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Host Compounds as Semiochemicals for Bark Beetles

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Abstract—In field tests, methyl chavicol is a strong anti-aggregant for several species of bark beetles. One low dose of methyl chavicol reduced aggregation by 40 to 68 percent for two species of *Dendroctonus* and two species of *Ips*. Methyl chavicol is a naturally occurring aromatic ether that is found in many species of hard pines. In ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*P. contorta* Loud.) that were stressed by smog or disease and preferentially attacked by bark beetles, a 43 to 70 percent decrease in methyl chavicol was the largest phytochemical change compared to healthy control trees. Methyl chavicol may provide an olfactory chemical link to the observed ecological association of bark beetles with stressed trees. Study of the responses of bark beetles to host compounds with and without beetle pheromones holds great promise for integrating basic plant/herbivore research with applied efforts to develop semiochemical-based bark beetle management.

Host plant odors pervade the atmosphere in forests where bark beetles occur. The remarkable olfactory acuity of bark beetles to semiochemicals in their environment has been well demonstrated in pheromone research (Borden 1985; Wood 1982). However, our understanding of bark beetle responses to plant odors is in its infancy. Investigation of host plant odor and biochemistry with new biochemical analytical abilities should provide—and has already suggested—new semiochemical tools such as stereospecific attractants and interruptant kairomones. Such chemical tools can augment pheromone-based approaches to bark beetle management. Investigation of bark beetle response to host volatiles also provides a close link with basic plant/herbivore and plant stress studies. Recognizing the evolution of host and herbivore biotypes, and understanding the mechanism of herbivore selection of diseased or susceptible hosts are challenges we can address with detailed knowledge of the dynamics of plant secondary compounds and insect response to these changes.

In: Salom, Scott M.; Hobson, Kenneth R., tech. eds. 1995. Application of semiochemicals for management of bark beetle infestations—proceedings of an informal conference. Annual meeting of the Entomological Society of America, 1993 December 12-16; Indianapolis, IN. Gen. Tech. Rep. INT-GTR-318. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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A Case Study: Methyl Chavicol

In the late 1960's a group at the University of California at Berkeley including R. W. Stark, D. L. Wood, J. R. Parmeter, Jr., F. W. Cobb, Jr., P. R. Miller, and others examined smog damaged trees that were being heavily attacked by western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*D. ponderosae* Hopkins) in the San Bernardino Mountains (Stark and others 1968). In papers that followed from that work, Cobb and others (1968, 1972) discussed methyl chavicol (= estragole), the second most abundant volatile of the foliage of healthy ponderosa pines (*Pinus ponderosa* Laws.). The 70 percent drop in methyl chavicol was by far the largest biochemical change detected in the damaged trees preferred by beetles.

More recently, T. E. Nebeker and others examined the biochemistry of lodgepole pine (*P. contorta* Loud.) diseased with comandra stem rust (*Cronartium comandrae* Pk.) or infected with armillaria root disease (*Armillaria* sp.). These are the trees in the Intermountain West most likely to be infested with mountain pine beetles (Amman and Schmitz 1988; Tkacz and Schmitz 1986). Nebeker and others (in preparation) found 43 and 62 percent reductions, respectively, in the level of methyl chavicol in these diseased trees. This was again the greatest biochemical change that occurred among the most abundant host compounds (all those present at greater than 0.1 percent).

Methyl chavicol or estragole is known by several other chemical synonyms including: allylanisole, isoanethole, p-allylmethoxybenzene, chavicol ether, esdragon, tarragon and 1-methoxy-4-2 (2-propenyl) benzene (Material Data Safety Sheet, Aldrich Chemical). It is a simple, licorice-smelling, aromatic ether or phenylpropanoid. Methyl chavicol is found in the xylem resin of many of the hard pines in the subgenus *Pinus* including ponderosa, lodgepole, loblolly (*P. taeda* L.), longleaf (*P. palustris* Mill), slash (*P. elliottii* Engelm.), Scots (*P. sylvestris* L.), black (*P. nigra* Arnold) (Mirov 1961), and Caribbean (*P. caribaea* Morelet) (Smith 1975). It is common in foliage of spruce, *Picea* spp. (E. Zavarin personal communication); and is distributed widely among other plant families. It also contributes to the flavors of several strongly scented herbs: fennel (*Foeniculum vulgare* Mill.), basil (*Ocimum basilicum* L.), clove (*Syzygium aromaticum* L. Merrill. L.M. Perry), tarragon (*Artemisisia dracunculus* L.), and star anise (*Illicium verum* Hook.f.) (Duke 1988). The most well known example of methyl chavicol as an insect kairomone is its role in the Cucurbitacae as an attractant of corn root worm beetles (*Diabrotica virgifera* LeConte) (Metcalf and Lampman 1989).

The responses of several bark beetle species to methyl chavicol have been observed in laboratory tests. In a variety of olfactometer tests, Werner (1972a,b) used host extracts and pure host compounds alone and in combination with pheromones and found that methyl chavicol decreased the response of female and increased the response of male southern pine engravers (*Ips grandicollis* Eichoff). Payne and others isolated methyl chavicol from bolts infested with southern pine beetle (*Dendroctonus frontalis* Zimmermann) in the late 1970's. They tested southern pine beetle response to methyl chavicol in a walking bioassay and electroantennogram (EAG) (Payne, personal communication). In laboratory tests Gries and others (1988) identified methyl chavicol emanating from new galleries of the spruce beetle (*Dendroctonus rufipennis* Kirby); but no tests of its behavioral activity were conducted. In 1988 White measured the EAG response of the red turpentine beetle (*Dendroctonus valens* LeConte) to 11 of the most abundant volatiles from ponderosa pine resin (White and Hobson 1993). Methyl chavicol produced the third highest response for males and females. Whitehead, in preliminary work in 1993 tested mountain pine beetle's EAG response with methyl chavicol and found the fourth highest response of all host compounds tested (Whitehead personal communication).

At the 1992 national meeting of the Entomological Society of America, Hayes and others (1992) described the anti-aggregant effect of a "novel host compound" from southeastern pines that was strongly reduced in trees treated with metham-sodium and dimethyl sulfoxide. Treated trees were preferentially attacked by southern pine beetle after the level of this host compound was reduced. In field tests with Lindgren traps the repellency of the host compound compared well with verbenone. Hayes and others (in preparation) later reported on additional laboratory tests of this compound with several species of scolytids and revealed it to be 4-allylanisole (= methyl chavicol).

Metcalf and Lampman (1989) explored chemical variations of methyl chavicol with different simple side chains to discover the most potent attractant known for corn root worm—a "parakairomone" in their terms. In theory at least, one might test quite a large number of non-host compounds for interruption of attraction. Perhaps peppermint, wintergreen, or naphthalene moth balls would be super repellents. Hayes and others (in preparation) used several chemical analogues to methyl chavicol in laboratory repellency tests with southern pine beetle and found three that were at least as repellent as methyl chavicol.

Field tests of the response of five western bark beetles to methyl chavicol began in 1993. I tested western pine beetle, red turpentine beetle, and California fivespined ips (*Ips paraconfusus* Lanier) in California and mountain pine beetle and the pine engraver (*Ips pini* Say) in Idaho. Tests were designed to detect a positive or negative response to methyl chavicol with four treatments: (1) a blank control, (2) a sample of methyl chavicol, (3) an attractive pheromone or kairomone bait, and (4) the bait attractant plus methyl chavicol together. The test used a randomized block design with Lindgren traps. Treatments were randomly reassigned to traps after every collection of beetles. Methyl chavicol significantly reduced the catch of beetles with active bait by: 60 percent for western pine beetle, 68 percent for mountain pine beetle, 29 percent for pine engraver, and nonsignificantly by 21 percent for red turpentine beetle. In my preliminary work *I. paraconfusus* catch was reduced in five of six trials with too few replicates for a test. However, in additional preliminary work, Storer (1994) has since tested methyl chavicol on California fivespined ips at Berkeley using a similar experimental design and found an approximate 40 percent reduction in catch.

These results are preliminary; nevertheless the conclusion is clear. Methyl chavicol, a natural host compound, interrupts scolytid aggregation and decreases in concentration in the diseased or stressed trees that are most often attacked by aggressive bark beetles. This conclusion is exciting because it sets repellency by a host plant odor into the ecological context of what we already know about bark beetle association with diseased, stressed trees and it provides new possibilities for bark beetle management. There are of course caveats:

1. These data are from traps and not trees. Trees are notoriously difficult to protect from beetles.
2. Dose-response tests are needed to compare my release rate to natural emissions from healthy trees. But the release rate I used, approximately 0.5 ml/day is likely to be in the low range of what would be coming from healthy foliage.
3. This compound is in the foliage of ponderosa pine (and the cortical resin of lodgepole). Most bark beetle host selection work has considered volatiles from the xylem or cortical resin of the bole. However, there is something quite logical about beetles being influenced by foliage volatiles as that is where gas exchange takes place, where host volatile emissions mostly come from, and where biochemical changes are most pronounced with plant stress.
4. Deterrents/repellents/interruptants likely are only effective at short range, where an odor gradient from the tree exists. In contrast, attractants, even in broken up packets in moving air, can trigger anemotactic flight behavior that can draw insects to an attractive source 100's of meters away. A new mental model of how antiaggregants might work at distances greater than a few centimeters is needed.
5. Finally, this is probably not "the silver bullet" of host selection for these species. Trees are complicated sensory objects. Other host stimuli, including visual and olfactory cues, also play a role. To paraphrase Metcalf and Metcalf (1992): it is probable that no totally definable (host selection) message exists, since the chemical extent of the message is dependent on so many variables.

Nevertheless plant odor repellents do provide some interesting management possibilities. Pheromone repellents/interruptants such as verbenone have been plagued with still unexplained inconsistency (L. Rasmussen personal communication); and may, by themselves, be intrinsically unable to reliably protect trees because of their multifunctional nature, they also serve as attractants at low concentrations. Verbenone, produced by bark beetles, always signals the presence of bark beetles. This in itself may increase the probability that bark beetles will be drawn to the locality of the verbenone even if they are interrupted from aggregating on the tree where verbenone is being released. In contrast, host antiaggregation compounds, such as methyl chavicol, signal only the presence of the (normally resistant) host and would not be likely to attract bark beetles at normal concentrations.

The reduction in trap catch with methyl chavicol for western pine beetle was of the same order of magnitude as that for verbenone. Methyl chavicol is one fifth as costly as verbenone ($77/kg versus $375/kg), much more abundant naturally, and readily available commercially. If the repellency of a plant odor is additive with the antiaggregation of verbenone, it may be possible by combination to come up with more dependable semiochemical protection.

Related Studies of Bark Beetles and Plant Volatiles

Recently other work has been published that shows antiaggregation by plant odors. Dickens and others (1992) showed that a combination of nonhost "green leaf volatiles" from broad-leaved plants significantly reduced the attraction of the southern pine engraver, the four spined engraver (*Ips avulsus* Eichoff), and southern pine beetle to their respective pheromones. Wilson (personal communication) in 1993 found significant reduction of attraction of female mountain pine beetle to green leaf volatiles. Similarly, Schroeder (1992) showed that the attraction of the European pine shoot beetle (*Tomicus piniperda* L.) and *Hylurgops palliatus* Gyll. to ethanol was interrupted or reduced by volatiles from wood of nonhost aspen (*Populus tremula* L.). *Trypodendron domesticum* L. and *Anisandrus dispar* F. are repelled by α-pinene from nonhosts Norway spruce (*Picea abies* L. Karst) and Scots pine (Nijholt and Schonherr 1976).

The somewhat random progress in elucidating bark beetle response to host odors is evidence of the need for basic research on a number of pertinent questions:

1. Which groups of compounds would most likely elicit a response from bark beetles? Are there classes of chemicals, such as aromatic ethers or alcohols, that most often are behaviorally active?
2. Is the probability of bark beetle response to a compound related to the frequency with which it is encountered? For example, are nonhost compounds more likely to produce antiaggregation when the non-host is frequently encountered by the beetle?
3. Several insect herbivores are attracted by allylisothiocyanate to their cruciferous hosts (Free and others 1978). Are unique or unusual, relatively host-specific compounds used by bark beetles to locate hosts or avoid nonhosts?
4. Are more general compounds such as the decomposition product ethanol often behaviorally active?
5. Do beetles respond to chemicals that increase or decrease strongly when trees are vigorous or are placed under stress?
6. Visser (1986) cited several examples of insect herbivores that are sensitive to the ratio of a blend of host odors. Is the ratio of several host compounds important in producing a response by bark beetles?
7. Are major host compounds such as α-pinene and β-pinene more or less likely to be behaviorally active than minor compounds?
8. Is the tendency of a compound to produce antiaggregation related to its toxicity to the beetle?

We also need to know about variability of bark beetle response to host odors. How does response vary regionally, seasonally, by sex, by dose or concentration, by beetle age and physiological state or by population phase (for example epidemic or endemic)?

Other basic questions that have practical importance include:

1. What other sensory stimuli, such as visual cues, combine synergistically with olfaction to increase bark beetle response?
2. Are different kairomones synergistic with each other?
3. Are kairomones additive or synergistic with various pheromones?
4. How far away from a source can plant odors cause beetle avoidance or attraction?
5. When in the host selection process do plant compounds have their effect, prior to landing or later after feeding?

Many of these questions have been addressed in the study of bark beetle pheromones and methods exist to answer them. Others are being explored in studies of other herbivores. Insights from these studies should be incorporated in our study of bark beetles. When we better understand the role of host odors in scolytid chemical ecology, we will be able to better implement practical semiochemical-based management of bark beetles.

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