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Chemical ecology of bark beetles

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Summary. The purview of chemical ecology and the recent criticisms of improper application of theory to bark beetle phenomena is briefly discussed. Seven levels of research in chemical ecology are presented as well as their relationship to research on bark beetles. The biology and chemical ecology of several pest bark beetles from North America and Europe are discussed in regard to host tree selection theories of random landing on trees or attraction to semiochemicals. The diversity and similarities of pheromone components among species are presented in relation to their biosynthesis from host tree precursors and in relation to the ecological implications of de novo or precursor syntheses. Individual variation in biosynthesis of, response to, and release of pheromones is discussed. Olfactory perception of semiochemicals at both the electrophysiological and behavioral levels is presented. Orientation to semiochemicals during walking and flying is discussed with reference to the significance of dose-response curves for determining a compound's functionality in short- or long-range communication. The regulation of attack density, termination of the aggregation, mechanisms of attack spacing, and recognition of host suitability are presented in the context of an individual's avoidance of intra- and interspecific competition. Finally, a brief summary of topics where our understanding of the chemical ecology of bark beetles and their associates is poorly known is presented.

Key words. Scolytidae; semiochemical; pheromone; allomone; kairomone.

Chemical ecology and ecology

Ecology is the science of the relations of an organism to both its biotic and abiotic environment which influence the organisms' distribution and abundance[77]. The biotic factors are included in the disciplines of physiology, behavior, genetics and evolution; ecology is especially concerned with the interface of these areas. Chemical ecology then concerns any aspect of ecology but involves the external chemicals which mediate the interactions. This definition is actually more comprehensive than many would accept, for instance, it could include macrophage antibody – microbe interactions, nutrient cycling, and much of biology. Traditionally, chemical ecology has been restricted to studies of the chemicals (semiochemicals) which mediate interactions between individuals of a species (pheromones) or between co-evolved species (allelochemicals, such as kairomones and allomones).

Alcock[1] criticized several bark beetle (Scolytidae) researchers for what he thought was their inadequate application of ecological theory in the explanation of bark beetle phenomena. His primary concern was that bark beetle mass-attack and colonization of host trees was often misunderstood in terms of 'species-selection' when in fact 'individual selection' was now the dominant theory. Today most realize that a deeper knowledge of bark beetle biology can be obtained if both the proximate and ultimate causes for the phenomena are considered.

Levels of research in chemical ecology

Research in chemical ecology of insects can be described with seven hierarchial levels which to some extent are chronological. The following examples will refer to the western pine beetle, *Dendroctonus brevicomis,* which aggregates en masse in response to an aggregation pheromone. The first step in the research is to (1) observe the biological phenomenon – e.g. demonstrate that *D. brevicomis* are attracted to odor from the infested host tree[89]. Once the biology is partially understood, one can design bioassays which are used to (2) isolate and identify at least one semiochemical component – e.g. *exo*-brevicomin was isolated from female frass by solvent extraction, concentration, gas-liquid chromatographic (GC) fractionation (collecting into discrete fractions the continuous successive elution of chemicals from the GC) and bioassay (testing each of the several fractions for attractive activity)[129]. Once a relevant compound is isolated, enough must be obtained for structure elucidation via GC-mass spectrometry (GC-MS), and often other spectrographic methods[127–129]. The third step involves (3) isolating and identifying all participating semiochemical components. For example, *D. brevicomis* males were shown to produce frontalin[73] which was synergistic with *exo*-brevicomin (i.e. neither compound alone is very attractive but together the blend is highly attractive), and the host tree monoterpene, myrcene, further enhanced the attraction[11, 12].

Once one chemical part of the ecological system, in this case the aggregation pheromone, is described, then (4) other pheromones, which may also act as kairomones or allomones, can be identified with respect to the biological phenomena. For example, intraspecific pheromone inhibitors of attraction such as verbenone[13, 109] and *trans*-verbenol[13, 32] cause individuals to avoid colonizing in high attack density patches and thus function in terminating the aggregation[45]. To further understand the chemical ecology, which appears to grow ever more complex, one must (5) quantify the rates of production and release of semiochemicals over the period of colonization. Some studies have measured the release rates of some semiochemicals from *D. brevicomis* over short periods[27], and others have followed the production of pheromone components in the beetle's guts during the colonization period[45].

Once the release rates of semiochemicals are known, the (6) mechanisms of pheromone production, olfactory perception, and the sites of biosynthesis and perception can be investigated – these areas will be discussed later. However, these topics become increasingly more peripheral to chemical ecology as they become more involved in physiology, behavior, genetics and evolution. Finally, one can (7) attempt a synthesis of the knowledge concerning known semiochemicals, release rates, interspecific interactions and biological phenomena in order to construct a working theory on how the semiochemicals mediate the interactions between individuals of various sexes and species.

Chemical ecology of bark beetles

Reviews of various aspects of bark beetle chemical ecology since 1980 have concerned semiochemicals in host selection and colonization[147], host odorants and pheromones[78], orientation[23], aggregation[18], aggregation pheromones[22, 23], stridulation and pheromones[117], biosynthesis[59], and competition and semiochemicals[38]. These reviews cover the field in more detail than can be done here. Instead this paper will highlight the chemical ecology of a few economically important systems: the pine beetles of the western and southern United States and the pine and spruce beetles of Europe in regard to selected topics.

The diversity of bark beetles and their biology can be appreciated in the taxonomic compilation of Wood[152] and in discussion of mating systems[74]. However, pest bark beetles are included in three categories: 1) 'aggressive' phloem-feeding beetles which must attack en masse living trees and kill them in order to reproduce, 2) vectors of tree diseases such as Dutch elm disease, and 3) wood boring beetles which weaken and stain lumber. Beetles in all three groups utilize pheromones but much of the following discussion will best apply to those in the first group. A generalized life cycle of these bark beetles, including many non-pest species, is depicted in figure 1. Before bark beetles begin their host tree and mate seeking flight, there may be a period of required dispersal flight before they become responsive to pheromone[4, 51, 65]. However, several species appear responsive to pheromone or host attractants soon after emerging from brood logs[40, 46] or overwintering sites[47].

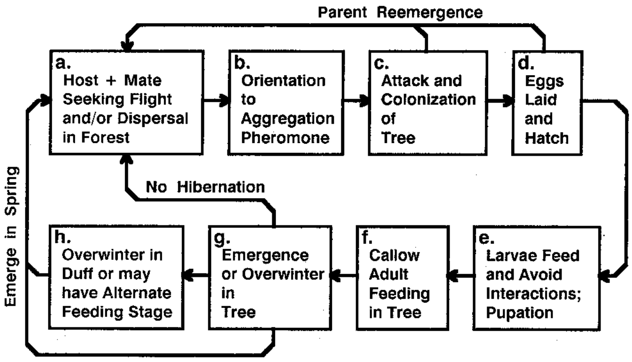

Figure 1. Generalized life cycle of a pest bark beetle. The letters refer to the order of discussion in the text.

Host selection. Little is known about dispersal and host selection except for the stages immediately preceding landing on the tree. Host selection for several pest species of the western United States is thought to be a random process in regard to landing on host and non-host trees[92, 147]. Ponderosa pines that were killed by freezing and screened to prohibit beetle attack, did not exhibit higher landing rates for *I. paraconfusus, D. brevicomis* or *D. ponderosae*, among others, than did healthy trees. Landing rate differences also were not observed between healthy trees and trees with diseased roots. Other studies have shown that population densities of *D. ponderosae*[71] and *Ips typographus*[3, 42] are often high enough to allow nearly every tree in a stand to be visited by at least one beetle. If beetles test the defenses of host trees (although there is as yet no evidence of this) then in theory stronger trees will repel beetles while weaker trees will allow pheromone production and mass colonization. It is well known that conifers can be induced to exude copious amounts of resin which can entrap beetles[45, 86, 89, 125] and has some toxic properties as well[131]. Healthy trees are able to exude more resin at a higher pressure[141] while weaker trees, diseased or drought-stressed, are less able to produce resin. In late summer when trees in California are drought-stressed it is often observed that attacks of *D. brevicomis* are not defended by resin flow and trees easily succumb[89]. Thus, in many bark beetle species host selection appears to occur after landing on the bark, and in *I. paraconfusus* it was shown that a rejection of the non-host white fir did not occur until after penetration of the phloem[57].

In other species, however, there is a long-range influence of host tree volatiles on host selection. *D. rufipennis* are attracted to volatiles from white spruce[91], *Scolytus multistriatus* to volatiles from American elm[103], and *D. valens* to volatiles from ponderosa pine[139]. Other bark beetles, often termed 'secondary' because they infest trees in more advanced stages of decay or are sapwood-infesting species, have been shown to respond to volatiles from their host trees[49, 64, 90, 92] and especially to ethanol[76, 90]. Ethanol is the most commonly occurring kairomone attractant for the 'secondary' species[76] and is supposed to be released from natural sources due to microbial activities, although this has not been quantified. In many cases it is known that a pheromone is released by the first arriving beetles which accounts for most of the subsequent aggregation of the population.

Also in contrast to a random landing process during host selection, *Tomicus piniperda* is strongly attracted by monoterpenes from Scots pine (terpinolene, α-pinene, and 3-carene) volatilizing from wound oleoresin[47]. A GC fractionation and subtractive-combination bioassay was performed on volatile air collections of logs infested by *T. piniperda* in order to find an aggregation pheromone but none was detected, however, the host tree monoterpenes (kairomones) were attractive[47]. This phenomenon was also suggested to function in the beetle's recognition of host susceptibility. Fallen trees or broken tops injured during winter storms have wounds with oleoresin that release the attractive monoterpenes and these trees are less resistant to beetles since they have a reduced ability to produce more resin (lower turgor pressure). Ironically then, the beetle is selecting a susceptible tree based on the very components normally used by the tree as part of its resistance mechanism.

Once the first individuals of the 'pioneer' sex arrive at the tree (males of *Ips* and *Pityogenes* or females of *Dendroctonus* and *Tomicus*) they are induced to begin boring into the tree. Little is known about what chemical stimuli are involved, few feeding stimulants or deterrents have been reported with the exception of *S. multistriatus*[56, 63, 97]. During the development of an artificial diet for *I. paraconfusus* it was found that sucrose stimulates feeding in a cellulose-based diet but not as much as sucrose plus 22% host phloem particles in the diet[41]. Other studies have demonstrated feeding stimulant properties in extracts of host phloem[58, 71]. The pheromone is released from fecal pellets after the bark beetles have fed on the phloem (and some xylem tissue)[149].

Biosynthesis and release of pheromone. Ips species generally must feed for several hours in order to produce detectable attractants in their fecal pellets[149], and significant attraction may not result until males have fed for more than 24 h[149]. The site of pheromone biosynthesis within bark beetles is still uncertain but the largest amounts of semiochemicals are found in the hindgut[17, 28–32, 39, 69, 80, 104, 107, 142]. Male *Ips* acquire α-pinene from vapor absorbed during breathing in galleries and from ingested phloem and then convert it to *cis*-verbenol (fig. 2) or *trans*-verbenol depending on whether the precursor is of *S* or *R* chirality[75, 110]. *Dendroctonus* species generally convert the respective *S* or *R* enantiomers of α-pinene to the corresponding enantiomers of *trans*-verbenol[32]. In contrast to *trans*-verbenol, the quantities of verbenone (fig. 2) in male *D. brevicomis* are not affected by exposure to α-pinene vapors[32].

Myrcene is converted to pheromone components hydroxylated at carbon 4 (ipsdienol and ipsenol) in various *Ips* species[29, 69] or to amitinol in *I. amitinus* (fig. 2)[60]. The bioconversion of myrcene to ipsdienol and ipsenol in *I. paraconfusus* is inhibited by the antibiotic streptomycin while other myrcene metabolites are not quantitatively affected[41]. However, no direct evidence has been found for microbe involvement in pheromone production. The biosynthetic enzymes appear to vary between individuals, populations, and species since the enantiomers of ipsenol and ipsdienol vary quantitatively and qualitatively between individuals of a population[70, 130] and between populations[79] of *I. pini* compared to other even larger differences between species[142]. *D. brevicomis*[30] and *D. ponderosae*[70] also are capable of transforming myrcene to (+)-ipsdienol which inhibits attraction to aggregation pheromone in *D. brevicomis*[30]. In addition to the commonly used α-pinene and myrcene-derived pheromone components, bark beetles in the genera *Dendroctonus, Scolytus* and *Trypodendron* utilize bicyclic ketals and tricyclic acetals (fig. 3)[73, 87, 104, 129]. In figure 3 it is easy to see the structural similarities of certain enantiomers of frontalin, *exo*-brevicomin and multistriatin. The importance of the correct enantiomer for each component in a pheromone was clearly demonstrated by Wood et al.[151] wherein only (−)-frontalin and (+)-*exo*-brevicomin were active in causing *D. brevicomis* to aggregate. The biosynthesis of these components is uncertain but appears different between the sexes; in *D. brevicomis*

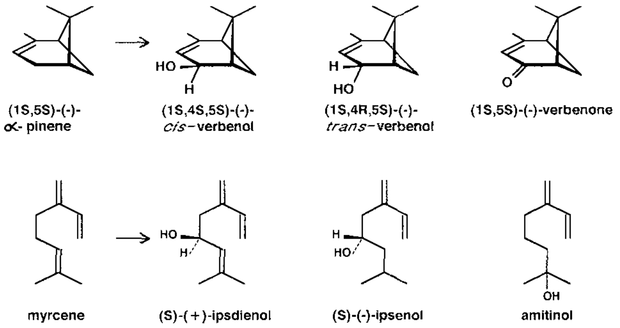

Figure 2. Biosynthesis of the tree monoterpenes (−)-α-pinene to corresponding enantiomers of *cis*-verbenol (an attractant pheromone component in *Ips*)[110, 150], *trans*-verbenol (an inhibitory or attractant pheromone component in *Dendroctonus*)[32] and possibly to verbenone (an inhibitory pheromone, allomone, and kairomone in several genera)[13, 39]; and conversion of the tree monoterpene myrcene to ipsdienol (pheromone component in *Ips* and *Dendroctonus*[30], ipsenol (pheromone component of *Ips*)[69, 150] and probably (unproven) to amitinol (a pheromone component of *I. amitinus*))[60].

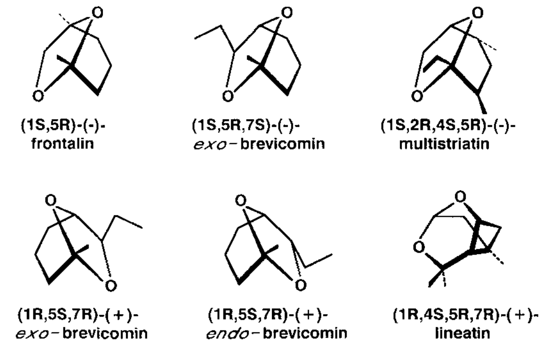

Figure 3. Structural similarities of *Dendroctonus* pheromone component enantiomers (frontalin, *exo*-brevicomin and *endo*-brevicomin)[129] to those of *Scolytus multistriatus* (multistriatin)[104] and *Trypodendron lineatum* (lineatin)[87].

the female produces *exo*-brevicomin after feeding whereas the male contains the largest amounts of frontalin upon landing on the tree[45].

Other structures of pheromone components of bark beetles are shown in figure 4. Short-chain terpenoid compounds are found in some European species (*I. typographus, I. cembrae*)[8,111] but not in the most important American pest species. 3-Methyl-2-cyclohexen-1-one (MCH) is a well-known inhibitor of *D. pseudotsugae* aggregation (fig. 4)[112,115]. A spiroketal, chalcogran, is found in several species of *Pityogenes*[61,123], while recently a unique acetogenic pheromone component, *E,Z*-2,4-methyl decadienoate (*E,Z*-MD), was found in *P. chalcographus* (fig. 4)[44,46]. The biosynthesis of beetle pheromones, with many examples for Scolytidae, has recently been reviewed by Vanderwel and Oehlschlager[138] in regard to biosynthetic pathways (largely speculative) based on a suspected precursor. Much of the speculation concerns the origin of the pheromone components – whether they are terpenoid (fig. 2), fatty acid, polyketide (fig. 3), hydrocarbon, or amino acid (2-phenylethanol)[138]. The physiological mechanisms of biosynthesis and hormonal control are also reviewed[138]. However, the ecological implications of the use of host plant precursors compared to the de novo synthesis of pheromone components is of interest here.

The advantages to an individual using de novo synthesis of a pheromone component is that control of the stereo configuration and quantity can be precisely regulated resulting in the optimal benefit in the specific environmental context. The possible cost is that more biosynthetic machinery is necessary with additional costs of energy required for linking the simple building blocks. The advantages in using an exogenous precursor in which only a small change, such as hydroxylation, is needed to make a pheromone are obious from an energetic standpoint. Also it seems that α-pinene and myrcene are routinely de-toxified by increasing their water solubility (hydroxylation or oxidation, fig. 2), so the products were available in evolutionary time to be used as pheromones. The risk for the beetle is that the host tree could influence the availability of monoterpene precursor or that variation in these compounds would confer a degree of resistance to those hosts with lower titers of precursor[30]. Sturgeon[135] and Smith[132,133] have shown how host precursors of pheromones vary geographically in ponderosa pine and the question is whether tree resistance might also vary due to pheromone quantity or, as they suggest, due to toxic resistance properties of monoterpenes, especially limonene[133,135].

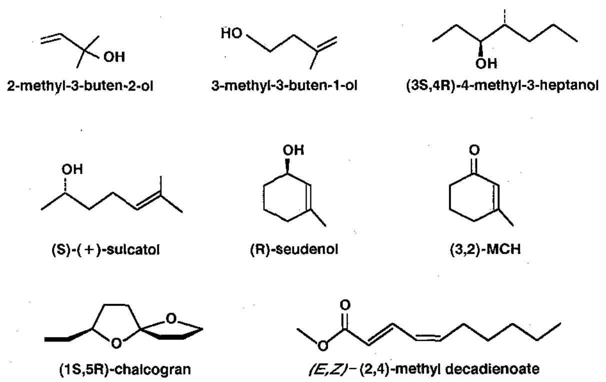

Figure 4. Examples of other pheromone components in *Ips typographus* (2-methyl-3-buten-2-ol)[8], *Ips cembrae* (3-methyl-3-buten-1-ol)[111], *Scolytus multistriatus* (4-methyl-3-heptanol)[104], *Gnathotrichus sulcatus* (S-(+)-sulcatol)[24,48], *Dendroctonus rufipennis*[62] and *D. pseudotsugae*, (R-seudenol)[83,145] and (3,2-MCH)[115], and *Pityogenes chalcographus* (*S,R*-chalcogran[61] and (*E,Z*)-(2,4)-methyl decadienoate[44,46]).

I. typographus and *D. brevicomis* have been attracted to pheromone blends that have varied greatly in the ratio of components[37,120]. At least in the case of *I. typographus*, this variation is due in part to host precursors[16,17,75] which are not under the control of the insect. Byers[30] suggested that myrcene and α-pinene were utilized by California bark beetles as precursors to pheromones because they were the most consistently present of the monoterpenes in host trees throughout a wide geographic range. Then, due to stabilizing selection[50] (communication requires conforming individuals) and gene flow, the species would tend to equilibrate genetically in response to the availability of host monoterpenes, which were de-toxified and then used as pheromone components.

The rather large variation in monoterpene precursors would, however, produce selection pressures that would necessitate the evolution of some degree of behavioral tolerance of variations in pheromone quantity (and component ratios) in beetles utilizing myrcene and α-pinene. The inherent individual variation in component production would be further amplified proportionally by the monoterpene variation. Although behavioral tolerance of varying pheromone component ratios derived exclusively from host monoterpenes has not been tested, bark beetles seem rather more tolerant[37,120] than moths[50] of pheromone component ratios.

Bark beetles even appear somewhat tolerant of variations in the ratios of enantiomers of an attractive component. The percentages of (+)- and (−)-ipsdienol in the natural ipsdienol of individuals in a local population of *I. pini* (east Kootenay region, British Columbia) were found to vary. About half the individuals had nearly pure (−)-enantiomer, 20% had about 10% (+), while 5% had about 35% (+)[130]. Over the geographic range of *I. pini*, the western population (British Columbia) averaged nearly 100% (−)-ipsdienol while the eastern population (New York) produced about 65% (+)-ipsdienol[79]. The response of the western population is inhibited by the (+)-enantiomer, not because of an avoidance of eastern individuals but because of avoidance of its competitor *I. paraconfusus* which produces (+)-ipsdienol[20]. The eastern population would not be attracted to western individuals because insufficient (+)-enantiomer is produced[20].

Few studies of bark beetles have measured the release of semiochemicals from natural sources due to the small amounts of semiochemical relative to contaminating host compounds. Browne et al.[27] quantified the release of attractive and inhibitory pheromone components of *D. brevicomis* boring in ponderosa pine by liquefaction of air. Since then porapak Q has been used as an adsorbent for attractive volatiles from *T. piniperda*[43, 47, 80], *I. typographus*[15, 122] and *P. chalcographus*[46]. This type of data is necessary to formulate theoretical models of semiochemical interactions during colonization of the host tree.

Observations of the immediate attraction of *D. frontalis* to incipiently colonized trees under high beetle densities caused Vité et al.[142] to propose a 'contact' pheromone whereby beetles would release pheromone upon landing on an attractive tree. While there have been no studies to determine the actual time of release, from an individual beetle's point of view it would seem better to release pheromone after acquiring an entrance tunnel with a female before committing resources (pheromone) to help in the colonization of the tree. Otherwise, a beetle might lose the advantage of arriving earlier and be outcompeted for access to females. In *D. brevicomis* males, which also contain frontalin and some inhibitors in the largest amounts upon landing (*trans*-verbenol, verbenone, and ipsdienol)[45], it would only make sense to an individual to release inhibitors from a place that is to be 'defended against' competitors rather than just anywhere on the tree. This also applies for release of 3-methyl-2-buten-2-ol (MB) by male *I. typographus* who contain relatively large amounts upon landing[17].

Olfactory perception of semiochemicals. The chirality of semiochemicals in bark beetles is important both in communication and in insect-plant interactions. The enantiomeric specificity is obtained by 1) the availability of chiral precursors of the host tree, 2) the chiral specificity of synthesizing enzymes, and 3) the enantiomer-specific acceptors on olfactory cells[55].

The electrophysiological response of an insect to chemicals can be measured using the electroantennogram (EAG) of the whole antenna or the single-cell technique which measures electrical responses of specific receptor cells. The antennal receptor cells each contain multiple acceptor sites that physically interact with the chemicals. Bark beetle olfactory cells on the antennae have been shown to be of several functional types, all of which generally are found in each species: 1) a 'labelled-line' or highly specific receptor cell such as the ipsdienol-sensitive cells in *I. paraconfusus* and *I. pini* which are responsive only to one or the other enantiomer[94], 2) a pheromonal cell which is also responsive to some other synergists or inhibitors such as the frontalin cells of *D. frontalis* (the cells have at least two acceptor types specific for each enantiomer of frontalin)[54, 102], and 3) 'generalist' receptor cells which respond to host monoterpenes as well as pheromones to some extent[54, 55]. However, the possibility that impurities in the monoterpenes account for the receptor activity has not been definitively ruled out.

The technique of 'differential adaptation', in which a receptor cell (or antenna) is first adapted with a compound by saturation of specific acceptor sites and then exposed to a different volatile to see if an electrical response can be elicited, has been used to determine the types of semiochemical acceptors on a cell[55, 99, 100]. By using this technique with single-cell recordings it has been shown that *D. pseudotsugae* has at least four olfactory cell types[55]. Three types are each most sensitive to either MCH, seudenol, or frontalin, although they are all stimulated somewhat by all of these pheromone components[55]. The fourth cell type is most sensitive to beetle-produced synergists and host attractants and is less sensitive to pheromone compounds[55]. Acceptors are specific for one enantiomer of a chiral mixture[101] and there may be either only one type of acceptor per cell (e.g. (+)- or (−)-ipsdienol in *I. paraconfusus*[94]) or both types of chiral acceptors on the same cell (e.g. (+)- and (−)-frontalin in *D. frontalis*[102] and *D. pseudotsugae*[55]).

In *I. paraconfusus*, both sexes have equal receptor sensitivity (EAG) to natural pheromone and to (+)-ipsdienol[85]. However, the males have been shown to be relatively less attracted by higher concentrations of synthetic pheromone components and were also not as likely to fly directly to the pheromone source as were females[33]. Thus, the sexual differences in behavioral response appear to be the result of differences in central nervous system (CNS) integration. Both sexes of *I. typographus* have similar dose-response curves for *cis*-verbenol but some differences for MB[53]. Similar to *I. paraconfusus*, males of *I. typographus* also are less directed to pheromone at the final landing than are females[121]; this behavioral difference could be due either to CNS differences between the sexes or to the lesser receptor sensitivity of males to MB.

Mustaparta et al.[94] have shown that eastern U.S. populations of *I. pini* have separate cells for the two ipsdienol enantiomers that are synergistic attractants[79]. However, the exposure of the two cells to the enantiomers together did not synergistically increase the nerve impulse rate so it was concluded that synergism here acts at the CNS level[94]. In contrast, Dickens et al.[55] have shown that the behavioral effects of MCH on *D. pseudotsugae* may be due in large part to peripheral receptors rather than as a result of CNS discrimination. At low concentrations MCH has acted as an attractant synergist[112] and certain olfactory cells have been found which are highly specific and sensitive to MCH in both sexes[55]. The dose-response curve was judged to be relatively wide, suggesting a long-range orientation effect. However, at higher concentrations, MCH caused a decrease in spontaneous activity of other receptor cell types sensitive to other components[55]. Thus, the behavioral inhibition of attraction by MCH[112, 115] could be the result of CNS reception of the impulse frequency of the specific receptor type and also the peripheral inhibition of receptor activity[55]. Whether this peripheral inhibition is a general phenomenon of semiochemical inhibitors is not known, although the ipsdienol inhibitors of *Ips*, mentioned above, appear to function only at the CNS level.

Of the three or four receptor types found in most species[54, 55, 94, 95] it appears that individual receptors within a type also can vary in their response spectrum to various chemicals[94, 95, 137]. In the few cases so far known, the host-responsive cells are present in both sexes but the host-selecting sex (males of *Ips* or females of *Dendroctonus*) is slightly more sensitive to plant compounds[53-55]. However, the role of plant compounds in long-range orientation of *Ips* is not certain; while short-range behavior is probably influenced, it also is poorly understood. *I. typographus* is purported to be sensitive to *exo*-brevicomin since it increased response to the pheromone components[137], although it is not present in this species[15-17]. However, sympatric *D. micans* and/or *Dryocoetus* sp. produce *exo*-brevicomin and thus *I. typographus* could locate susceptible host trees by responding to species that colonize weakened hosts[137]. This same phenomenon, on the behavioral level, was suggested for *D. brevicomis* and *I. paraconfusus*[40]. However, the effects of 'unnatural' semiochemicals on bark beetle receptors must be considered with caution. Lanne et al.[80] have shown that *T. piniperda* shows EAG responses to *exo*-brevicomin, ipsenol, and other compounds not known to be associated with the beetle or any competing species.

The difficulties with electrophysiological methods for unraveling ecological phenomena are two-fold: (1) the electrical responses may not be correlated to the relevant behavior and (2) the nerve impulse patterns vary even within a cell type[94], all of which are not located and tested, and the patterns are further integrated in the 'black-box' CNS. It remains a great challenge to understand even incompletely the 'cross-talk' interactions and 'decoding' of nerve impulses from receptor cells at the peripheral level, a nearly impossible challenge when the CNS is considered.

Orientation to semiochemicals. Compared to moths[5, 72], much less is known about orientation mechanisms of flying bark beetles in part due to their small size and difficulty of study in wind-tunnels[51]. A rotating wind-vane trap has been used to confirm the belief that bark-beetles fly up-wind in response to a pheromone[36], however, little more is known of flight behavior. Byers[33] used grids of traps distant from a natural pheromone source and found that male *I. paraconfusus* do not fly directly to the source as females do, the reason being that males avoid patches densely colonized with potentially intense competition. This phenomenon has been observed in other polygynous species, e.g. *I. typographus*[120] and *P. chalcographus*[44]. Sex-specific differences in *D. brevicomis* induced by *trans*-verbenol were observed when females were found to be inhibited from entering holes in artificial hosts releasing synthetic pheromone attractants while males were not. Sexual differences were not found in long-range orientation to pheromone component mixtures[32], but single components (either *exo*-brevicomin or frontalin) caused the sexes to respond differently[35, 37]. The orientation of flying bark beetles is expected to use optomotor (visual) self-steered counterturning and anemotaxis in accordance with moth studies[5, 72], although we have little evidence to support this belief.

Orientation by walking has been studied more often[19, 20, 30, 32, 33, 40, 46, 47] but with the objectives of observing attraction or inhibition by semiochemical blends. Recent studies have shown that bark beetles can orient in still air up a diffusion gradient[148]. Although still air does not normally occur in nature this chemotactic mechanism may operate a few millimeters from an entrance hole. Host monoterpenes (camphene, α-pinene, β-pinene) of Norway spruce caused *P. chalcographus* to enter 'beetle-sized' holes in cylindrical 'tree-sized' traps more so than controls (both released pheromone components also)[44].

It has been proposed that a long-range orientation function for a semiochemical was indicated if the compound had both a low threshold and a wide range of concentrations which elicited an electrophysiological response using EAG or single-cell recording. Conversely, a short-range function was indicated for a semiochemical if the electrophysiological activities were observed only with a relatively high threshold concentration and over a narrow range of concentrations[53]. However, the evolution of an ability to detect a certain threshold concentration would depend on the absolute amounts available in nature, and thus a specific threshold (low or high) is not a valid indicator of the distance over which a semiochemical functions. Still, the breadth of the dose-response range (often shown to cover 5 orders of magnitude) does appear to be a valid indicator of a compound's role in distance orientation since a wider response to concentrations would be required over a wider range of distances from the source[53]. Since (*S*)-(−)-*cis*-verbenol had an effect on receptor cell response over a wide range, it was suggested to function in long-range attraction in *I. typographus*, while MB had a narrow range (two orders of magnitude) and was thought to be a close-range signal[53]. Field tests with various ratios of these two components were reported to support the concept[121]. However, when either component was released alone there was no significant difference in catch on traps 3 m from the source and few beetles were attracted[121]. Holding either component constant and varying the other caused a synergistic increase in attraction at the source[121]. Thus the theory of dose-response range width as an indicator of orientation range function needs more investigation – especially since the responses to MB were not tested at higher concentrations which ultimately would saturate the acceptors[53].

A possible complication when attempting to ascribe a short- or long-range function to a semiochemical is that receptor response to a wide range of dosages may also have evolved due to the natural variation in release rates of the semiochemical. MB synthesis is under endogenous control in male *I. typographus* and relatively large amounts are found in the gut (up to 4 μg/gut) relative to *cis*-verbenol[16, 17]. Thus it may be expected to vary less than *cis*-verbenol which is dependant on the quantity of (−)-α-pinene[75], a function of genetics and vigor of the tree[17] in addition to the beetle's enzymes. The ability to respond to a wide range of concentrations would be required not only for orientation, where concentration decreases with distance[93], but also because aggregations of beetles vary in size and pheromone release rates[37].

A third possible factor complicating the interpretation of dose-response curves is that not all semiochemicals are equally volatile. MB is one of the most volatile of bark beetle pheromones and is found in one of the largest amounts per beetle ($\bar{x} = 0.5$ μg/male), while *cis*-verbenol is produced in small amounts (0.06 μg/male) and is less volatile[17]. *E,Z*-MD is one of the least volatile of bark beetle pheromone components (having a volatility comparable to moth pheromones) and is produced in the smallest of amounts (0.01 μg/male)[46]. Whether this quantitative-volatility relationship holds more generally for bark beetle pheromones is not yet clear.

Attack density regulation and termination of aggregation/attack mediated by semiochemicals. In response to the pheromone from the pioneer beetles resident in the tree, flying beetles orient to the tree, some joining established galleries while others begin excavations in the bark. The release of pheromone from these many new attacks increases perhaps as a logistic function such that the resinous defenses of the tree are overwhelmed[45, 68, 108, 147]. Once the tree has been rendered effectively defenseless, the functional cooperation among beetles ends and competition for the two-dimensional phloem becomes progressively more severe as the aggregation and attack continues[2, 14, 34].

This intense competition has provided strong selection pressures for the evolution of individuals adept at avoiding or reducing the degree of competitive interactions with conspecifics and with individuals of competing species[34, 38]. As mentioned previously, *I. paraconfusus* males can determine the likelihood of competition based on the strength of the pheromone signal. They avoid orientating to the highest release sources while females prefer these areas of the tree[33]. At the peak of the female landing period on a felled tree, the male landing rate actually declined indicating that males may have been attracted (as shown in long-range orientation through a grid of traps) but did not land and then chose to fly elsewhere[33]. These behaviors would serve to spread the colonization area in *Ips*[33, 120, 121] and *P. chalcographus*[44] as well as by a more simple 'spill-over' or imprecision in orientation to pheromone. This latter mechanism may also account primarily for the switch of attack focus to surrounding trees by *D. frontalis* and other pest species[3, 52, 119].

Bark beetles appear to have behavioral mechanisms which space the attacks and gallery systems in order to reduce competition to tolerable levels. The mechanisms by which beetles choose whether to attack near previously attacked sites and at what distance are poorly known. Spacing of attacks has been shown in *D. ponderosae*[118, 124], *D. frontalis*[88], *D. pseudotsugae*[67], *T. piniperda*[96] and *I. typographus*[34]. A computer method of comparing simulated attack densities at various minimal spacings between nearest neighbors to the natural attack patterns has been developed[34]. It showed that *I. typographus* attacks would have the observed average nearest neighbor distances if the beetles initiated entrance holes at least a minimum allowed distance (MAD) of 2.5 cm from other holes. This distance was apparently the same regardless of the natural attack density and thus appears to be an inherent biological distance characteristic of the species[34].

The possible mechanisms that account for these spaced attack distributions and the MAD are (1) olfactory communication[34], (2) stridulation/acoustic communication[67, 112–116], (3) selection of bark structures[57, 118], and (4) visual inspection of attack sites or beetles, or various combinations of these. Olfactory communication between *Ips* males has been discussed above and could also function even more strongly at close-range. In *D. pseudotsugae*, an arriving male stridulates at the female's entrance hole and stimulates her to release MCH[113, 115]. The male also releases MCH[83, 106] which has an inhibitory effect at long-range and apparently also at close-range[112–115]. Verbenone, *trans*-verbenol and (+)-ipsdienol have been shown to inhibit attraction of *D. brevicomis* to pheromone components at long-range[13, 30] and (−)-*trans*-verbenol at close-range[32]. Female stridulation alone has been implicated in the spacing of *D. brevicomis*[113]. Bark structure does influence the selection of attack site[57, 118] as well as the density of attacks, but it may have little affect on the spacing patterns or MAD.

Termination of aggregation and attack may be the result of saturation of the available bark areas as constrained by the spacing mechanism (MAD)[34]. After the sexes pair, the production of pheromone declines as shown experimentally in *I. paraconfusus*[28] and by observations of gut volatile contents in tree-colonizing *I. typographus*[17] and *D. brevicomis*[45]. Thus, a spacing mechanism and cessation of attractant release after mating could explain the mechanism of termination of the aggregation. However, in *T. piniperda* termination may also be influenced by verbenone emanating from infested logs with only a small portion from the beetles themselves[43, 80]. Similar studies with *I. typographus* have shown that

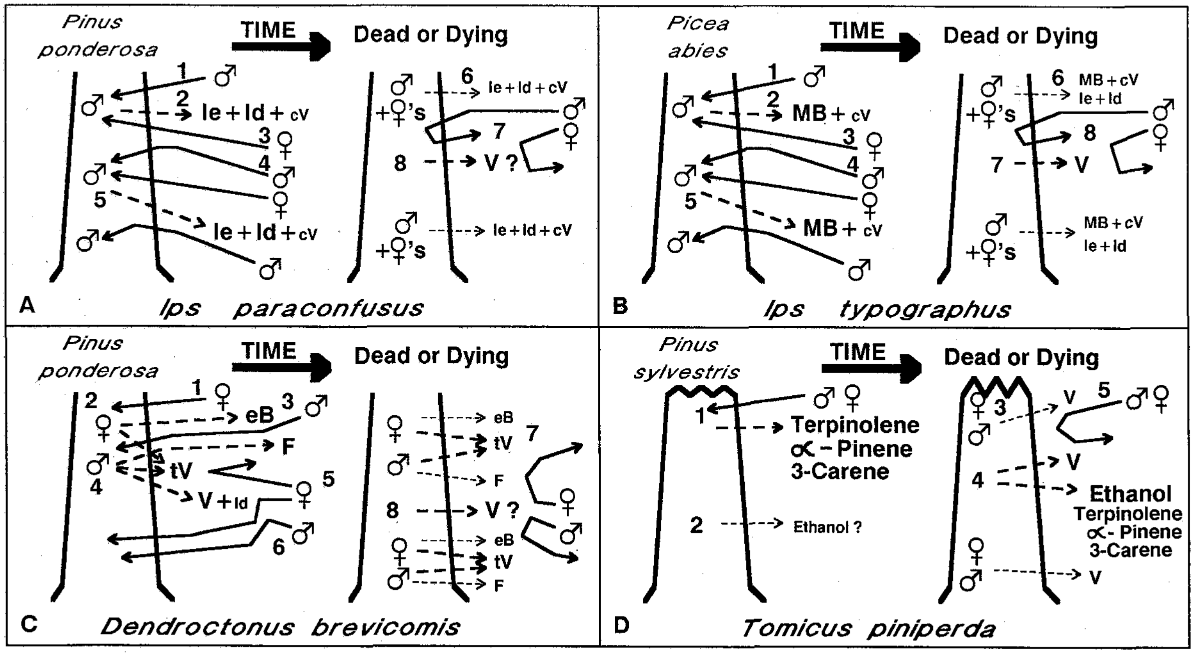

Figure 5. Theoretical mechanisms for regulation of aggregation and attack density (intraspecific competition) and termination of aggregation in four species of bark beetles. *A Ips paraconfusus* colonization of ponderosa pine. The male beetle arrives first [1] and constructs a nuptial chamber in the phloem layer. His release of ipsenol (Ie), ipsdienol (Id) and cis-verbenol (cV) [2], attracts both sexes [3][126–128, 150], but at higher concentrations near the source, males are inhibited in close-range orientation and thus land in adjacent areas of lower male attack density [4][33]. This process is repeated and serves to evenly spread the colonization and regulate attack density [5][33]. After males are joined by several females, their production of the pheromone components, Ie and Id, declines rapidly [6][28] and the tree becomes unattractive to beetles [7]. However, it appears that an additional mechanism (verbenone, V, from microbes in the tree?) is needed to both regulate density and terminate attack initiation during the later stages of colonization [8]. V has been shown to inhibit attraction to natural pheromone[39]. *B Ips typographus* colonization of Norway spruce. The male arrives first [1] and releases 2-methyl-3-buten-2-ol (MB) and cis-verbenol (cV) [2] which attracts both sexes from a distance [3][8], but as males approach high concentrations of pheromone they become less precise than females in close-range orientation and so land in adjacent areas [4][120, 121]. These sex-specific behaviors function to spread the attack and limit attack density in a way similar to *I. paraconfusus*. Males of *I. typographus* also reduce their release of pheromone components after 'mating' [5][17] but in addition they release small quantities of ipsenol (Ie) and ipsdienol (Id)[15, 17], which inhibit response of both sexes probably only at close range [6][6, 119]. These compounds could function to both regulate attack density and terminate aggregation (along with a decline in attractants). However, verbenone (V) from microorganisms in the bark beetle galleries [7] could be the more general inhibitor responsible for termination of aggregation [8][6, 81, 82, 119]. *C Dendroctonus brevicomis* colonization of ponderosa pine. The female beetle arrives first [1] and bores into the trunk and after feeding produces exo-brevicomin (eB) [2][129], which primarily attracts males [3][35, 37]. Males, upon locating a female gallery, soon release frontalin (F) [4][74], which synergizes with eB to elicit a mass aggregation [5][11, 12]. However, at the same time females and males produce *trans*-verbenol (tV)[32] and males produce verbenone (V) and (+)-ipsdienol (Id)[30, 45]. At close range these compounds apparently inhibit the attraction of beetles to eB and F (tV appears to primarily affect females while Id and V affect both sexes), which would regulate the attack density[13, 30, 32]. After several days the production and release of eB and F diminishes to levels that are unattractive at long range[45]. The few females attracted during this latter period may be inhibited from attacking by the still significant, although reduced levels of tV [7][45]. The few males would not find any unpaired females and so would continue searching elsewhere. Verbenone may also increase in release rate as the tree decays and so inhibit beetles [8], although measurements have not been done. *D Tomicus piniperda* colonization of Scots pine. Both sexes arrive simultaneously en masse on the first day in spring above 13 °C in response to host monoterpenes, terpinolene, (±)-α-pinene and (+)-3-carene, released from resinous wounds incurred during winter storms [1][47, 80]. Females and males pair up under bark flakes and the females tunnel into the bark followed immediately behind by the male. Trees that have fallen earlier in the winter and are beginning to decay probably release ethanol which in relatively small amounts may enhance the attraction to monoterpenes [2][76] but at higher amounts is inhibitory[76]. Both sexes contain verbenone (V) in the largest amounts shortly after entering the tree and amounts decline thereafter [3][80] while V released from the tree continues to increase [4][43] possibly due to microbial activity in the tissues surrounding the galleries. Ethanol may increase in release rate due to fermentative processes (unproven) while monoterpene release gradually decreases[43]. V released in traps at rates comparable to rates released from infested sections of a tree was able to inhibit attraction of both sexes to the attractive monoterpenes also released at natural rates[43]. V may serve both to space attacks (when released from individuals) and to terminate the aggregation (when released generally by microbial decay).

verbenone from microbial activity in infested trees may play a major role in termination of the aggregation[6, 15, 81, 82, 119].

In figure 5, semiochemical mechanisms which mediate the aggregation, attack density and termination of aggregation are presented for four species of bark beetle.

Interspecific interactions mediated by semiochemicals. Semiochemicals function in interactions between bark beetles in primarily two ways: (1) as allomones for interspecific communication of resource use in order to avoid competition and (2) as kairomones for use in locating weakened hosts colonized by another species. In California and other regions of the western United States, four pest bark beetles compete more or less for ponderosa pine (fig. 6). Verbenone released by male *D. brevicomis*, in addition to its intraspecific effects, appears to inhibit the response of its competitor, *I. paraconfusus*, to pheromone[39]. Verbenone has also been found in *I. pini* males from Idaho that had fed in red pine logs, but no behavioral role was ascribed[79]. However, I suggest here that

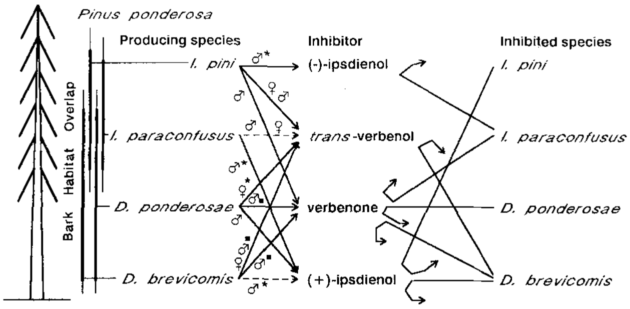

Figure 6. Inhibition of the attraction response to conspecific pheromone by allomones produced by four sympatric bark beetles, *Dendroctonus brevicomis, D. ponderosae, Ips paraconfusus*, and *I. pini* which appear to function in reducing interspecific competition for ponderosa pine in California. Response inhibition by the pheromones *trans*-verbenol, verbenone, and (+)-ipsdienol may also reduce intraspecific competition in *D. brevicomis*. The asterisks indicate pheromone attractants and black squares indicate pheromone inhibitors of attraction.

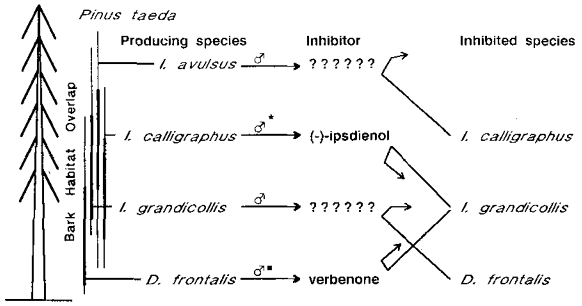

Figure 7. Inhibition of the attraction response to conspecific pheromone by allomones produced by four sympatric bark beetles, *Dendroctonus frontalis, Ips grandicollis, I. calligraphus*, and *I. avulsus* which appear to function in reducing interspecific competition for southern pines in the southeastern United States[21, 136]. Verbenone also acts as a pheromone in *D. frontalis* that reduces response to aggregation pheromone. The asterisks indicate pheromone attractant and the black square a pheromone inhibitor.

the observed inhibition of attraction of *I. paraconfusus* to its pheromone by logs infested with *I. pini*[19] appears due in part to verbenone, a major volatile component in *I. pini*[79, 142]. Earlier it was reported that only (−)-ipsdienol from *I. pini* was responsible for inhibition of *I. paraconfusus*[84]. Thus, the inhibitory effect of verbenone on *I. paraconfusus* may have resulted from selection pressures to reduce interspecific competition from both *D. brevicomis* and *I. pini* (fig. 6). Similarly, the inhibitory effects of verbenone on *D. brevicomis* could be the result of selection pressures from both intra- and interspecific competition (from *I. pini*). Multiple selection pressures could also account for the inhibitory effects of *trans*-verbenol on *D. brevicomis*[32] (fig. 6) which is produced in significant amounts by *D. brevicomis*[32], by *I. pini*[79, 142] and by *D. ponderosae*[107]. The (+)-ipsdienol produced by male *I. paraconfusus*[126] and by male *D. brevicomis* in the early stages of colonization[45] may function both to reduce intraspecific competition in both species[30, 33] and to reduce interspecific competition from *I. pini* in both species (fig. 6)[20, 30].

A similar situation of competitive interactions exists among four sympatric bark beetles of southern pines (fig. 7). *I. calligraphus* produces (−)-ipsdienol as one of the attractive components[142, 144] and this also acts as an allomone to inhibit *I. grandicollis* attraction to its pheromone[21, 143]. Allomonal volatiles from *I. avulsus* are inhibitory to *I. calligraphus*[21]. Verbenone, produced by *D. frontalis*[106, 109] acts as a pheromone that inhibits attraction as well as an allomone that inhibits attraction of *I. grandicollis*[21]. The use of allomones appears to reduce competitive interactions among the southern pine beetles just as they do in the western pine beetles.

The bark beetles attacking pines in the southern United States are different from their western counterparts[18, 19, 39], however, in that they are cross-attractive to each others' pheromones (fig. 8)[21, 136]. The reason for the strongest interspecific attraction, *I. avulsus* attraction to pheromone of *I. calligraphus*, is probably that *I. avulsus* locates weakened hosts already infested by *I. calligraphus* and that the potential competition is tolerable since both species utilize somewhat different levels of the tree (fig. 7)[98, 136].

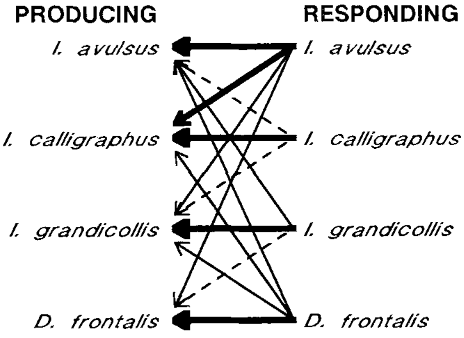

Figure 8. Cross-attraction of four sympatric bark beetles colonizing pines in the southeastern United States[21, 136]. Thick-line arrows indicate strong attraction (65% – 100% of conspecific attraction), thin lines indicate weaker attraction (5 – 12%) and dashed lines little attraction (2 – 5%).

Therefore, the above discussion indicates that olfactory systems evolve as a result of the relative benefits of multiple factors including avoidance of intra- and interspecific competition. Coevolution would favor the sharing of semiochemicals so that specific compounds could serve in communication both intra- and interspecifically. There would also be a selection pressure for use of biosynthetic pathways that produce the semiochemicals from host precursors, as long as the precursors were consistently available. Thus (+)-ipsdienol, from myrcene, and *trans*-verbenol (and possibly verbenone), from α-pinene, may have become pheromone components and allomones for a growing list of species. However, another hypothesis is that verbenone was already consistently present in decaying hosts due to microbial activity[25, 26, 43, 82], and then was subsequently used over evolutionary time by bark beetles as pheromones and allomones[38].

The predators, parasites and other associated insects interacting with bark beetles comprise a complex guild of species. During the course of aggregation of *D. brevicomis* on ponderosa pine, over 100 species of insects were collected[134]. Associated insects of bark beetles locate the breeding habitat either by landing at random, or using kairomones from the beetle (often their pheromones)[7,12,140,146,147] or other kairomones from the dying tree[76] or possibly other associated insects. The primary requirements of a kairomone are that it be a reliable indicator of host condition or presence and that the host (or fermentative process) can not dispense with its use. Thus, pheromone components of bark beetles are the most likely volatiles to be utilized as kairomones by predators and parasitoids since the adaptive advantages for the emitter outweigh the disadvantages as a kairomone, and so not net selection pressure for changing to other compounds will occur.

The chemical ecology of adult and larval interactions under the bark (e.g. they appear to avoid intersecting galleries[38]), callow adult movements, emergence, and overwintering (fig. 1, d–h) are practically unknown. Gregoire et al.[66] indicated that larval *D. micans* maintained a feeding aggregation in response to *cis*-verbenol. Fungal interactions with bark beetles in regard to host tree resistance[68,108,125], nutrition of larvae[10] and host unsuitability[25,26,43,81] are not well understood. Sexual recognition and species recognition are due in part to stridulation[9] but probably more so by specific cuticular chemicals[105] – a subject not yet investigated in bark beetles.

The field of chemical ecology of bark beetles encompasses much more than can be covered here, but it is hoped that one can appreciate that bark beetles and their associates are among the best of model systems for the study of chemical ecology.

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