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Interrupting the response of *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae: Scolytinae) to compounds that elicit aggregation of adults

Elizabeth E. Graham[1] and Andrew J. Storer[2]

Abstract

The eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae: Scolytinae), is a native bark beetle that has caused significant mortality to tamarack, *Larix laricinia*, in the Upper Peninsula of Michigan. The effectiveness of potentially attractive chemicals for *D. simplex* was tested and the most attractive compound, seudenol, was used in subsequent studies to test interruptants against *D. simplex*. Verbenone, methylcyclohexenone (MCH), and 4-allylanisole were tested as potential interruptants in combination with seudenol. Catches of *D. simplex* in traps baited with seudenol and MCH were not significantly different from catches in unbaited control traps, indicating successful interruption of the response to seudenol by MCH. Verbenone released at commercially available doses significantly increased catches of *D. simplex* in traps baited with seudenol, however it did not catch significantly more *D. simplex* than the unbaited control traps when released alone. Traps baited with 4-allylanisole did not significantly reduce the number of *D. simplex* captured compared to traps baited solely with seudenol. The potential for MCH to be used to protect individual trees and in stand level management of *D. simplex* is discussed.

Infestations of the eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae: Scolytinae), have been recorded in North America since 1883 (Seybold et al. 2002). *D. simplex* is a native bark beetle and is considered a secondary pest of tamarack, *Larix laricina*, generally attacking already weak or wounded trees (Langor and Raske 1987). The geographic range of *D. simplex* coincides with that of tamarack, extending from Maine to Minnesota, throughout most of Canada, and as far west as Alaska (Johnston 1990). *D. simplex* caused tamarack mortality of >1.4 million m^3 in northeastern North America during outbreaks between the mid 1970s and 1980s (Langor and Raske 1989). Outbreaks of *D. simplex* may occur when trees are under physiological stress such as defoliation, flooding, drought, fire, age, etc. (Seybold et al. 2002). When outbreaks occur, *D. simplex* may attack apparently healthy trees (Langor and Raske 1989). Tamarack is not a major commercial timber species. However it is used for pulpwood, posts, poles, mine-timbers, and railroad ties (Johnston and Carpenter 1985). Tamarack is also valuable as an ornamental tree because of its rapid growth and fall colors (Johnston 1990).

Dendroctonus simplex generally has one generation per year although in extreme conditions it may complete two generations per year (warmer climates) or one generation every two years (colder climates) (Seybold et al. 2002). Adult *D. simplex* females tend to emerge first from host trees, generally between

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April and June, and initiate attack on weakened or stressed trees (Langor and Raske 1987). The males and additional females begin to emerge about two days later, and are attracted to an aggregation pheromone produced by the pioneering females (Seybold et al. 2002). Seudenol (3-methyl-2-cyclohexen-1-ol) may be a component of this aggregation pheromone because when released in combination with α-pinene (2,6,6-Trimethylbicyclo[3.1.1]hept-2-ene) it has been shown to be an effective attractant for *D. simplex* in Alaska (Werner et al. 1981). The result of pheromone-mediated aggregation is mass attack of individual trees.

Many species of bark beetles (Scolytinae) release an antiaggregation pheromone once a tree is successfully colonized that acts as a interruptant and deters further attack, thereby reducing intraspecies competition (Wood 1982). Antiaggregation pheromones have been exploited as a management tool for multiple scolytine species. Successful management strategies for *Dendroctonus pseudotsugae* Hopkins, a sister species of *D. simplex*, involves a combination of attractant-baited traps and protecting trees from infestation with the interruptant compound MCH (3-Methyl-2-cyclohexen-1-one) (Ross and Daterman 1995, Ross et al. 2001). MCH was identified as a pheromone released by male *D. pseudotsugae* to deter additional beetles of the same species from attacking already colonized trees (Kinzer et al. 1971). *D. pseudotsugae* is closely related to *D. simplex* taxonomically (Wood 1982), and similar management strategies may be effective for controlling *D. simplex* in outbreak areas. MCH has already been shown to interrupt the response of *D. simplex* to traps baited with both seudenol and α-pinene (Werner et al. 1981). However, the effect of MCH on the response of *D. simplex* to seudenol has not been tested in Michigan.

The compounds verbenone (4,6,6-Trimethylbicyclo[3.1.1]hept-3-en-2-one), and 4-allylanisole [1-Methoxy-4-(2-propen-1-yl)benzene;methyl chavicol; or estragole] can also interrupt the responses of a number of scolytine species to their attractive compounds (e.g., Dyer and Hall 1977, Hayes et al. 1994, Ross and Daterman 1995, Werner 1995, Holsten et al. 2001, Huber and Borden 2001, Rappaport et al. 2001, Haack et al.2004). Verbenone-baited trees significantly reduced attacks by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, on single trees and groups of trees (Huber and Borden 2001). Verbenone interrupts the responses of several other *Dendroctonus* spp. such as the western pine beetle, *Dendroctonus brevicomis* LeConte (Betram and Paine 1994a; 1994b), southern pine beetle, *Dendroctonus frontalis* Zimmermann (Payne and Billings 1989), and the red turpentine beetle, *Dendroctonus valens* LeConte (Rappaport et al. 2001) to their respective aggregation pheromones. In the laboratory, 4-allylanisole can repel *D. frontalis*, *D. brevicomis, D. ponderosae*, and *D. rufipennis* Kirby (Hayes et.al. 1994). The vapors of 4-allylanisole are toxic to *D. simplex* adults when exposed at certain doses for 24 hours (Werner 1995).

Previous experiments have tested attractive and interruptive compounds for *D. simplex* in Alaska (Werner et al. 1981, Werner 1995). However, some scoyltine species exhibit variation in their chemical ecology when populations are widely distributed. For example, the pheromone of *Ips pini* (Say) in New York and Wisconsin is strongly synergized with the addition of lanierone, however this effect was not significant in California (Miller et al. 1997). The goal of this study was to examine the chemical ecology of *D. simplex* in Michigan as very little work has been conducted on *D. simplex* outside of Alaska. We had three objectives: (1) to compare chemical compounds alone and in combination for attractiveness to *D. simplex*; (2) to test chemical compounds that have the potential to reduce the response of *D. simplex* to attractant, i.e., interruptants; and (3) determine whether *D. simplex* is attracted to any of the potential interruptants in the absence of the attractants tested in objective 2.

Materials and Methods

Site Description

Trapping studies were conducted during the summers of 2002 and 2003 at sites in Luce and Schoolcraft counties in the Upper Peninsula of Michigan. The sites were located in areas with *D. simplex*-associated *L. laricina* mortality, identified during aerial surveys in early 2002 by the Michigan Department of Natural Resources. All sites were dominated by *L. laricina* with dead, declining and healthy trees. Stands were located on poorly drained, wet lowlands, which is typical for *L. laricina* (Johnston 1990). Other species present included: black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and paper birch (*Betula papyrifera*). The study sites were located between 85.95º W, 46.34º N and 85.68º W, 46.33º N, and were separated by a minimum of 100 m and a maximum of 33 km.

Trap Description and Experimental Design:

We used 12-unit multiple-funnel traps (Lindgren 1983) laid out in a complete randomized block design. The traps were hung from branches of *L. laricina* approximately 1.5-2 m off the ground. Branches and foliage surrounding the traps were removed to allow beetles easy access to the traps. Traps were placed ≥5 m in from the edge of the stand and were separated by ≥10 m to reduce potential interference from other chemicals on adjacent traps. Baits were hung outside of the fourth funnel from the top on all traps. A small block of Vapona No-Pest Strip (Greencross, Fisons Horticulture Inc., Missassauga, Ontario) was placed in each collecting cup to minimize escape and predation by other arthropods. Trap contents were emptied and the position of the traps was randomized within each block every 3-10 days, to control for location effects. Entire traps and their baits were moved during randomization to ensure there was no residual effect from the previous bait.

Bait Descriptions:

All baits for this study were provided by PheroTech Inc. (now Contech Enterprises Inc., Victoria, British Columbia, Canada), except for 4-allylanisole that was provided by Penta Manufacturing Co. (Livingston, New Jersey). The PheroTech baits were packaged in controlled-release devices with known release rates (Table 1) and did not need to be replaced during the experiments. The 4-allylanisole baits consisted of open 2-ml micro-centrifuge tubes containing 1.5 ml of compound and were renewed when traps were rotated (every 3 d). Five micro-centrifuge tubes were used in each trap, and the release rate of 4-allylanisole was determined gravimetrically (Table 1).

Table 1: Release rates of compounds used in Experiments 1-3 at 20ºC. Data provided by PheroTech Inc. except, * determined gravimetrically.

Chemical	Release Rate
Ultra High Release α-Pinene	1-2 g per day
Ultra High Release Ethanol	275 mg per day
Frontalin	2.5 mg per day
Seudenol	.2 mg per day
Verbenone	2 mg per day
Methylcyclohexenone (MCH)	3.5 mg per day
4-allylanisole	29.7 ± 0.0001 mg per day *

Experiment 1: Comparison of potential attractants for *D. simplex*. Three replicate blocks were used to test potential attractants for *D. simplex*. Each block contained six traps, one with each of the following treatments assigned at random: α-pinene, α-pinene + ethanol, frontalin, frontalin + seudenol, seudenol alone, and an unbaited trap (negative control). The baits were selected because of their success as attractants for related species of bark beetles and in previously reported studies of *D. simplex* (Seybold et al. 2002, Werner et al. 1981). Trap contents were emptied and the number of *D. simplex* adults counted every 9-15 d. The trapping treatments were randomized within each block after the insects were collected. Four rounds of trapping were carried out between 1 August and 12 September 2002 (n = 12). Date and block combinations that collected fewer than 10 *D. simplex* were eliminated from the analysis, resulting in n = 11.

Experiment 2: Interruption of the response of *D. simplex* to seudenol using MCH, verbenone, and 4-allylanisole. Six blocks of traps were used to test the interruption of the response of *D. simplex* to the most attractive lure from experiment 1, seudenol (see Results), in Luce County, Michigan in June 2003. The distance between blocks was between 50 m and 8 km. The blocks were located in stands with characteristics similar to those used in Experiment 1 and all study sites contained trees known to be infested with *D. simplex*. Treatments were randomly assigned to the traps in each block. Each block contained the following treatments: seudenol (positive control), seudenol + verbenone, seudenol + MCH, seudenol + 4-allylanisole, and an unbaited trap (negative control). Traps were emptied every 3 d and the positions of the treatments within each block were randomized. Five rounds of trapping took place between 10 June and 25 June 2003 (n = 30). Date and block combinations that collected fewer than 10 *D. simplex* were dropped from the analysis, resulting in n = 16.

Experiment 3: Attractiveness of MCH, verbenone and 4-allylanisole released without seudenol. A further study was conducted in the six blocks used in Experiment 2 to test the attraction of *D. simplex* to the potential "interruptant" compounds when released without an attractant in Luce County, Michigan in July 2003. Each block contained the following treatments: seudenol (positive control), verbenone, MCH, 4-allylanisole, and an unbaited trap (negative control). Treatments were randomly assigned within each block. Trap contents were emptied every 3 d and the position of the treatments were randomized within each block. Three rounds of trapping took place between 8 July and 17 July 2003 (n = 18).

Data Analysis. Mean number of *D. simplex* adults captured per trap in each experiment were compared with the nonparametric Friedman's test (PROC FREQ with CMH option; SAS Institute, 2001) because assumptions of analysis of variance (ANOVA) were violated by heteroscedasticity (Sokal and Rohlf 1995). Differences between pairs of means were tested with the REGWQ means-separation test to control maximum experiment-wise error rates (SAS Institute, 2001).

Results

Experiment 1: Comparison of potential attractants for *D. simplex*. Overall, 14,778 *D. simplex* beetles were collected in Experiment 1. Significant differences were detected among treatment types (Fig. 1, Friedman's $Q_{5,71}$ = 31.03; $P < 0.0001$). Traps baited with seudenol and the combination of seudenol + frontalin caught significantly more beetles than the other treatments (Fig. 1). Traps baited with only frontalin did not capture significantly more beetles than the unbaited control. Differences in catches of *D. simplex* among the remaining treatments were not significant.

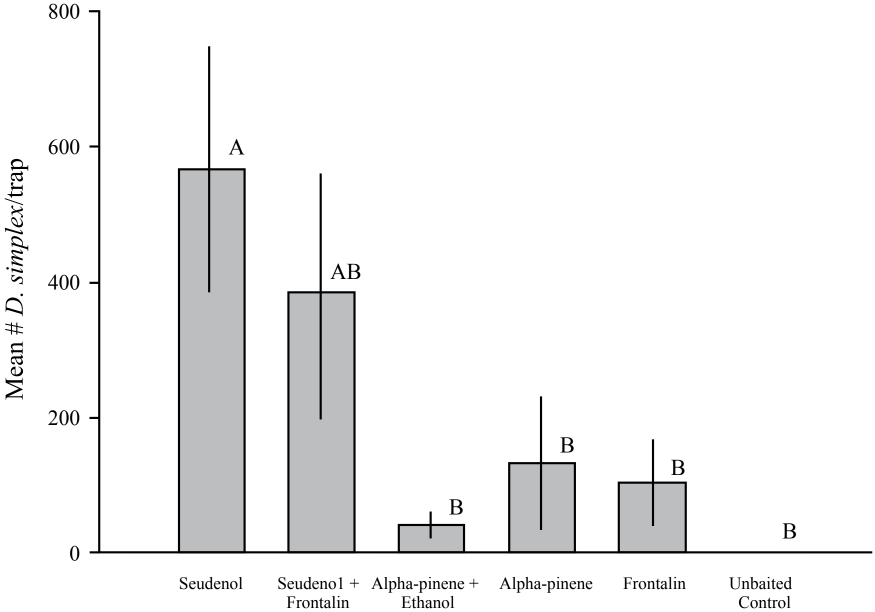

Figure 1. Mean ± SEM number of *D. simplex* adults captured per trap during Experiment 1 in funnel traps baited with seudenol, frontalin, seudenol + frontalin, α-pinene + ethanol, α-pinene, frontalin, or unbaited (control). See Table 1 for release rates of each compound. Bars designated with different letters were significantly different (REGWQ test P <0.05). The study took place between 1 August and 12 September 2002 in Luce and Schoolcraft counties, MI.

Experiment 2: Interruption of the response of *D. simplex* to seudenol using MCH, verbenone, and 4-allylanisole. In Experiment 2, 1225 *D. simplex* were collected. Significant differences were detected among treatments (Fig. 2, Friedman's $Q_{4,149} = 43.52$; $P < 0.0001$). Traps baited with 4-allylanisole did not catch significantly fewer beetles than traps baited with seudenol (Fig. 2). Verbenone was also an ineffective interruptant, given that traps baited with seudenol + verbenone captured significantly more beetles on average than those baited with seudenol alone (Fig. 2). MCH, however, was successful in shutting down the beetle's response to seudenol as indicated by no significant difference in mean trap count between traps baited with seudenol + MCH and the unbaited control traps (Fig. 2).

Experiment 3: Attractiveness of MCH, verbenone and 4-allylanisole released without seudenol. Overall, traps baited with the interruptants or seudenol caught only 44 beetles. This study tested compounds that are not known to be attractive to *D. simplex*, with the exception of seudenol as a positive control; therefore large trap captures were not expected. Regardless, enough beetles were captured to analyze statistically and the results were significant (Fig. 3, Friedman's $Q_{4,59} = 33.28$; $P < 0.0001$). Mean trap catches in response to seudenol were significantly higher than to any of the other compounds tested; in fact 89% of the beetles were captured in traps baited with seudenol (Fig. 3). Differences among the number of *D. simplex* captured in traps baited with the interruptant compounds and the unbaited control were not significant.

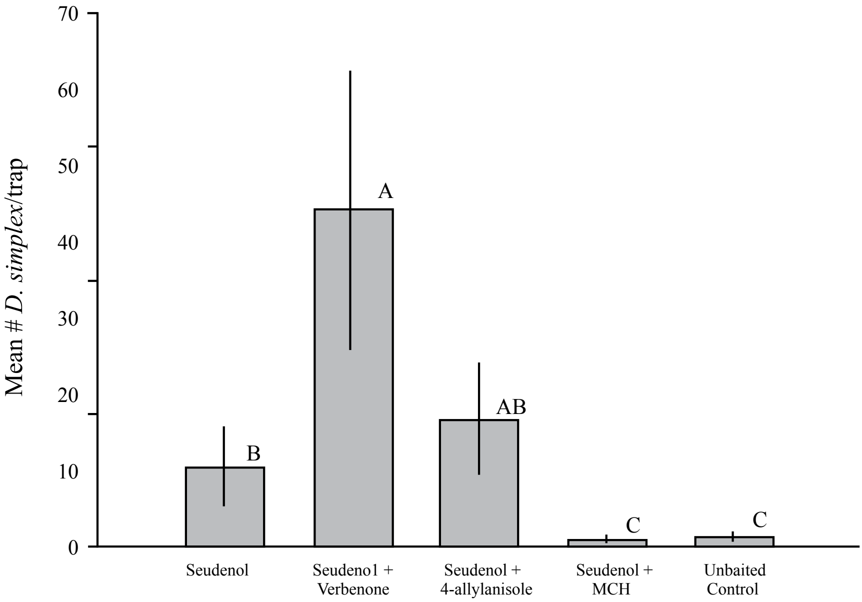

Figure 2. Mean ± SEM number of *D. simplex* adults captured per trap during Experiment 2 in funnel traps baited with seudenol, seudenol + verbenone, seudenol + 4-allylanisole, seudenol + MCH, or blank (control). See Table 1 for release rates of each compound. Bars designated with different letters were significantly different (REGWQ test $P < 0.05$). The study took place between 10 June and 25 June 2003 in Luce County, MI.

Discussion

Seudonol was the most attractaive compound tested for *D. simplex* in Michigan. Ethanol is commonly produced and released by weaken or stressed conifers (Kimmerer and Kozlowski 1982) and α-pinene is a major component of *L. laricina* (Rudloff 1987). In combination the two compounds are attractive to some *Dendroctonus* spp. (Shroeder and Lindelöw 1989); however this was not the case for *D. simplex* in this experiment. Demonstrating attraction of bark beetles to host volatiles is often problematic given that the attraction effect may be very small (e.g. Warren et al. 1996). Although not tested in the present study, Werner et al. (1981) found a synergistic effect on the number of beetles captured in trap baited with α-pinene and seudenol. We refrained from using these combinations because traps were hung from trees that were naturally producing these compounds.

Frontalin is a known attractant for *D. pseudotsuage*, which is closely related to *D. simplex* (Pitman and Vite 1970, S.L. Wood 1982). However attraction to the frontalin-baited traps was not significantly different from the unbaited traps. Similar results were reported from a study in Alaska suggest that this phenomenon may help ensure reproductive isolation between the two species in areas of sympatry (Werner et al. 1981). Traps baited with the combination of frontalin and seudenol caught more *D. simplex* than the unbaited traps, but not more than the traps baited with seudenol alone. Seudenol alone was used as the attractant in Experiments 2 and 3, given that the addition of frontalin

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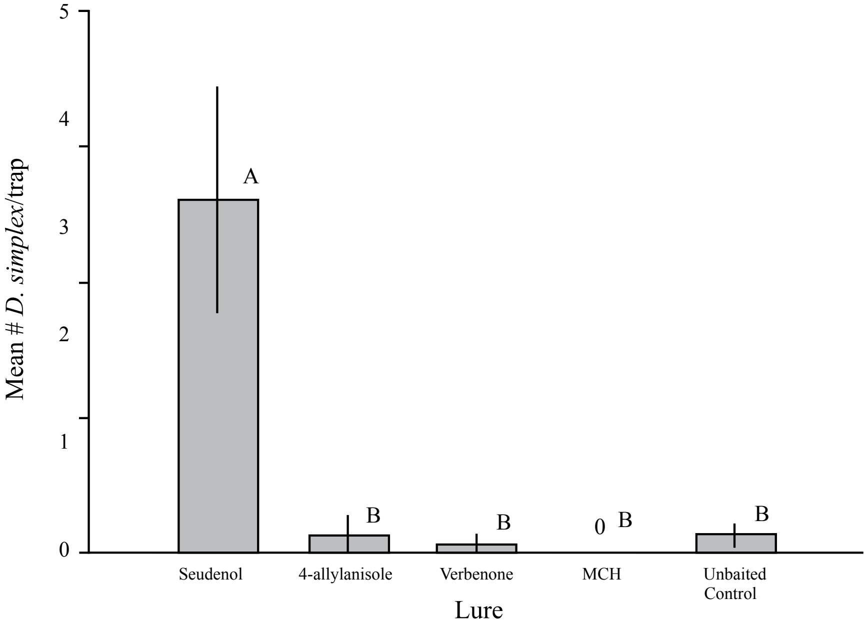

Figure 3. Mean ± SEM number of *D. simplex* adults captured per trap during Experiment 3 in funnel traps baited with seudenol, verbenone, 4-allylanisole, MCH, or blank (control). See Table 1 for release rates of each compound. Bars designated with different letters were significantly different (REGWQ test $P < 0.05$). The study took place between 8 July and 17 July 2003 in Luce County, MI.

did not significantly increase trap catch of *D. simplex*. This finding is consistent with other studies involving *D. simplex* in Alaska and Minnesota (Werner et al. 1981; Seybold et al. 2002).

Dramatically fewer beetles were caught in Experiments 2 and 3 than Experiment 1 (1269 combined versus 14,778 respectively). This may be because the outbreak was subsiding and the number of adult beetles decreased region-wide. Alternatively, these numbers may be the result of using a different field site in Experiments 2 and 3 than in Experiment 1, which may have had a lower population. Another possible factor is that Experiments 2 and 3 took place earlier in the summer than Experiment 1. *D. simplex* generally overwinter as adults and emerge between April and June and immediately initiate attacks in new host trees. The parent brood may then emerge again during the summer to attack a new host tree and some of the newly formed adults will emerge in the fall (Seybold et al. 2002). It is possible that Experiments 2 and 3 were conducted after initial emergence, whereas Experiment 1 was conducted during peak flight of the reemerged parent brood and newly formed adults.

MCH was extremely successful in shutting down the response of *D. simplex* to traps baited with seudenol in Michigan. This is consistent with the reported interruption of the response of *D. simplex* to seudenol and α-pinene baits by MCH in Alaska (Werner 1981). MCH is known to be released by female *D. pseudotsugae* upon a sonic signal from the males and has been widely used as an anti-attractant for that species (Rudinsky et al. 1972, Rudinsky 1973a, Rudinsky et al. 1973, Ross and Daterman 1995). It is also an effective anti-

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attractant for *D. rufipennis;* another closely related species that uses similar pheromones (Dyer and Hall 1977, Holsten et al. 2003). Further testing should be conducted to determine if female *D. simplex* also produce MCH and to test its ability to protect individual, high-valued tamarack trees from *D. simplex* attack. In addition, the potential for MCH to be used in stand-wide protection programs using techniques similar to those employed against *D. pseudotsugae* should be considered.

In our study looking at seudenol in combination with potential interruptants, trap catches of *D. simplex* with seudenol + verbenone were significantly higher than trap catches with seudenol alone. Other than seudenol, none of the potential interruptants released alone were attractive to *D. simplex.* Verbenone is an interruptant for numerous scolytine species including, *D. ponderosae* (Huber and Borden 2001), *D. brevicomis* (Betram and Paine 1994a; 1994b), *D. valens* (Rappaport et al. 2001), and *D. frontalis* (Payne and Billings 1989). However, in other studies involving verbenone, interruptant properties were not evident for *D. ponderosae* (Bentz et al. 1989), *Conophthorus coniperda* (Schwarz), and *Conophthorus resinosae* Hopkins (de Groot and DeBarr 2000).

The synergistic effect of verbenone on the attraction of *D. simplex* to traps baited with seudenol has not been reported in previous studies. Traps baited with seudenol + verbenone consistently captured more beetles than seudenol alone despite their location within the block. Further studies should be conducted to determine what dosage of verbenone is needed to gain a synergistic effect with seudenol. For example, low doses of MCH increased *D. pseudotsugae* attraction to its pheromones (Rudinsky 1973a). It is possible that verbenone is acting as a mixed function pheromone for *D. simplex*, and would interrupt attraction at higher doses. Rudinsky (1973b) demonstrated that the behavioral effect of verbenone on *D. frontalis* depends upon the concentration. The baits used in the present study are commercially available and marketed as an anti-attractant dose for various scolytines. A dose response test for verbenone combined with seudenol needs to be conducted for *D. simplex* to clarify this effect.

Conclusion

This study has shown that seudenol is an effective attractant for *D. simplex* and can be used to monitor *D. simplex* activity in Michigan and likely throughout the East. The combination of seudenol and verbenone as an enhanced bait for *D. simplex* should be verified and if confirmed, considered for use in *D. simplex* survey efforts. MCH effectively interrupted the response of *D. simplex* to seudenol and should be further studied for its ability to protect individual high value trees and stands during outbreak periods. The results of this study are consistent with experiments involving *D. simplex* in Alaska thereby demonstrating that the response of *D. simplex* to the compounds tested does not vary across large geographical areas.

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