

Review

Composition of Attractant Semiochemicals of North American Species of *Dendroctonus* Bark Beetles: A Review

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Abstract: The 19 species of *Dendroctonus* bark beetles native to North America include several of the most significant biotic mortality agents of conifers in this region, and they have impacted millions of hectares of forest in recent decades. Semiochemical attractants play several vital roles in the biology of these insects including host finding, host assessment, and mate finding. They are key to the virulence of these insects, since they mediate the mass attacks that enable killing and reproduction within healthy trees. These attractants consist of combinations of thirteen identified pheromone components in three primary chemical classes and at least ten host-associated compounds dominated by monoterpene hydrocarbons in host defensive resin. Due to their potential for use in pest management technologies, semiochemical attractants for *Dendroctonus* have received extensive research into their chemical compositions and effects on insect behavior. This paper is intended as a synthesis of this research over the past 60 years as well as a critical examination of approaches to investigation of this topic and interpretation of experimental results. Its purpose is to assist practitioners in formulating suitable attractive lures for use in applications and identify gaps in knowledge of the semiochemistry of *Dendroctonus* that should be addressed if the practical potential of attractants is to be fully realized.

Keywords: pheromone; kairomone; bark beetle; monoterpene; host location; aggregation; conifer



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1. Introduction

The bark beetle genus *Dendroctonus* (Curculionidae: Scolytinae) includes some of the most destructive native insect pests of conifer forests in North America [1,2]. In the last 30 years, they have impacted millions of hectares of forestland [3,4], having major economic and social consequences [5–8] and producing long-term impacts on ecosystems and their services [9–13]. For dispersing bark beetles, long-range attractive chemical signals can mediate a range of critical life activities including host location, host assessment, mass-aggregation, and mate location [14–17]. Importantly, attractants that mediate mass-aggregation are essential to the ability of the more aggressive species to colonize healthy trees [18,19], since only with sufficient numbers of attacks can the beetles neutralize the resin defenses of vigorous hosts [20,21]. Due to the potential of semiochemicals to alter bark beetle behavior in beneficial ways, there have been extensive efforts to incorporate synthetic semiochemicals into technologies for pest management [22–24]. Bark beetle attractants are used for delimiting the range of individual species [25,26], assessing diversity of bark beetles and their natural enemies [27–29], detecting inadvertent introductions of exotic pest species [30–33], forecasting beetle population trends [34–36], mass trapping and “trap tree” procedures for population reduction [37–40], “push-pull” tactics with both attractants and repellants for protecting resource patches [39,41,42], creating snags for wildlife habitat [43,44], and addressing a wide range of research questions. The following review is intended as a compilation and integration of nearly 60 years of published studies aimed at identifying compounds for attracting North American *Dendroctonus* species when in flight. The review will also summarize and provide a critical assessment of

procedures used for identifying attractants and characterizing their behavioral influence on *Dendroctonus* and other bark beetles.

2. Natural Sources of Attractants in *Dendroctonus*

Semiochemical attractants for *Dendroctonus* consist of both pheromones (compounds released by the beetles for interactions with conspecifics) and kairomones (compounds released by other organisms including host trees, associated species of bark beetles, and microorganisms) [14,19]. Bark beetles generate pheromone components in their fat body and midgut tissues, accumulate them in their alimentary tract, and release them from their anus [45–47]. Some species emerge and arrive on the host tree with attractive pheromone components already in their gut [48–50], and these compounds can be released prior to feeding [51,52]. However, entry into the host may be necessary for the production and release of some or all attractive pheromone components or may alter quantities of those already being produced [51,53,54]. For beetles initiating galleries, pheromone is mixed with excrement and expelled from the gallery entrance along with borings (frass) [55,56]. Released pheromone components may have either attractive or repellant (or attraction-inhibiting) effects, and both types of pheromone components may be released simultaneously or sequentially [48,54]. Females are the gallery-initiating (“pioneer”) sex in *Dendroctonus* and release pheromone components that are attractive to males and sometimes to both sexes. Males may release their own pheromone components following arrival on the host or pairing with a female, and these may be the same or different from the female pheromone components. Pheromones of other bark beetle species may also be a source of attractants (as kairomones), either when the emitting species utilizes some of the same pheromone components of the receiving species [57–59], or when the responding species has evolved the capacity to “eavesdrop” on heterospecific pheromones for the purpose of orienting toward and exploiting a host resource located by the emitting species [60–63].

The most abundant and diverse host odors known to influence *Dendroctonus* attraction are the volatile components of the constitutive resin of host trees, whose composition is dominated by monoterpenes [64–66]. These fragrant volatiles evaporate from the resin expelled into breaches of the phloem tissue and sapwood of living trees caused by insect attacks as well as damage to the bole and branches from weather disturbances and forest management operations [67–69]. Fire damage and disease may also result in resin exudation through the bark or from fungal cankers [70–72]. Resin volatiles are concentrated in pitch tubes formed at beetle gallery entrances and in bark beetle frass [73,74]. They are also released continuously in significant quantities from healthy trees and contribute to the odor background in forests [72,75]. Resin exudation represents the “first line” of defenses against bark beetle colonization, as rapid release into beetle attacked tissue can flush beetles out or kill them through entrapment or toxic effects [21,76–78]. Despite being major impediments to host colonization and agents of beetle mortality, these compounds can be strong attractants or attractant pheromone synergists for dispersing bark beetles including *Dendroctonus* [64,79–81]. The composition and concentrations of resin odors may function as long-range indicators of host location, taxon, suitability, and susceptibility [82–85]. Ethanol is an attractive compound for at least three species of *Dendroctonus*. This host compound is released by trees placed under stress by factors such as fire, flooding, disease, and drought [86–90] and, as such, may serve as a signal of greater susceptibility of a tree to colonization.

Microbes living in association with bark beetles both externally and internally can produce semiochemicals including some *Dendroctonus* attractants [91–97]. However, the importance of compounds from microbial sources to attraction of *Dendroctonus* species in nature has not been demonstrated conclusively.

3. Analytical Techniques for Identification of *Dendroctonus* Attractants

Demonstration of positive chemotaxis by a particular species to natural sources of semiochemicals is the starting point for investigation of attractants of any insect. For bark

beetles, this may involve observation of locations of concentrated beetle landings and attacks [98–102] or use of volatiles derived from suspected attractive substrates as lures in suitably-controlled trapping experiments [103–106] or laboratory bioassays [46,73,107,108]. The odor source utilized in field and laboratory experiments may be the substrate itself, its extracts, or air passed over the substrate or its concentrates [103,104,107–109]. With *Dendroctonus* and other bark beetles, the substrates typically investigated as semiochemical sources have been live beetles [49,51,110–112], crushed beetles [51,58,103,113,114], the alimentary tract [115–118], frass produced during mining [56,107,119–121], individual gallery entrances [74,108,122–124], whole infested or uninfested logs [125–129], and distilled or whole host tree resin [80,81,130,131]. Once natural sources of semiochemical attractants are identified, odorants are isolated from them typically by either direct solvent extraction of the material (in particular, the insects, their tissues, frass, host tissue, and resin [51,56,98,118]) or use of chemical adsorbents to concentrate organic molecules in the air surrounding or passed across the odor source [49,111,122,132]. Concentration of odorants from moving air has typically been accomplished with cartridges filled with particles of chemical adsorbent, in particular, Porapak QTM (Waters, Milford, MA, USA) or TenaxTM (Buchem B.V., Apeldoorn, The Netherlands), through which odor-laden air is passed [74,111,122,133]. Alternatively, solid phase microextraction (SPME, Supelco, Bellefonte, PA, USA) fibers coated with adsorbent can concentrate and trap odorants from static or moving air [110,122,134,135]. Odorant molecules are recovered from the adsorbents either through solvent extraction or heat desorption. Solvent extracts and fractions may be tested in behavioral bioassays to confirm that the semiochemicals were successfully isolated [55,136–138], however, the small quantities of compounds normally obtained by these methods are typically only suitable for laboratory bioassays.

Volatiles collected from natural substrates indicated above tend to be highly complex in their composition, with dozens of compounds present at potentially behaviorally active concentrations [139–141]. However, typically, most of these compounds are not semiochemicals, and steps should be taken to screen sample components as much as possible before resources are expended on extensive identification steps or behavioral bioassays are pursued with individual compounds. Separation of candidate semiochemicals can be performed with gas chromatography (GC) with the separated compounds eluting sequentially and usually directly from this instrument into three primary types of chemical detectors: flame ionization detector (FID), mass spectral detector (MSD), and/or electroantennographic detector (EAD). In the EAD, the living antenna of an insect is exposed to the sequentially eluting compounds from the GC, and electrodes attached to the antenna produce a voltage deflection in response to an eluting olfactory stimulant [142,143]. The timing of the deflections can be correlated to compounds detected in the chromatogram of a “universal” detector for organic molecules (typically an FID) operating in parallel with the EAD, and compounds detected simultaneously with antennal voltage pulses are presumed to be the olfactory stimulants. These presumptive odorants can be identified with GC-MSD, with which a diagnostic mass spectrum is generated for each compound eluting from the GC. If the mass spectrum and elution times of an unknown olfactory stimulant match those of an identified “standard” (purified or synthesized compound, commonly obtained from commercial suppliers), the identity of the stimulant can be established generally with a high degree of confidence. If the olfactory stimulant cannot be identified through mass spectrum and elution time matches to available standards, additional analytical steps (such as nuclear magnetic resonance and infrared spectroscopy) may be required, often followed by laboratory synthesis of a standard for GC-MSD and GC-EAD confirmation of data matches with those of the natural odorant. The identified olfactory stimulants may then be tested in behavioral assays (discussed below) to determine whether they are semiochemicals and characterize their behavioral effects on the insect. It should be noted that most of the original identifications of bark beetle semiochemicals (and many recent ones) were performed without the benefit of GC-EAD, as this technology was generally not available before the 1980s.

Candidate, attractive semiochemicals in complex, natural samples can be screened with steps in place of or in addition to electroantennographic analyses. These include comparisons of the GC chromatograms of samples of either beetle sex (individual components of an attractive pheromone are typically produced only, or predominantly by, one sex) [50,144], or contrasts of the composition of samples from attractive substrates to those that lack attractiveness but are similar in other respects (e.g., contrast of volatiles from infested and uninfested logs). *Dendroctonus* bark beetles appear to utilize the same, relatively few compounds in their attractive pheromone blends and as attractive host kairomones (Figures 1 and 2), and, after the original research on the chemical ecology of *Dendroctonus* was completed in the late 1960s through 1970s, very few additional compounds have been discovered. Hence, it is likely that future identifications of attractive semiochemicals of insufficiently or unstudied *Dendroctonus* species will be possible without sophisticated analytical and synthetic steps.

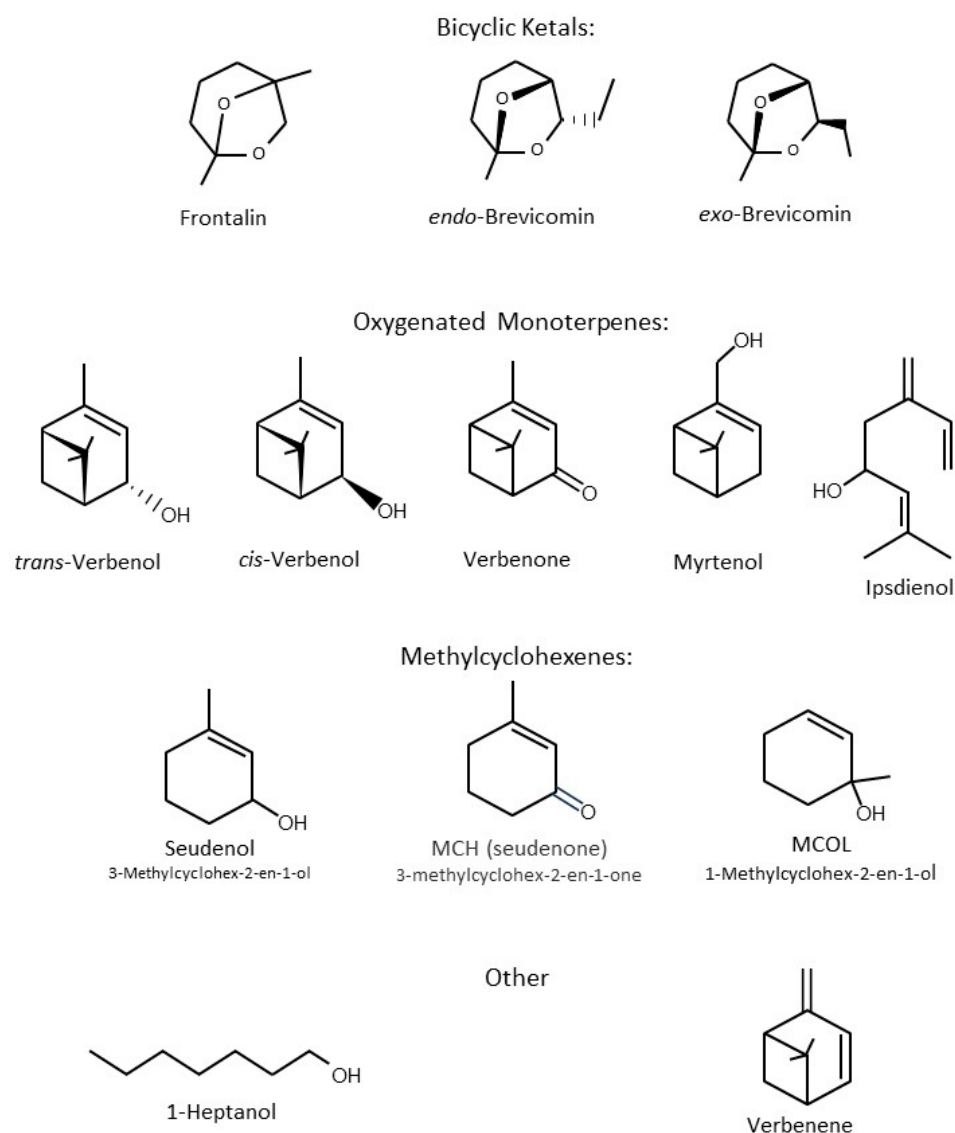


Figure 1. Attractive pheromone components for species of *Dendroctonus*.

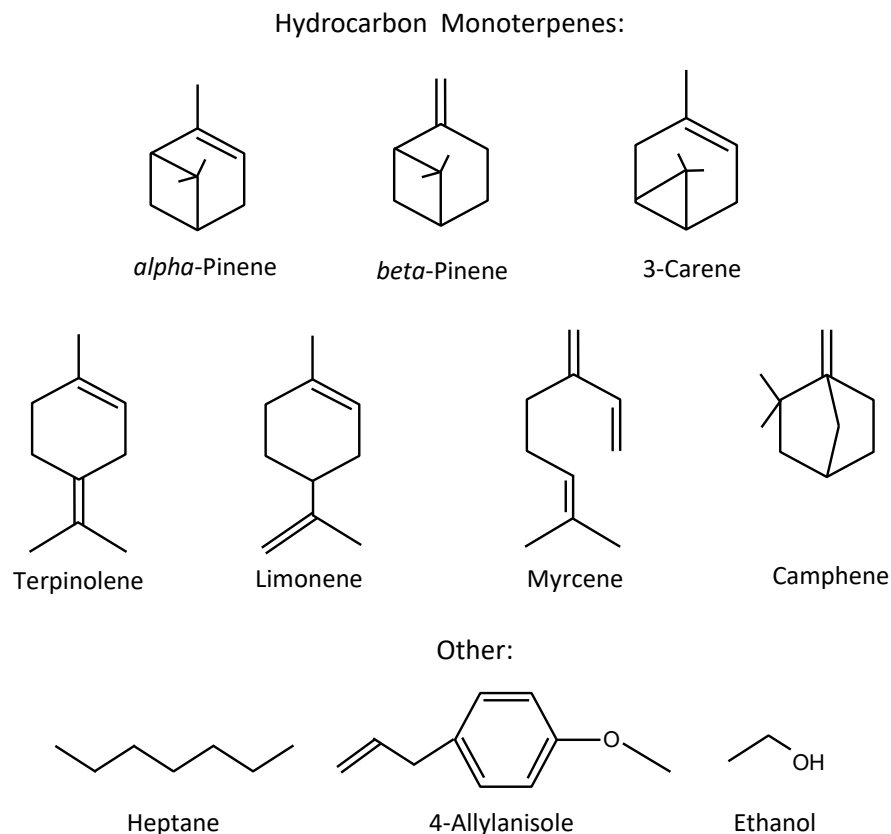


Figure 2. Attractive host odors for species of *Dendroctonus*.

4. Behavioral Bioassay Techniques for Identification of *Dendroctonus* Attractants

Bioassays for characterizing the long-distance attractive effects of bark beetle semiochemicals have typically been field experiments with baited traps. The most common statistical design for these experiments is randomized complete block where different lure compositions are assigned randomly within groups (blocks) of proximate traps equal in number to the lure treatments, and then blocks are replicated at multiple sites in a forested landscape [145]. This design reduces confounding effects of often strong variation in site-associated abundances of the target insect. Additionally, confounding spatial effects can be further reduced by rotating or re-randomizing positions of traps or lure treatments within blocks periodically during the experiment. The basic statistical model for the analysis of the resulting trap catches is a two-way ANOVA with factors lure treatment and block [145]. If catches in traps to which a compound is added are higher than for identical traps lacking only this compound, the compound is concluded to be attractive. Another common assay has involved contrasts of landings and attacks of beetles on trees baited or not baited with a candidate attractant [146–148]. However, results of these tests can be confounded by attractants released by beetles attacking the baited trees. Nonetheless, baited tree experiments have identified attractive effects of pheromone components not discovered in trapping experiments [149–151].

Early field research on bark beetle attractants was typically conducted with adhesive traps where the candidate attractant was placed within or adjacent to hardware cloth cylinders or panels coated with insect adhesive [133,152,153] (Figure 3A). All-direction, non-adhesive barrier traps, particularly the Lindgren funnel trap and the cross-vane panel trap, are currently the most common trap designs used in semiochemical research and applications with *Dendroctonus* and other bark beetles in North America [154–156] (Figure 3B,C). Release devices of candidate semiochemicals are placed on or within the barriers (funnels or panels), and deflected beetles are collected within a cup or similar container at the base

of the trap. For convenience of manipulation, traps are typically deployed at head height or lower, either from free-standing poles, tree branches, or cables strung between trees.

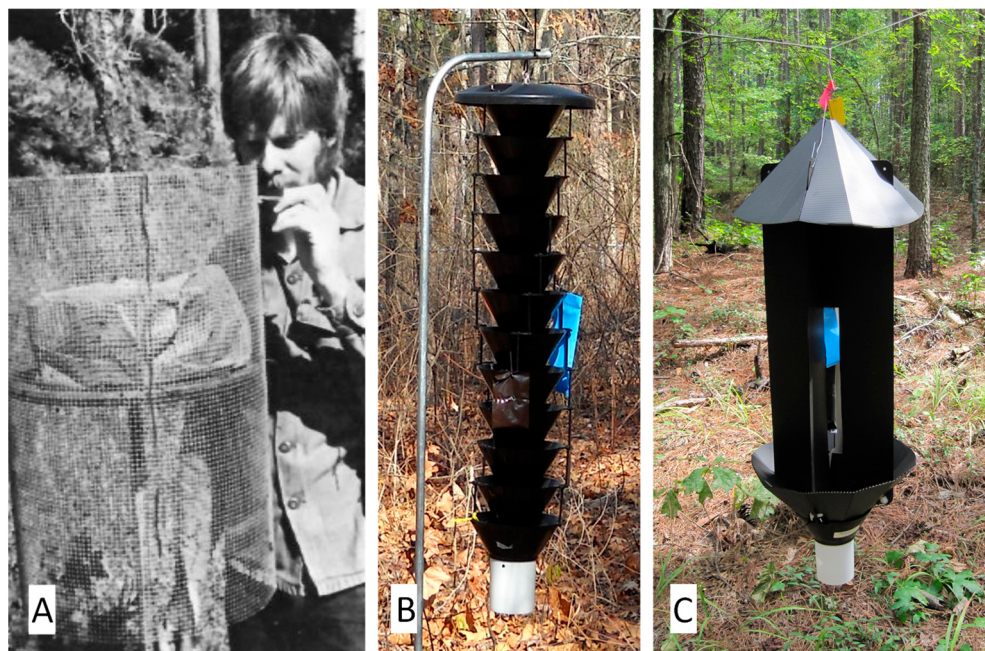


Figure 3. Major trap designs used for evaluating attractive lures for North American species of *Dendroctonus*. (A) Adhesive-coated screen cylinder [152], (B) Lindgren funnel trap, (C) Cross-vane panel trap. Photos (B,C) courtesy of Dan Miller, USDA Forest Service.

Particularly in the early literature on *Dendroctonus* attractants, laboratory assays with walking beetles were commonly used for initial evaluation of suspected semiochemicals. The most common laboratory olfactometer designs have measured upwind movement (anemotaxis) when candidate semiochemicals are released into a flow of air directed at one or more beetles walking on a platform [119,157,158]. Attraction is demonstrated by motion toward a source of test compound-laden, but not compound-free, air presented consecutively to the same or different individuals. Alternatively, multiple, compound-laden or clean airstreams are directed at the insect simultaneously (such as in a Y-tube), and the insect is allowed to “choose” among them and then scored for its selections [108,110,159]. In another design, suspected semiochemicals are released beneath one or more permeable locations in a walking surface, and arrestment of the insect’s movement at or in the vicinity of the odor release point is considered evidence of an attractive response [73,160]. Olfactometer bioassays are inexpensive, produce data rapidly, require very small quantities of test compounds, and can establish definitively that a compound has behavioral activity with an insect species. However, responses to semiochemicals in these bioassays may not reflect those of flying beetles in the field (e.g., data collected in trapping bioassays) and thus can misrepresent the composition of longer-range attractants. For example, in ambulatory bioassays, the pheromone component *endo*-brevicomin has displayed attraction-inhibiting activity for *Dendroctonus frontalis* Zimmermann across a wide range of concentrations [108,140], whereas it is a potent attractant synergist at low release rates in trapping experiments [129,161]. *Dendroctonus frontalis* responded strongly to several analogs of its major pheromone component, frontalin, in a walking bioassay while exhibiting attraction to just one of these in traps [162]. *Dendroctonus ponderosae* Hopkins walked upwind in response to sources of both (+)- and (−)-ipsdienol, whereas there was no attractive response to these compounds in traps [119]. *cis*-Verbenol, *trans*-verbenol, *exo*-brevicomin, and frontalin alone were all attractive to *Dendroctonus valens* LeConte in Y-tube experiments, but alone they produced no attractive response to traps [163]. Although these contrasts could be explained by dosing effects and thus are not definitive demonstrations

of inconsistency, it is evident that responses in flight cannot be definitively inferred from laboratory assays with walking insects. For this reason, the discussion of attractive semiochemicals for individual *Dendroctonus* species later in this paper generally does not include evidence from olfactometer tests.

5. Mechanistic Classifications for Attractants Based on Experimental Data

Effects of attractive bark beetle semiochemicals are typically dose-dependent, often displaying increasing trap catches with increasing release rates within the limited range of rates typically tested in experiments [79,164–166]. The term “multifunctional” has been used for bark beetle semiochemicals that exhibit attractive effects when released at relatively low rates but attraction-reducing or repellent effects at high rates [167–170]. The term is relevant both to pheromones and to host odors [83,164,171]. With pheromones, this phenomenon may simultaneously mediate long-range attraction while regulating beetle attack densities on the host [172–174] or provide escape from natural enemies possessing a more linear, positive dose response to the beetles’ attractants [83]. With host odors, it may allow beetles to find locations with available hosts (host habitat) while avoiding hosts or portions whose levels of resin production would pose a threat to survival [83,175]. I suggest the replacement of the term “multifunctional” with “biphasic,” since the phenomenon being described is mechanistic (involving a type of dose response) rather than functional (entailing specific ecological roles). Furthermore, it is typically unknown whether the high, repellent/inhibitory concentrations of otherwise attractive compounds ever occur in nature, and thus whether the reversing of effects may genuinely play a role in the chemical ecology of the insects.

In interacting with other attractive semiochemicals, attractants can be classified as (1) “attractive synergists” if trap catches in combination with a second semiochemical (or blend) exceed the summed catches for each separately, (2) “attraction enhancers” if the two in combination are more attractive than either singly but are not synergistic, or (3) “redundant attractants” if addition does not produce greater attraction than either singly. For both synergists [176] and redundant semiochemicals, there is a statistical interaction in the effects of the two compounds. Accurate placement of attractive semiochemicals in these categories has practical implications. For example, lures should require only one of a redundant component, allowing omission or replacement of relatively more expensive, redundant components in a lure formulation [177,178].

6. Functional Classifications for Attractants Based on Experimental Data

Functional classifications (inferred ecological roles) of *Dendroctonus* semiochemicals have typically been assigned based on a limited amount of experimental data (as an example, [179]). An objective criterion for partial assignment of function to insect pheromones (and commonly applied to bark beetles) was proposed by Cardé [180]: attractants produced by one sex that attract predominantly the opposite are “sex pheromones” whereas those produced by one or both sexes that attract both sexes are “aggregation pheromones”. Due to their simplicity, such functional classifications can be consistently applied to trapping data. However, they fail to accommodate the remarkable diversity of *Dendroctonus* life activities that apparently employ the same array of attractive components in the same or distinct combinations. This functional overlap represents semiochemical parsimony, a common phenomenon in insects where different functions are served by the same semiochemicals [181], presumably reducing the evolutionary costs of metabolic pathways for unique pheromone components and olfactory receptors. For example, in many *Dendroctonus*, components of the female-produced attractants that attract both sexes and ostensibly contribute to mass-attacks (i.e., function as “aggregation pheromones”) also attract males to female attacks for pairing and thereby function as sex pheromones [103,108,129,182,183]. Likewise, one cannot readily distinguish compositionally the attractant that mediates mass attacks with that presumably used by dispersing beetles for locating and exploiting suitable host resources already colonized by conspecifics. Further doubt is cast on functional inter-

pretations of attractant-mediated behaviors by paradoxical variation in pheromone systems among *Dendroctonus* species despite the apparently similar life history demands addressed with semiochemicals. For example (citations below in discussion of individual species), in some *Dendroctonus* species, males produce no sex-specific, attractive pheromone components; in others, males produce a sex-specific synergist that is not attractive alone; in others, males produce a sex-specific pheromone component that is attractive alone and may also be an attraction enhancer or synergist. In some species, pheromone components produced by each sex are attractive to both, but in others they are almost exclusively attractive to the opposite sex. Females may produce a single attractive pheromone component or multiple components. Some attractive pheromone components are biphasic while others are not. Only a subset of species produces attractive pheromones prior to mining. Some of this interspecific variation may have arisen to enhance reproductive isolation among currently or ancestrally sympatric species or have resulted from genetic drift [170,184,185]. However, it is difficult to assign self-consistent and thus plausible functional significance to the differences among species in these and several additional distinguishing traits. Consequently, functional classifications for semiochemicals may provide limited assistance in making inferences or predictions about untested beetle behaviors. It is therefore perhaps beneficial to discuss semiochemical functions without attributing them to individual compounds or blends, and the summaries of research on attractants for individual *Dendroctonus* species below generally make no functional assignments to semiochemicals.

7. Pitfalls of Executing and Interpreting Trapping Experiments

Lack of attraction or even attraction inhibition or repellency by a semiochemical in a trapping experiment is not necessarily an indicator of the absence of attractive effects, and several experimental variables can influence detection of an attractive compound. Biphasic semiochemicals have attractive effects only within a limited range of release rates, hence these attractive effects may be overlooked if tests are performed only at higher, unattractive or inhibitory release rates. Typically, only a limited number of release rates have been tested for *Dendroctonus* semiochemicals, and it is common for semiochemical experimentation to be performed with commercially available lures that are sold within a limited range of release rates. Hence, it is likely that additional, known *Dendroctonus* attraction-inhibiting semiochemicals will be found to have a biphasic dose response and thus unrecognized attractive effects. Another possible dosing-related complication to assessing trapping results is that typical commercial lures have release rates equivalent to pheromone production by hundreds or thousands of individual beetles, however, this release is from a single point in space. Dispersion of the lure plume by artificial baffles [103,154,186] may help prevent exposure of responding insects to highly unnatural concentrations of the semiochemicals while orienting toward a trap.

Attractive effects of a synergist will not be detected if the compound with which it is synergistic is absent, and, as attractive synergists often have no attractive activity alone, failure to reproduce the necessary combination may lead to failure to identify an attractive semiochemical [131,187]. One approach to avoiding this problem is use of the “subtractive method” where all suspected semiochemicals are combined, and individual compounds are removed to determine if a decline (or increase, for attraction inhibitors) in attraction occurs [141,188]. Success of this method, however, depends upon inclusion of all attractant synergists in the total mixture, and selection of compounds to include is, to some extent, a matter of guesswork.

Insufficient trap spacing in tests of bark beetle semiochemicals can potentially prevent observation of attractive effects. In an experiment with *D. frontalis*, addition of its pheromone component *endo*-brevicommin to an attractant-baited trap resulted in catches that were greater than those in attractant-baited, unamended traps >100 m away but less than those in an unamended trap 4 m away [189]. Hence, depending on the distance of the control (unamended) from the experimental (amended) trap, *endo*-brevicommin would be interpreted either as an attraction enhancer or inhibitor. This “reversal” of apparent effects

is a likely consequence of *endo*-brevicomin's biphasic dose-response [190], such that, as airborne concentration declines with distance from a high-release *endo*-brevicomin source, this semiochemical's inhibitory effects on attractant baited traps decline, disappear, and reverse to enhancing effects. If such distance-associated reversal in behavioral effects is a typical property of biphasic semiochemicals, then confounding effects of trap spacing have significant potential to influence the outcomes and interpretations of trapping experiments for assessing semiochemicals.

Likewise, background semiochemicals can alter the effects of semiochemicals in trapping experiments. Addition of an *endo*-brevicomin device to a trap baited with *D. frontalis* attractant semiochemicals increased or reduced catches depending on presence of artificial *endo*-brevicomin background produced by dispersed releasers of this semiochemical [191]. Presumably, such a "background effect" could also occur in locations with a natural background of semiochemical, such as active bark beetle infestations. This was suggested by an experiment where addition of *endo*-brevicomin release devices was found to increase *D. frontalis* catches in attractant-baited traps located outside of active *D. frontalis* infestations but reduce catches inside of infestations [192]. Similarly, Borden, et al. [193] observed with *D. ponderosae* that synergistic, attractive effects of combining monoterpenes disappeared in tests performed within active infestations. Spillover attacks onto trees adjacent to attractant-baited traps can provide a competing or ameliorating source of attractant, biasing catches in the associated trap [27,194]. It is the author's experience that infested trees within tens of meters of a trap can cause sufficient changes in catches to prevent detection of lure effects in an experiment.

As many semiochemicals are close analogs of others and in some cases can be generated from them spontaneously, it is common for synthetic semiochemicals used in behavioral tests to be contaminated with others unless synthesis procedures are carefully designed, purification steps are taken, and preservation methods (e.g., cold storage, addition of preservatives, reduction of air and light exposure) are used [96,193,195]. Behaviorally active lure contaminants could misrepresent behavioral effects of a semiochemical. For some semiochemicals of *Dendroctonus*, one may be produced from the other through spontaneous oxidation or microbial activity. Notably, the host compound *alpha*-pinene in contact with atmospheric oxygen may spontaneously form the *D. frontalis* and *D. ponderosae* attractive pheromone component *trans*-verbenol and further oxidize into the attraction inhibitor, verbenone [96]. *exo*-Brevicomin lures are typically contaminated with *endo*-brevicomin and vice-versa, and this has challenged interpretation of some experiments [196,197]. The extent to which contamination, which the author has observed to vary considerably among lots of a commercial lure, can impact research and application of *Dendroctonus* semiochemicals deserves further investigation [198].

It is common for semiochemical tests to be performed within a radius of no more than several kilometers, whereas the species concerned may range over hundreds or thousands of kilometers. Geographic variation in bark beetle responses to semiochemicals is common [197,199–202]. Thus, tests at a single location may not give a representative picture of the responses of a species, although it is common practice to attribute behaviors observed at one or two locations to an entire species when data from additional locations are not available. Season may also interact with bark beetle semiochemical responses and limit the time of year during which experimental results are meaningful or specific effects can be expected [203–206].

It should be noted that increases of catches in traps due to semiochemicals is not necessarily caused by attraction (positive chemotaxis) in the strict sense, and this review takes some liberty in equating trap catches with evidence of attraction. Catches could change due to a variety of potentially semiochemical-influenced behaviors that do not produce positive or negative chemotaxis. For example, semiochemical-mediated behaviors that increase trap catches might include increased rates of movement of beetles already in the vicinity of traps (klinokinesis), or greater arrestment or other altered interactions with the trap surface.

8. Composition of Attractive Pheromones of *Dendroctonus*

Attractive pheromone components for *Dendroctonus* (Figure 1) fall into three major chemical classes: bicyclic ketals (*endo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane, “*endo*-brevicommin”; *exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane, “*exo*-brevicommin”; and 1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane, “frontalin”), oxygenated monoterpenes (*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol, “*cis*-verbenol”; *trans*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol, “*trans*-verbenol”; 4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one, “verbenone”; 6,6-dimethylbicyclo[3.1.1]hept-2-en-2-yl-methanol, “myrtenol”; and 2-methyl-6-methylene-2,7-octadien-4-ol, “ipsdienol”), and oxygenated methylcyclohexenes (3-methyl-2-cyclohexen-1-ol, “seudenol”; 3-methyl-2-cyclohexen-1-one, “seudenone” or “MCH”; and 1-methyl-2-cyclohexen-1-ol, “MCOL”). In addition, two species of *Dendroctonus* produce the hydrocarbon monoterpene 6,6-dimethyl-4-methylenebicyclo[3.1.1]hept-2-ene, “verbenene”; and one species (*D. jeffreyi* Hopkins) produces 1-heptanol. The oxygenated methylcyclohexenes occur only in the non-pine feeding *Dendroctonus* species [*D. pseudotsugae* Hopkins (primary host: *Pseudotsuga menziesii* (Mirbel) Franco), *D. simplex* LeConte (host: *Larix laricina* (Du Roi) K. Koch), and *D. rufipennis* (Kirby) (hosts: *Picea*)]. Brevicommin occurs only in pine feeding species, and frontalin occurs in both groups. The bicyclic ketals are produced *de novo* by the beetles [45], and the biosynthetic origin of the oxygenated methylcyclohexenes is unknown [207].

Oxygenated monoterpenes are produced by nearly all *Dendroctonus*, although only a subset of these are pheromone components and only for some species. In particular, the *Dendroctonus* semiochemicals verbenol, verbenone, and myrtenol—all derivatives of host-produced *alpha*-pinene [208–210]—have been detected from *D. frontalis* [49,53], *D. mesoamericanus* Armendáriz-Toledano and Sullivan [53], *D. mexicanus* Hopkins [211], *D. brevicomis* LeConte [59], *D. barberi* Hopkins [59,197], *D. adjunctus* Blandford [212], *D. ponderosae* [133], *D. rhizophagus* Thomas & Bright [118], *D. valens* [159], *D. terebrans* (Olivier) [50], *D. rufipennis* [122], and *D. simplex* [213]. Concentrations of oxygenated monoterpenes have been shown to increase following exposure of adult beetles to resin monoterpenes [209,214,215], consistent with their being the product of detoxification of the host’s defensive compounds [64]. To some extent, they may also be produced through the action of bark beetle microbial associates on host monoterpenes [93,216] or on other oxygenated monoterpenes [217,218], or they can be generated through spontaneous oxidation of these compounds in contact with the air [96]. Ipsdienol occurs in small amounts in *D. brevicomis*, *D. barberi*, *D. mesoamericanus*, some populations of *D. frontalis*, and in *D. ponderosae* exposed to myrcene vapors [53,59,73,214,215]. Ipsdienol is significant in being perhaps the most common attractive pheromone component among species of *Ips* bark beetles [185,219], including many that are sympatric with *Dendroctonus* species [1], and it influences interspecific interactions between these genera [60,109,220]. Only one species of *Dendroctonus* (*D. ponderosae*) utilizes an oxygenated monoterpene (*trans*-verbenol) as its primary attractant pheromone component.

The spectrum of compounds utilized as attractive pheromone components by *Dendroctonus* is small, and there is extensive overlap of their use among species (Table 1). For example, frontalin is an attractive pheromone component for 13 of the 14 species for which an attractive pheromone has been identified. Due to this overlap, cross-attraction among species is common [57–59,98,128,129,221]. Some degree of specificity may be conferred through differences among species in the effects of different combinations of compounds. However, cross attraction of sympatric, pine-infesting species to the same hosts may have benefits since simultaneous attacks by multiple species may increase likelihood of successful mass attack on healthy trees and outweigh costs of increased competition for available host resources [222,223]. Reproductive isolation may be enhanced in these instances of cross-attraction through differences in pheromone components produced by the sexes and different behaviors by walking and flying insects. For example, syntopic species *D. frontalis* and *D. mesoamericanus* produce, and in flight are attracted to, the combination of frontalin and *endo*-brevicommin [129]. However, gallery-initiating, solitary female

D. mesoamericanus produce both frontalin and *endo*-brevicomin, whereas female *D. frontalis* produce only frontalin (males produce *endo*-brevicomin) [53,73]. *endo*-Brevicomin inhibits response of walking *D. frontalis* males to the attractant frontalin, the pheromone component that ostensibly mediates their location of conspecific female entrances [108]. Hence, *endo*-brevicomin produced by *D. mesoamericanus* females presumably prevents inadvertent entry of *D. frontalis* males into female *D. mesoamericanus* gallery entrances despite this semiochemical's apparent role in cross-attraction of both species to the same trees. A similar situation likely exists for syntopic *D. frontalis* and *D. barberi*, which share the same in-flight attractive pheromone components frontalin and *endo*-brevicomin but have the producing sexes of these two semiochemicals reversed [59,224]. There is no evidence that synergistic effects among attractive pheromone components in *Dendroctonus* are dependent on a specific quantitative ratio among components, however, this possibility has received limited investigation [166].

Several of the attractive pheromone components for *Dendroctonus* are chiral compounds with a right- and left-handed form. For the bicyclic ketals, the enantiomeric compositions produced are generally similar among species: in nearly all species examined to date, frontalin has been predominantly the (−) and brevicomin predominantly the (+)-enantiomer. The enantiomeric composition of MCOL, on the other hand, has displayed substantial intraspecific variability in *D. rufipennis*, with production variably dominated by (+) or (−). While a stronger attractive response is usually observed to the predominantly produced enantiomer for chiral, attractive pheromone components [133,139,195,225–227], there is little evidence to suggest that the beetles prefer specific enantiomeric ratios or that antagonism exists between enantiomers possible exceptions: [171,226]. Due to this lack of enantiomer antagonism or preferences for the more attractive enantiomer over the racemate, commercial *Dendroctonus* lures with chiral pheromone components typically contain a racemic blend, as these lures are less expensive to produce than lures with single enantiomers.

Table 1. Attractive pheromone components for *Dendroctonus*.

	Females													Males												
	frontalin	endo-brevicommin	exo-brevicommin	trans-verbenol	cis-verbenol	verbenone	myrtenol	ipsdienol	seudenol	MCH	MCOL	1-heptanol	verbenene	frontalin	endo-brevicommin	exo-brevicommin	trans-verbenol	cis-verbenol	verbenone	myrtenol	ipsdienol	seudenol	MCH	MCOL	1-heptanol	verbenene
<i>D. frontalis</i>	X			X	X										X ^{1,2}	X	X									
<i>D. mesoamericanus</i>	X	X						X							X ¹											
<i>D. vitei</i>	X																									
<i>D. mexicanus</i>	X	X												X												
<i>D. brevicomis</i>		X	X ¹											X												
<i>D. barberi</i>		X ¹	X											X												
<i>D. adjunctus</i>	X															X										
<i>D. ponderosae</i>	X ^{2,3}		X ^{2,3}	X	X								X	X ²		X ²	X	X							X	
<i>D. jeffreyi</i>												X				X ²								X		
<i>D. valens</i>	X ²			X			X										X			X						
<i>D. terebrans</i>	X			X			X									X	X			X						
<i>D. rufipennis</i> ⁴	X								X		X		X	X			X					X			X	
<i>D. simplex</i>	X ²					X			X																	
<i>D. pseudotsugae</i>	X								X	X ²	X			X								X	X ²	X		

Compounds not indicated if only trace quantities detected. Producing sex is indicated. ¹ Dominant brevicomin isomer in production and/or response. ² Biphasic or possibly biphasic. ³ Evidence for female production: [51]. ⁴ Large intraspecific variation in production and response; not applicable to all populations.

9. Composition of Attractive Host Odors for *Dendroctonus*

Host compounds found to influence *Dendroctonus* attraction (Figure 2) have predominantly been the volatile constituents of host resin, including the monoterpenes *alpha*-pinene, *beta*-pinene, 3-carene, terpinolene, limonene, myrcene, and camphene; the phenylpropanoid 4-allylanisole; and n-heptane (produced by Jeffrey pine, *Pinus jeffreyi* Balf.). Typically, conifer resin contains a blend of volatile compounds, with compound identities and proportions having specific associations with tree species, population, and susceptibility to insect colonization [84,228–234]. Ethanol is a general attractant for bark and ambrosia beetle species that require weakened hosts for reproduction [235–238], and of the three *Dendroctonus* species that respond to ethanol (*D. valens*, *D. terebrans*, and *D. pseudotsugae*) only the final is considered aggressive within its native range.

In *Dendroctonus* species where it has been investigated, about half (in particular, the aggressive tree killers *D. frontalis*, *D. brevicornis*, *D. ponderosae*, and *D. jeffreyi*) display no responses to individual host odors, synthetic blends, or distilled resin when pheromones are absent; in contrast, *D. valens*, *D. terebrans*, and *D. rhizophagus*, which generally do not mass attack, display strong attraction to host odors alone but weak or no attractive responses to pheromones (citations below with details of individual species). Mass-attacking species *D. pseudotsugae* and *D. rufipennis* are intermediate, with strong pheromone responses combined with weak responses to host odor lures. The reason for these contrasts is unclear. Experimentation with host odor lures has focused largely on monoterpenes of defensive resin and ethanol, whereas conifer odor compositions may be far more complex [239,240]. It is possible that resin odors provide no or little useful information to pioneer individuals of the more aggressive species, or risks posed by responding to these compounds (such as from attracted predators) outweigh the benefits. Despite lacking a clear role in primary host location, host odors, particularly monoterpenes, can be potent synergists for the attractant pheromones of aggressive *Dendroctonus* species that do not respond to host odors alone. For example, high release of turpentine can increase *D. frontalis* catches in traps baited with their attractive pheromone components by 1–2 orders of magnitude [81,190], and combinations of monoterpenes can produce up to an approximately 30-fold increase in catches of *D. ponderosae* compared to pheromone alone [193].

Presumably, resin monoterpene blends specific to individual tree species may indicate a host of an appropriate taxon to a foraging beetle, and high concentrations of these compounds may indicate a vigorous, high-quality host which—as signified by the simultaneous presence of substantial quantities of attractant pheromone—is likely to be rendered susceptible by mass-attacking beetles. However, tests comparing selectivity of *D. rufipennis*, *D. pseudotsugae*, and *D. ponderosae* for volatile blends of their own host species (with and without pheromone) demonstrated limited preferences [82,241]. The composition of resin constituents also may be an indicator of host condition or susceptibility. Elevated concentrations of the resin semiochemical 4-allylanisole were found to be associated with *Pinus caribaea* Morelet experiencing either higher [242] or lower [230] rates of mortality from *D. frontalis*, and individual pines treated to render them more susceptible to *D. frontalis* attack had depressed levels of this compound [243]. Lower levels of 4-allylanisole were also found in trees attacked by *D. ponderosae* [84]. Despite the inconsistent associations of 4-allylanisole concentrations with attack susceptibility in these studies, the results suggest that relative proportions of volatile components in resin can communicate likelihood of attack success.

Typically, certain, individual host resin constituents have stronger attractive effects than others, but there may be limited correspondence between attractiveness and the predominance of the compound in the resin of host species of the beetle [82,118,193,197,201,244]. The lack of a clear pattern in monoterpene preferences among different *Dendroctonus* species may be due to the substantial intraspecific variation in resin compositions of conifers [228]. As with the pheromone components, *Dendroctonus* responses to individual host odors may be influenced by their chirality (as demonstrated with *alpha*-pinene in several *Dendroc-*

tonus species), with attractive responses sometimes being primarily, or only, to a single enantiomer [201,245,246].

10. Differences in Responses between the Sexes

The sexes may respond differently to components and blends of attractive semiochemicals, and it is common for the sex ratio caught in traps to differ significantly from 1:1 or the sex ratio of brood emerging from colonized hosts [247]. Certain pheromone components can be more attractive to one sex than the other. In particular, pheromone components produced by just one sex can be primarily or only attractive to the opposite sex [50,212,248]. Hence, representation of these compounds in lures can influence sex ratios trapped. Sex ratio may also be influenced by trap size and lure concentration. Females may be deflected from landing at locations with high concentrations of female pheromone components since these should signal competition with high densities of attacking females; in contrast, males should prefer landing at such locations due to likely greater availability of mates [249].

11. Composition of Attractants for North American Species of *Dendroctonus*

Below are summaries of past research on attractant semiochemicals for individual species of *Dendroctonus*. Behavioral results for sexes are generally not given separately, in part due to the fact that publications reporting responses for sexes separately frequently lacked statistical tests for interactions between beetle sex and lure response. Also, sex-specific differences in lure effects might not have been detected or have been incorrectly inferred if catches were too low in one sex for making statistical inferences. In the pheromone production data given below, I include only compounds with attractive effects unless otherwise noted.

11.1. *Dendroctonus frontalis* Zimmermann—Southern Pine Beetle

Attractive pheromone components frontalin and *trans*-verbenol are present in, and released by, females newly emerged from host bark or logs [53,114,161], arriving at mass-attacked host trees [250], solitary or paired inside a log or mass-attacked host [52,74,251], and reemerging from the host following brood production [252]. Frontalin is rarely reported in males during host colonization [250], but males artificially confined together may produce frontalin in significant quantities [140]. Small to moderate quantities of *trans*-verbenol are produced by emergent, landing, and paired males [49,53,250]. Females produce between 65% and 95% (–)-frontalin, and enantiomeric composition does not differ between emergent and mining beetles [161,253,254]. Brood females emerged from loblolly pine, *Pinus taeda* L., produced predominantly (–)-*trans*-verbenol (mean values: 70.5%, 74%) [177,254], however, quantities drop precipitously following entry of the host [251] and may be associated with considerable change in the enantiomeric composition [177]. *endo*-Brevicomin is detected from male *D. frontalis* that are newly emerged [53,114,161], arriving at a host [250], and mining with a female [161,224]. It is produced almost entirely as the (+)-enantiomer [161,255]. Much smaller amounts of the *exo*-isomer of brevicomin are detected in some males [53,196].

Racemic frontalin is slightly attractive in traps when presented alone [161,178], but this attraction is strongly enhanced by the presence of synergists (see below). The predominant, (–)-enantiomer of frontalin is significantly more attractive than the (+)-enantiomer in lures that include *alpha*-pinene, and racemic frontalin is not different in attractiveness from either (–) or the beetle-produced enantiomeric ratio [225]. *trans*-Verbenol is a synergist of frontalin [114,161,178], however, its effects are redundant with those of the host odor *alpha*-pinene [177,178]. Racemic and (+)-*endo*-brevicomin can strongly increase *D. frontalis* attraction to lures with frontalin and host odors [161,226], however, the (–)-enantiomer is reported to be an attraction inhibitor [226]. Tests deploying lures with identical release rates of (+)-*endo*-brevicomin indicated that the 1:1 blend of enantiomers was no less attractive than the (+)-enantiomer alone and thus demonstrated that the (–)-enantiomer in the racemate is not antagonistic with the (+)-enantiomer [189,192]. Racemic *endo*-brevicomin has a

biphasic dose response, with a 0.1–1 mg/d release rate producing greatest synergistic effects in one study [190]. High release rates (>1 mg/d) can interrupt attraction [190–192,256]. Release devices of *endo*-brevicomin located 32 m from traps baited with frontalin and host odors can still have synergistic effects on catches [189], and displacing *endo*-brevicomin devices several meters from baited traps can increase synergistic effects [189,203]. The author has observed that displacement-caused catch enhancement can occur across the range of *endo*-brevicomin release rates most attractive for the beetles but may be affected by time of year [203].

Racemic *exo*-brevicomin lures significantly enhanced attraction of *D. frontalis* to combinations of host odors and frontalin in both Mississippi and Arizona, USA [59,196]. In Arizona, attraction enhancement by *exo*- and *endo*-brevicomin lures did not differ, and in combination the semiochemicals were apparently redundant [59]. However, in these tests, lures were contaminated with the reciprocal isomer, and release rates differed somewhat, lessening confidence in the behavioral contrasts. *cis*-Verbenol, present in substantial quantities in emergent females, significantly increased *D. frontalis* catches when released at a high rate (60 mg/d at 22 °C) in combination with frontalin and *alpha*-pinene [49]. However, the lures were contaminated with significant quantities of attractant synergist *trans*-verbenol.

Host odors alone are not attractive to *D. frontalis* [81,114], but they can be strong attractive synergists. Raw and distilled (turpentine) pine resin, as well as individual turpentine constituents *alpha*-pinene, *beta*-pinene, and 4-allylanisole, can enhance *D. frontalis* attraction when combined with either frontalin and *endo*-brevicomin or frontalin alone [81,114,178,205,244]. High release rates (4–5 g/d) of turpentine or *alpha*-pinene, the dominant constituent of attractive turpentines, can increase *D. frontalis* catches by pheromone lures by 50 to 100-fold [190,244]. (+)-*alpha*-Pinene enhances attraction more than the (–)-enantiomer, but not more than the racemate [246]. A minor constituent of the resin of host pines for *D. frontalis*, 4-allylanisole, increased attraction to a pheromone component combination (frontalin and *exo*- and *endo*-brevicomin) in a positive dose-dependent manner when released at approximately 5 to 500 mg/d (causing up to a 50-fold catch increase), with or without *alpha*-pinene also present [165]. These results contrast with some studies which have reported 4-allylanisole to have repellant and attraction-inhibiting activity [257,258].

There is limited evidence suggesting geographic variation in the attractants for *D. frontalis*. Emergent males in central and southern Mexico produce substantially more *endo*-brevicomin than those in the southeastern USA [53,161,211], although an associated behavioral difference has not been observed. In laboratory bioassays, *D. frontalis* were more attracted to odors of attacks by beetles from their place of origin (Texas, Georgia, and Virginia, USA) [126], however, compounds potentially responsible for the discrimination were not reported.

11.2. *Dendroctonus mesoamericanus* Armendáriz-Toledano & Sullivan

Newly emerged females from Chiapas, Mexico contain and release no compounds known to influence conspecific attraction [53]. Following entry into a host, they produce large quantities of the bicyclic ketals frontalin and *endo*-brevicomin, as well as small amounts of ipsdienol [53,108]. Newly emerged males produce trace amounts of *endo*-brevicomin but large quantities following pairing in a log. The enantiomeric compositions are 95% (–)-frontalin, 99% (+)-*endo*-brevicomin, and >95% (+)-ipsdienol [108]. In trapping assays, the combination of *endo*-brevicomin, frontalin, and turpentine is attractive [53], and ipsdienol may further enhance attraction [129] although this has not been observed consistently (Alicia Niño-Domínguez, personal communication). Trap catches are typically low even when numbers of *D. mesoamericanus* are abundant in the forest, suggesting either that the lure blend is incomplete or that this species lacks a strong response to their attractive pheromone components.

The necessity of host odors in the attractive blend has not been tested directly, although attractive lure blends have always included a host odor component (turpentine or *alpha*-

pinene). GC-EAD analysis has confirmed this species' olfactory sensitivity to *alpha*- and *beta*-pinene and indicated probable sensitivity to multiple additional host odors [73,108].

11.3. *Dendroctonus vitei* Wood

In the early stages of attack, females produce frontalin, whereas males produce no compounds with identified behavioral effects [144]. In trapping tests in central Guatemala, frontalin was attractive, but no lures included host odors [144].

11.4. *Dendroctonus mexicanus* Hopkins—Smaller Mexican Pine Beetle

GC-FID analyses of hindguts indicated that females produce frontalin and possibly both *exo*- and *endo*-brevicomin and that emergent males produce frontalin [211]. Since these identifications were by retention times only, they should be considered tentative. In a trapping study in central Mexico, the combination of *alpha*-pinene and frontalin was attractive, and *endo*-brevicomin may have decreased response to this combination [211]. In another experiment in central Mexico, a lure that included both frontalin and *endo*-brevicomin trapped approximately 10-fold more *D. mexicanus* than a lure with frontalin as the only pheromone component, however, the host odor components of these lures differed, and no statistics were presented [259]. Lures with *alpha*-pinene and frontalin [260] and lures with host odors, frontalin, and *endo*-brevicomin [261,262] have been used in studies on flight timing, range, and antiattractants for *D. mexicanus*. Moser, et al. [263] trapped thousands of *D. mexicanus* with both a lure targeting *D. frontalis* (frontalin and *alpha*-pinene) and a lure targeting *D. brevicomis* (frontalin, *exo*-brevicomin, and myrcene) in Arizona. Although different host odor combinations have been used in *D. mexicanus* lures, their behavioral influence is unknown.

11.5. *Dendroctonus approximatus* Dietz—Larger Mexican Pine Beetle

No studies of pheromone production or responses to individual semiochemicals have been conducted with this species. However, when clusters of traps in northern Arizona were baited with lures for *D. brevicomis*, *D. frontalis*, *D. valens*, *D. ponderosae*, and *Ips pini* (Say), 89% of captures of *D. approximatus* occurred with lures for *D. brevicomis* and *D. ponderosae* [221]. These latter two lures shared *exo*-brevicomin and myrcene as common components.

11.6. *Dendroctonus brevicomis* LeConte—Western Pine Beetle

Emergent females contain small amounts of *exo*-brevicomin, whereas males correspondingly contain frontalin [47,58,114]. After entry into the host, production of both bicyclic ketals in the respective sexes increases [48,56,58,195]. Solitary and paired females in the host also produce quantities of *endo*-brevicomin [59,197]. Among four distant populations (two in California and one each in Idaho and Oregon, USA) the percentage of the *endo*-isomer in solitary feeding females was 13%–26% [197]. Beetles feeding in infested logs produce predominantly (–)-frontalin and (+)-*exo*-brevicomin although the precise enantiomeric ratios have not been reported [253].

In the presence of host odors, traps baited with frontalin and *exo*-brevicomin singly and in combination are attractive to *D. brevicomis*, and the two compounds are synergistic [113,120,264–266]. *exo*-Brevicomin alone and combined with frontalin are also attractive to flying beetles in the absence of host odor lures [120]. In traps baited with myrcene and racemic frontalin, (+)-*exo*-brevicomin was more attractive than (–), and with lures of myrcene and racemic *exo*-brevicomin, (–)-frontalin was more attractive than (+) [195]. (–)-Frontalin was equivalent in attractiveness to the racemate whereas (+)-*exo*-brevicomin was more attractive than the racemate [however, in the latter test, the quantity of the (+)-enantiomer was greater in the (+) than the racemic lure] [195]. *endo*-Brevicomin lures significantly increased attraction of *D. brevicomis* to frontalin and *alpha*-pinene, but there was no evidence of additive or synergist effects with *exo*-brevicomin [59]. At four of five

sites across three western states, lures dominated by the *exo*-isomer of brevicomin were significantly more attractive than those with the *endo*-isomer [197].

There is no evidence that host odors are attractive to *D. brevicomis* in the absence of pheromones [267]. Pine oleoresin increased attraction to *exo*-brevicomin and frontalin [266], and myrcene increased attraction to *exo*-brevicomin [120]. At only two of five sites across California, Oregon, and Idaho did *D. brevicomis* display a preference for trap lures that included myrcene rather than *alpha*-pinene as the host odor component; at the other sites no preference was apparent [197]. However, in this study, attractive effects were not confirmed with host odor-free checks. *Dendroctonus brevicomis* displays olfactory sensitivity to dozens of host-associated volatiles [268], and there are likely additional host compounds and combinations involved in attraction of this species.

11.7. *Dendroctonus barberi* Hopkins—Southwestern Pine Beetle

(Note: *Dendroctonus barberi* was synonymous with *D. brevicomis* from 1963 to 2019. As these species are believed to be allopatric, all semiochemical research nominally on *D. brevicomis* and conducted southeast of the Great Basin is considered here as applicable to *D. barberi*.)

Females either live-trapped or excised from ponderosa pine logs after mining 1–2 d (either paired or unpaired) release large quantities of *endo*-brevicomin and lesser quantities of *exo*-brevicomin [59,196,197,224]. In four southwestern USA states and one site in Mexico, the percentage of the *exo*-isomer was 1.1%–10% and did not differ significantly among sites [197]. Live-trapped or paired in a log, males release large quantities of frontalin [59,196]. Both *exo*-brevicomin and frontalin separately and combined are attractive in combination with *alpha*-pinene [269]. In traps baited with frontalin and a host odor, *endo*-brevicomin or the combination of *endo*- and *exo*-brevicomin enhanced *D. barberi* catches more than *exo*-brevicomin, and no additive effects of the isomers were apparent [59,197]. The preference for *endo*-brevicomin was observed across four southwestern states [197].

In Arizona, host odor *alpha*-pinene enhanced catches of *D. barberi* by frontalin, whereas myrcene did not [269], and catches with pheromone lures were typically higher if *alpha*-pinene rather than myrcene was included in the lure [60,197,269], although release rates were generally unequal. However, this result was not consistent within the range of *D. barberi*, with the reverse preference observed in southern Nevada, USA, and no preference observed in either western Texas or northern Colorado, USA [197].

11.8. *Dendroctonus adjunctus* Blandford—Roundheaded Pine Beetle

Newly emerged females from an unreported location contained small amounts of frontalin, and newly emerged males contained large quantities of *exo*-brevicomin [212]. Females feeding 2 d in fresh pine phloem also contained frontalin, however, data for paired beetles of either sex have not been reported. Frontalin and *exo*-brevicomin, either alone or combined, significantly increased catches by a mix of major pine monoterpenes (*alpha*-pinene, *beta*-pinene, and myrcene), and combining the bicyclic ketals did not increase total beetle catches over those by each semiochemical individually [212]. Males and females were primarily or only attracted to the bicyclic ketal pheromone component produced by the opposite sex, and male attraction was significantly reduced by the addition of *exo*-brevicomin to frontalin [212]. In central Mexico, a lure with frontalin and *alpha*-pinene was more attractive to *D. adjunctus* than lures that included frontalin, *exo*-brevicomin, and myrcene or *trans*-verbenol, *exo*-brevicomin, and myrcene [270]. The combination of frontalin and *alpha*-pinene was used in both central and central-eastern Mexico for studies of annual flight activity of *D. adjunctus* [271,272].

11.9. *Dendroctonus parallelcolis* Chapuis

No data have been published on the chemical ecology of this species.

11.10. *Dendroctonus ponderosae* Hopkins—Mountain Pine Beetle

Emergent females contain no attractive pheromone components (unfed females may begin producing *trans*-verbenol after several days), whereas females allowed to attack pine logs in the laboratory produce substantial amounts of *trans*-verbenol which may decline post-pairing with a male [51,98,139]. Emergent males contain substantial amounts of *exo*-brevicomin, and paired males contain lower amounts of *exo*-brevicomin, large quantities of frontalin, and small amounts of *trans*-verbenol [51,273]. This pattern was similar for beetles reared from infested lodgepole (*Pinus contorta*, Douglas ex Loudon), ponderosa (*Pinus ponderosa* Douglas ex C. Lawson), western white (*Pinus monticola* Douglas ex D. Don), and sugar (*Pinus lambertiana* Douglas) pines from Oregon [133]. However, *exo*-brevicomin and frontalin were not detected from pairs infested onto jack pine (*Pinus banksiana* Lamb.) [124], and production of oxygenated monoterpenes was influenced by resin composition of this host [274]. When removed from logs cut from naturally-infested trees, both solitary and paired females contained some frontalin and *exo*-brevicomin [51]. Either sex may produce small amounts of *cis*-verbenol and verbenene [51,133,275]. For populations sampled in southern British Columbia, females produced 89% (–)-*trans*-verbenol, and males produced 98% (+)-*exo*-brevicomin and 93% (–)-frontalin [51].

trans-Verbenol is the primary attractive pheromone component for *D. ponderosae*, and, with the possible exception of *cis*-verbenol, is the only pheromone component that in the absence of others can attract this species to traps. *trans*-Verbenol in combination with host odors is highly attractive to flying beetles [103,133] and increases attraction to female infested logs [98]. In Oregon and southern British Columbia, (–)-*trans*-verbenol was more attractive than the (+)-enantiomer when released with myrcene or myrcene and *exo*-brevicomin [133,276]. *exo*-Brevicomin is a biphasic pheromone component, enhancing attraction to combinations of *trans*-verbenol and host odors at low release rates but reducing attraction at high rates [133,140,276–278], although this effect is not consistent in all trials or studies [164,279] and may vary geographically [276]. Attractive effects have been observed for *exo*-brevicomin at a release rate of approximately 0.05 mg/d and are significant only for females [276,277]. Inhibitory effects for high rates of *exo*-brevicomin were similar for both the (+) and (–)-enantiomers, whereas the influence of chirality on attractive effects has not been established [276]. Although a strong inhibitor of *D. ponderosae* attraction at intermediate to high release rates [133,273,276], in one experiment racemic frontalin at a low release rate (0.05 mg/d) significantly increased female responses to a lure composed of myrcene, *trans*-verbenol, and *exo*-brevicomin, suggesting that frontalin is biphasic [276]. Although not attractive alone or with host odors in traps, both frontalin and *exo*-brevicomin alone can induce higher rates of attack on initially uninfested trees [149–151]. *cis*-Verbenol significantly increases attraction to myrcene and *exo*-brevicomin, although its effects may be redundant with those of *trans*-verbenol [280].

Catches of *D. ponderosae* in traps baited with screened lodgepole pine logs, either stripped of their bark or intact, indicated primary attraction to host odors [281]. However, attraction to resin, turpentine, or terpene mixtures in traps has not been reported in the absence of pheromone components [82,133,281]. Responses to pheromone components (*trans*-verbenol with or without *endo*-brevicomin) are strongly enhanced by fresh resin of host species [130], turpentine from host resin [193], as well as host terpenes singly and in combinations [82,130,193,277,282]. In general, myrcene alone or with terpinolene has been found to be the best attractive pheromone synergist for *D. ponderosae*, with evidence of superiority of myrcene alone over *alpha*-pinene, *beta*-pinene, 3-carene, and limonene [130,193,279,283]. In some tests, the combination of myrcene and terpinolene was a superior synergist to either compound singly, but not in others [193,283]. Addition of 3-carene to myrcene and terpinolene can either enhance or decrease attraction [284]. Some of this variability might be attributable to geographic variation or time of year [130,283]. Dose-response tests in traps baited with verbenols and *exo*-brevicomin found that 3-carene and myrcene (but not *alpha*-/*beta*-pinene, *gamma*-terpinene, or terpinolene) exhibited log-log increases in responses to release rates ranging from 0.7 and 5.2 mg/d up to 609 and

6463 mg/d, respectively [79]. Synthetically reconstituted bole and foliage volatiles of host species lodgepole pine were no more synergistic than volatile blends of some sympatric, non-host conifers, including Douglas-fir, spruce, and fir [82].

11.11. *Dendroctonus jeffreyi* Hopkins—Jeffrey Pine Beetle

Females excised from pitch tubes and initial galleries in Jeffrey pines [285] and both sexes fed phloem [136] produce 1-heptanol. Phloem-fed males additionally produce >99% (+)-*exo*-brevicomin and 67% (–)-frontalin [136]. In combination with host odor heptane, 1-heptanol attracted beetles to traps [136,286]. Increasing the proportion of heptanol in heptane (released at 250 mg/d) from 0.01% to 5.0% caused a positive dose-dependent increase in beetle catches [136]. Frontalin reduced attraction of beetles to traps baited with heptane and heptanol in a dose-dependent manner, whereas *exo*-brevicomin significantly increased catches at a single intermediate dose (i.e., when 0.1% of the total semiochemical blend, producing a six-fold catch increase), suggesting a biphasic response [136]. The combination of frontalin and *exo*-brevicomin was likewise biphasic, enhancing catches at an intermediate release rate (0.01%) but reducing catches at high rates ($\geq 0.1\%$) [136]. Although apparently a necessary component of attractive lures, the major resin odor of Jeffrey pine, heptane, was not attractive alone [136].

11.12. *Dendroctonus rhizophagus* Thomas & Bright

This species may lack an attractive pheromone. Solitary and paired females and paired males initiating egg galleries on hosts in the field or pine logs in the laboratory produced five oxygenated monoterpenes that elicited responses from antennae in GC-EAD studies: myrtenal, *cis*-verbenol, *trans*-verbenol, verbenone, and myrtenol [118,287]. No bicyclic ketals were detected in either sex. GC-EAD analyses with resin from a host species (*Pinus arizonica* Engelm.) identified three constituents active with antennae of both sexes: *alpha*- and *beta*-pinene and 3-carene [118]. Traps positioned at ground level in areas experiencing a *D. rhizophagus* infestation and baited with 3-carene alone or a 1:1:1 mix of all three terpenes were attractive, but addition of the five oxygenated monoterpenes either singly or combined did not enhance beetle attraction to the three-component hydrocarbon monoterpene mix [118].

11.13. *Dendroctonus valens* LeConte—Red Turpentine Beetle

In a study of a population in Shanxi, China (where *D. valens* is an exotic species), seven of 14 solitary females and three of 17 paired females released frontalin following excision from logs infested in the laboratory [110]. Both sexes produce oxygenated monoterpenes *trans*-verbenol and myrtenol when feeding [110,159,288], and trapped insects were also found to contain trace or low quantities of *trans*-verbenol and myrtenol [117].

Frontalin released at a very low rate (less than 3 $\mu\text{g/d}$) enhanced catches in traps baited with *beta*-pinene and ethanol or 3-carene and ethanol in Oregon [289] and with 3-carene in Shanxi [110]. However, with a more typical release rate for frontalin in attractive *Dendroctonus* lures (>1 mg/d), it either reduced or had no effect on catches in traps baited with 3-carene (two sites in Shanxi) and had no effect on catches with ethanol and *beta*-pinene (Oregon) [163,290]. Both *trans*-verbenol and myrtenol (at 1 and 8 mg/d, respectively) significantly increased attraction to a three-component host odor lure in one study in Shanxi [159], although they had no effect on catches with 3-carene in subsequent studies [110,163]. Pheromones of sympatric *Ips* species (ipsenol or ipsdienol with lanierone) increased *D. valens* attraction to (–)-*alpha*-pinene-baited traps in Wisconsin, USA [63].

Monoterpenes of the resin of its hosts, singly or in blends, are attractive to *D. valens* without pheromone components: turpentine from ponderosa pine resin; *alpha*-pinene, *beta*-pinene, 3-carene, and myrcene alone; and *alpha*-pinene, *beta*-pinene, and 3-carene combined [163,245,291–293]. Preferences for individual monoterpenes in trapping trials have varied, and this may be due to a variety of factors potentially including geographic variation, composition and history of the stands where tests were conducted, and lure release

rates. In a study that applied uniform testing procedures at multiple locations, 3-carene was more attractive than *beta*-pinene and either enantiomer of *alpha*-pinene in northern, southern, and central California, Wisconsin, and Shanxi, although no significant difference was detected in Pennsylvania, USA [201]. 3-Carene alone also exceeded attractiveness of a three-component lure (3-carene, and *alpha*- and *beta*-pinene in a 1:1:1 blend) at these same locations and Pennsylvania, but not in one of three trials in Shanxi where there was no difference [201,292]. These findings of widespread superiority of 3-carene contrast with results in northern California and Oregon where *beta*-pinene exceeded the attractiveness of 3-carene [245,294]. With ethanol as a component of the lure, *beta*-pinene was more attractive than 3-carene or *alpha*-pinene in southern and central Oregon and northeastern Washington, USA [295]. In the absence of other semiochemicals, (+)-*alpha*-pinene was more attractive than (−)-*alpha*-pinene in northern California, Wisconsin, and Pennsylvania [201,245], however, the (−)-enantiomer was more attractive in one of two trials in Shanxi [201]. Attractive release rates of monoterpenes have typically been in the hundreds of milligrams per day.

Host odor ethanol alone is attractive to *D. valens* [293,294] and when released at hundreds of milligrams per day can enhance responses to host monoterpenes [290,294]. However, a high release of ethanol (1–2 g/d) did not increase response to an attractive three-component monoterpene lure in northern California [291].

11.14. *Dendroctonus terebrans* (Olivier)—Black Turpentine Beetle

Females trapped in flight, dissected from host trees, or infested onto logs in the laboratory produce frontalin, whereas males under similar conditions produce *exo*-brevicomin [50,248,296]. They produce 91% (−)-frontalin and >98% (+)-*exo*-brevicomin [296], respectively. Both sexes produce *trans*-verbenol and myrtenol. Pheromone components are apparently not attractive in the absence of host odors released at a high rate [50,248]. Frontalin increased attractiveness of turpentine for males but not females [50,248], whereas *exo*-brevicomin increased attraction of females in some experiments but not males [50,227]. Addition of *exo*-brevicomin to frontalin and turpentine reduced responses or had no effect on males, whereas addition of frontalin to *exo*-brevicomin and turpentine had no effect on females [50,227]. Activity of the predominant enantiomer produced by the insect was similar to the racemate for both pheromone components [227]. In some tests, *trans*-verbenol was found to produce a small but significant increase in catches in traps baited with turpentine or turpentine and ethanol [297], but it did not enhance attractiveness of lures of turpentine and frontalin [50]. Myrtenol enhanced male attraction to lures with turpentine, *trans*-verbenol, and frontalin, but had no effect on other attractive lure combinations [50]. Ipsdienol, produced by sympatric bark beetles *Ips avulsus* (Eichhoff) and *I. calligraphus* (Germar), was found to enhance attraction of *D. terebrans* when trapping results were analyzed across multiple lure combinations that included different *Ips* pheromone components [62].

Dendroctonus terebrans are strongly attracted to turpentine released at high rates (grams per day) [80,248,298,299], and turpentine is synergized by high release rates of ethanol, which is not attractive alone [80,300]. Ethanol may be synergistic only if it is mixed with turpentine rather than released from a separate device [300]. Six predominant monoterpenes in an attractive turpentine failed to attract *D. terebrans* in significant numbers when released singly or recombined [299]. Catches in traps baited with a ternary combination of bicyclic ketals (*exo*-brevicomin, *endo*-brevicomin, and frontalin) were increased by *alpha*-pinene, *beta*-pinene, and myrcene separately (released at 3–4 g/d), as well as 4-allylanisole (released at 0.05 g/d) [244]. Two oxygenated monoterpenes without a known natural origin relevant to *D. terebrans* biology, 1,4-cineole and eucalyptol, increased attraction to the bicyclic ketal combination with or without *alpha*-pinene also present [244]. 4-Allylanisole released from approximately 5 to 500 mg/d enhanced attraction to the combination of the ternary bicyclic ketal combination and *alpha*-pinene in a positive dose-dependent manner [165].

11.15. *Dendroctonus murrayanae* Hopkins—Lodgepole Pine Beetle

No data have been published on the chemical ecology of this species.

11.16. *Dendroctonus punctatus* LeConte —Boreal Spruce Beetle

No data have been published on the chemical ecology of this species.

11.17. *Dendroctonus rufipennis* (Kirby)—Spruce Beetle

Based on beetle production and trapping data, four compounds have been proposed as attractive pheromone components for *D. rufipennis*: frontalin, seudenol, MCOL, and verbenene. All four compounds have been isolated from feeding beetles [54,122,202,301–305]. Gries [301] reported that *D. rufipennis* from an unstated source population produced pure (+)-frontalin, 66% (+)-seudenol, and 58% (+)-MCOL. However, at four of six sites sampled in eastern and western Canada, mean enantiomeric composition of frontalin was >90% (–)-enantiomer in both sexes; in two locations females produced a mean 62% (–) [305]. Among these sites, seudenol and MCOL were a mean 80% and 69% (+)-enantiomer, respectively, with minimal variation among sites [305]. Verbenene was a mean 89% (+) [305], although the enantiomeric composition of verbenene is likely governed by the *alpha*-pinene precursor from the host [301].

Geographic variation in production of pheromone components by *D. rufipennis* is suggested by differences in the composition of pheromone blends isolated at different beetle collection sites. However, substantial differences in beetle treatments and pheromone isolation methods could account for at least some of the contrasting results. Extracts of frass of solitary females collected in east-central British Columbia and boring 3 d in a host log revealed MCOL and seudenol in similar amounts, whereas whole-body extracts of paired males revealed neither of these compounds [202]. Frontalin was found in hindguts of solitary and paired, feeding females in eastern British Columbia and western Alberta, Canada [305]. Aerations (72–96 h duration) of beetles from Newfoundland, Canada feeding in glass tubes detected seudenol in females but neither MCOL nor frontalin from either sex [303]. Hindgut extracts of beetles from Nova Scotia, Canada indicated that feeding solitary and paired females produced MCOL and seudenol, whereas paired males produced both seudenol and frontalin [54]. Proportions among compounds differed substantially 24 and 48 h following introduction into logs, implying that timing of sampling might explain disparate results of some studies [54].

Isitt, et al. [305] performed the first systematic study of geographic variation in pheromone production by *D. rufipennis*. To simplify the characterization of pheromone composition of individual beetles, the authors used K-means clustering to divide the pheromone blends into four distinct profiles of the proportions among frontalin, MCOL, seudenol, and verbenene. The “frontalin profile” was disproportionately frontalin with MCOL generally absent; the “frontalin/verbenene profile” disproportionately contained both these semiochemicals; the “MCOL profile” was dominated by MCOL with lesser amounts of seudenol; and the “seudenol profile” was dominated by seudenol with small amounts of MCOL and frontalin entirely absent. Hindguts of feeding solitary females and paired beetles were sampled from infested trees at six different sites in both eastern and western Canada. The representations of the profiles among the sample sites differed significantly, with a higher frequency of the MCOL and seudenol profiles among females east of the Rocky Mountains and a higher frequency of the frontalin profile within or west of the Rocky Mountains. Isitt, et al. [305] also discovered significant differences in the pheromone profiles of beetles emerged from logs of different trees at the same site.

Frontalin (racemic or with enantiomeric composition unreported), alone or with *alpha*-pinene, was attractive to one or both sexes in traps or on baited trees in one or more experiments in south-central and interior Alaska, southeastern and south-central British Columbia, and northwestern Alberta [171,202,306–308]. However, in Newfoundland and in some experiments in interior Alaska and south-central British Columbia, the combination of *alpha*-pinene and frontalin was unattractive alone [171,202,303] and in northern British Columbia had only weak attractancy [309]. *Dendroctonus rufipennis* displayed a negative dose response to frontalin lures releasing more than 0.1 mg/d in Alaska, whereas no dose response was apparent with release rates between 0.06 and 5 mg/d in northern British

Columbia [171,309]. Seudenol alone or with *alpha*-pinene attracted *D. rufipennis* to traps in Alaska [152,171], and seudenol increased responses to frontalin and *alpha*-pinene in Newfoundland [303]. In contrast, seudenol had no effect on responses to frontalin and *alpha*-pinene in Utah, USA [310].

MCOL has alternatively displayed attraction enhancement or inhibition, sometimes observed in experiments repeated at the same sites, and no clear relationship to geography has emerged. Activity (attractive or inhibitory) for MCOL when added to traps with lures containing frontalin has been detected in at least some tests in south-central and interior Alaska; southeastern, southwestern, and northern British Columbia; northwestern Alberta; Newfoundland; and Utah [171,202,303,309,310]. Likewise, there is little consistency in enantiomeric preferences for MCOL, with attractive responses displayed for both the (–) and (+)-enantiomers, although preferences have typically been for the (+)-enantiomer [171, 202,309]. A trapping study in Alaska with releasers of MCOL ranging from 0.6–4.5 mg/d failed to detect a dose-response trend, and thus did not support the hypothesis that some of the variability in behaviors to MCOL is due to a biphasic dose response [171]. Releasers of (+)-MCOL significantly increased attacks on trees also baited with frontalin and *alpha*-pinene in both south-central British Columbia and northwestern Alberta [202].

At a release of 2 mg/d, verbenene was reported to enhance *D. rufipennis* attraction to the combination of frontalin and *alpha*-pinene in southeastern British Columbia [302], however, later tests at this location and in southwestern British Columbia and northeastern Alberta failed to demonstrate activity [202]. In separate studies in interior Alaska, verbenene enhanced attraction to frontalin, *alpha*-pinene, and MCOL [171,202].

The large variability in both pheromone production and response by *D. rufipennis* lacks a consistent relationship with geography, and evidence that beetles reared from nearby trees can possess different pheromone production profiles suggests coexistence of distinct pheromone lineages [305]. A study of mitochondrial DNA and nine microsatellite loci identified three major haplotype groups for *D. rufipennis*, one occurring along the Rocky Mountains from British Columbia south to Arizona, and two that substantially overlap geographically from Newfoundland to Alaska but are nonetheless 3%–4% divergent in their mtDNA sequences [311]. Intraspecific variability in semiochemistry may coincide with these genetically distinct subpopulations, and this possibility deserves further investigation.

In central British Columbia, monoterpene blends representing the composition of volatiles from either the bole or foliage of spruce (blends including some combination of *alpha*-pinene, *beta*-pinene, 3-carene, camphene, limonene, myrcene, or bornyl acetate) released at approximately 140 mg/d were attractive alone to *D. rufipennis* [82]. However, this spruce blend did not significantly increase attraction to a lure that included attractive pheromone components and *alpha*-pinene, although a blend duplicating Douglas-fir resin did enhance catches [82]. However, a different blend of spruce volatiles released at 2 g/d significantly enhanced catches by a frontalin and seudenol lure in Nova Scotia [303]. There are few studies where monoterpenes have been tested individually for effects on *D. rufipennis* attraction. In an experiment where the most attractive pheromone-lure treatments caught hundreds of beetles, the monoterpenes, *alpha*-pinene, *beta*-pinene, camphene, carene, limonene, myrcene, and *beta*-phellandrene alone and at an unreported release rate failed to catch a single insect [171]. At low release rates (≤ 2 mg/d), *alpha*-pinene did not enhance trap catches by the combination of frontalin and seudenol or frontalin and MCOL in Utah and Newfoundland [303,310]. Werner [171] indicated that *alpha*-pinene at an unreported release rate significantly enhanced attraction to lures containing frontalin alone but reduced attraction to seudenol.

11.18. *Dendroctonus simplex* LeConte—Eastern Larch Beetle

Pheromone production by *D. simplex* has not been systematically investigated. Francke, et al. [213] reported several potentially attractive *Dendroctonus* semiochemicals in female hindguts including (–)-frontalin, MCH, *trans*-verbenol, and verbenone. However, they did not indicate feeding status or geographic origin of the insects. Barkawi, et al. [112]

confirmed that females in Minnesota produce frontalin. Seudenol has recently been identified in female beetles in Minnesota (Emily Althoff, personal communication). Traps baited with seudenol alone or in combination with *alpha*-pinene are attractive to *D. simplex* populations in Alaska, Michigan, and New York, USA [128,312–314]. Lures with seudenol, *alpha*-pinene, and MCOL were also attractive, although MCOL did not have a significant effect on attraction [314,315]. Frontalin has alternatively been reported to be attractive [213], inactive either alone or in combination with seudenol or *alpha*-pinene [128,171,312], or inhibit responses to sources of attractant [313]. Verbenone, typically a bark beetle attraction inhibitor or repellant, significantly (approximately 4-fold) enhanced *D. simplex* attraction to traps baited with seudenol [312]. *alpha*-Pinene, although not attractive alone, significantly enhances catches in traps baited with seudenol [128,171,312,313]. 3-Carene was also found to increase attractiveness of seudenol, but its effect was not significantly different from *alpha*-pinene [314].

11.19. *Dendroctonus pseudotsugae* Hopkins—Douglas-fir beetle

Trapped or emerged, unfed females produce frontalin which decreases in quantity following entry into a host [316–320]. Males produce variable amounts of frontalin following pairing or forced, prolonged contact with other males [317,321]. Seudenol is produced by feeding females and may occur in emerged females and paired males of some populations [182,317,318,320,322]. MCH occurs in variable amounts in unfed females but is generally present in feeding females [317–319,322,323]. It also occurs in unfed males of some populations and in males confined with other males [317,322,324]. MCOL is produced by both unfed and feeding females and by paired males [317,325]. Feeding females additionally produce 3-penten-1-ol [tentative, unconfirmed identification, 323]. Aerations of frass of feeding female beetles from south-central British Columbia contained 66% (+)-seudenol and 55% (+)-MCOL [326]. Differences in results among some of the above studies suggest geographic variability in pheromone composition, particularly between coastal Pacific and inland populations, with this variability possibly corresponding to genetic differences between the populations [327]. However, studies of pheromone production have largely been limited to western Oregon, Idaho, and southwestern British Columbia, and differences in production initially detected in coastal and inland populations were not reproduced when examined in a single study [320].

Frontalin, seudenol, and MCOL can be attractive without other pheromone components. Frontalin alone or with ethanol attracted *D. pseudotsugae* to traps in southern British Columbia and northwestern Oregon [153,326,328]. In combination with the host terpene camphene, it attracted flying beetles in Idaho [316] and, with *alpha*-pinene and camphene, attracted beetles to traps in western Oregon [182]. During the early semiochemical research on this species, this latter combination was called “doughlure” and used experimentally to induce *D. pseudotsugae* attacks on trees in Idaho [148,329]. When the only semiochemical, (–)-frontalin was more attractive in traps than (+) but did not differ significantly from the racemate in both interior and coastal British Columbia [326]. In western Oregon, seudenol dissolved in ethanol or released with *alpha*-pinene and camphene attracted beetles to traps [182], and it significantly increased responses to frontalin in northeastern Oregon [330] and to doughlure in Idaho and western Oregon [182,187]. In northeastern Oregon, catches by a combination of frontalin and seudenol held at a 2:1 ratio were maximum when the total release rate was 15–30 mg/d [331]. MCOL alone or with host odors (resin, *alpha*-pinene, or ethanol) was attractive to *D. pseudotsugae* in traps, and it significantly increased response to frontalin alone or with host odors at interior and coastal sites [132,325,330]. Frontalin and MCOL were additive in their effects at two coastal sites in southern British Columbia and synergistic at an interior site [328]. MCOL did not enhance attractiveness of seudenol and frontalin in northeastern Oregon [330]. When the only lure component, (+)-MCOL attracted more beetles than (–), with possibly additive effects of the enantiomers [132]. When combined with frontalin, both (+) and (–)-MCOL enhanced attraction similarly [132]. Response to MCH appears to be biphasic: at relatively low release

rates it significantly increased catches of *D. pseudotsugae* in traps baited with lures including frontalin, host resin components, and/or ethanol, whereas it reduced responses at higher rates [167,168,182]. Some results have suggested attractive effects for *trans*-verbenol and verbenone with *D. pseudotsugae* [153,182,332]. The compound 3-penten-1-ol was reported as having attractive effects but its identity as a *D. pseudotsugae*-produced compound or other natural compound in the environment of the insect was never confirmed [320].

The host odor ethanol, although not attractive alone [101,131], enhances attraction to frontalin as well as combinations of frontalin, seudenol, and host resin odors in Oregon and Idaho [187,330]. However, it eliminated the enhancing effect of adding MCOL to frontalin [330]. Combinations of ethanol and other host odors including Douglas-fir resin and its constituents *alpha*-pinene, limonene, and camphene were attractive to *D. pseudotsugae* in Oregon and Idaho [101,131,187]. Monoterpenes significantly increased attraction to frontalin in Idaho, with highest attraction being achieved with *alpha*-pinene and limonene, whereas mixtures of these and additional monoterpenes did not exceed responses to these monoterpenes singly [333]. In a study where synthetic blends of monoterpenes were mixed to duplicate odors of either interior or coastal Douglas fir [82], *D. pseudotsugae* of the two regions did not discriminate between the blends when they were combined with a pheromone lure (racemic frontalin and MCOL). However, attraction by the blends when alone or combined with the pheromone lure was inconsistent and may have been influenced by whether the blends were modelled with odors from either the bole or foliage of the host trees [82].

12. Conclusions

For several species of North American *Dendroctonus*, the body of research on attractants is overwhelming in its quantity and level of detail, but it is nonetheless rife with conflicts and inconsistencies that do not lend themselves readily to interpretation or resolution. As these “troublesome” species are those that have received the greatest research focus (e.g., *D. rufipennis*, *D. ponderosae*, *D. pseudotsugae*, and *D. valens*), it seems likely that similar but unrecognized complexities also exist in the attractant semiochemistries of less studied *Dendroctonus* species. Some of the complexities and conflicts may be resolved in future with taxonomic revisions to the genus. However, this review has highlighted some underappreciated sources of complexity that pose unique challenges to establishing fully reliable outcomes for deployment of attractants: unpredictable interactions among components of semiochemical blends, time of year, local beetle population densities, alternative sources of semiochemicals in the environment, and spatial arrangement of semiochemical sources. Data from trapping experiments may not reflect effects of a semiochemical in applications such as tree baiting [149,150], yet current understanding of the semiochemistry of *Dendroctonus* is derived almost entirely from trapping experiments. It is also remarkable that several species, including ones that can cause catastrophic levels of damage (notably, *D. mexicanus* and *D. simplex*), have received very limited study of their semiochemical systems despite over 60 years of availability of the necessary research tools. Nonetheless, despite the limitations of the current body of research, semiochemical attractants have been identified for 16 of 19 species of North American *Dendroctonus*, which is a noteworthy accomplishment.

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