortenson, L.A.; Mafra-Neto, A. MCH-based semiochemical repellents for protecting Engelmann spruce trees from *Dendroctonus rufipennis* (Coleoptera: Curculionidae). *J. Econ. Entomol.* **2022**, *115*, 187–192. [CrossRef] [PubMed]
84. Robbins, Z.; Xu, C.; Jonko, A.; Chitra-Tarak, R.; Fettig, C.J.; Costanza, J.; Mortenson, L.A.; Aukema, B.H.; Kueppers, L.M.; Scheller, R.M. Carbon stored in live ponderosa pines in the Sierra Nevada will not return to pre-drought (2012) levels during the 21st century due to bark beetle outbreaks. *Front. Environ. Sci.* **2023**, *11*, 1112756. [CrossRef]