**ABSTRACT** I report on the attraction of the white pine cone beetle, *Conophthorus coniperda* (Schwarz) (Coleoptera: Scolytidae), to traps baited with the host monoterpane limonene in western North Carolina. Both (+)- and (−)-limonene attracted male and female cone beetles to Japanese beetle traps in an eastern white pine, *Pinus strobus* L., seed orchard near Murphy, NC. Catches of cone beetles were directly proportional to the release rate of (−)-limonene; (+)-limonene was not tested for dose response. Attraction of cone beetles to the pheromone (±)-trans-pityol was increased significantly by both enantiomers of limonene. In all experiments, catches of *C. coniperda* were strongly male biased with no treatment effect on sex ratio. (−)-Limonene had no effect on trap catches of the predator *Enoclerus nigripes* (Say) to pityol, whereas (+)-limonene interrupted the attraction of *E. nigripes* to traps baited with pityol. Of six monoterpene commonly found in white pine cones, only (−)-α-pinene elicited attraction of *E. nigripes* to Japanese beetle traps.

**KEY WORDS** *Conophthorus coniperda*, Scolytidae, kairomone, Cleridae, *Enoclerus nigripes*

Some species of insects pose significant threats to the production of valuable seed crops in conifer seed orchards throughout North America (Hedlin et al. 1981). In eastern white pine, *Pinus strobus* L., the white pine cone beetle, *Conophthorus coniperda* (Schwarz) (Coleoptera: Scolytidae), can cause seed losses of up to 100% within seed orchards (Graber 1964, Odera 1968, Morgan and Mailu 1976, DeBarr et al. 1982). Such losses can be particularly acute as seed orchards are generally limited to only a handful per region. The loss of cones and seed also can impact natural regeneration of eastern white pine after forest fires (Godwin and ODell 1965). Prescribed fire can be used to reduce populations of cone beetles within seed orchards (Wade et al. 1989). However, such efforts are constrained by environmental conditions, susceptibility of trees to mortality from scarph and costs of application (Wade et al. 1989). Control tactics using semiochemicals could provide cost-effective protection of seed resources with minimal environmental costs (Rappaport et al. 2000, Trudel et al. 2004).


Host odors play an important role in the chemical ecology of cone beetles. The common pine monoterpane, (−)-α-pinene, synergizes attraction of male and female *C. coniperda* and *C. ponderosae* to pityol-baited traps (de Groot et al. 1998; de Groot and DeBarr 2000; Miller et al. 2000, 2003) but not *C. resinosae* (de Groot et al. 2002). Moreover, de Groot et al. (2002) found that attraction of *C. resinosae* to pityol was interrupted by (−)-α-pinene.

To date, catches of *C. coniperda* in traps with attractants have been largely male biased with no strong attractant yet identified primarily for females. de Groot et al. (1991) found that female *C. coniperda* were attracted to volatiles emitted by eastern white pine cones, *Pinus strobus* L., in both laboratory walking bioassays and field trapping studies. Miller et al. (2003) found that the monoterpane blends released by un-
attacked cones of several eastern white pines in western North Carolina in March differed in composition from blends released by cones from the same trees in May. Specifically, the relative proportion of limonene was high in volatiles from March cones but low in volatiles from May cones in the same year. Overwintering adult cone beetles typically start to emerge from fallen cones in March in western North Carolina (D.R.M., unpublished data).

My objective was to test both enantiomers of the host monoterpenes, limonene, as attractant kairomones for *C. coniperda* in an eastern white pine seed orchard in western North Carolina. The ultimate goal is to develop a lure that is significantly attractive to female beetles, thereby providing an opportunity for a mass-trapping program in white pine seed orchards (Rappaport et al. 2000, Trudel et al. 2004). The effects of (+)- and (−)-limonene on the responses of the beetle predator *Enoclerus nigripes* (Say) (Coleoptera: Cleridae) also were determined. Previously, Miller et al. (2003) found that attraction of *E. nigripes* (misreported as *Thanasimus dubius* L.) was strongly influenced by (−)-α-pinene.

### Materials and Methods

#### Chemicals and Release Devices

Chemicals and environmental conditions were studied at Beech Creek Seed Orchard (USDA Forest Service, Nan-tahala National Forest) near Murphy, NC, over a 3-yr period (2002–2004). The trapping period was 1 March–30 May 2003. The following treatments were randomly assigned to traps within each block: 1) unbaited control; 2) (−)-limonene; 3) (−)-β-pinene; 4) (−)-3-carene; 5) myrcene; 6) (−)-limonene; and 7) (−)-limonene, resulting in 10, 12, 10, 11, 12, 11, and 9 replicates of each treatment, respectively. Except for control traps, each trap was baited with one closed LDPE bottle (device 1) filled with an appropriate monoterpenene. In spite of differences in release rates among the various monoterpenenes (105–295 mg/d at 23–25°C), the LDPE bottle was chosen as the standard device, because devices releasing α-pinene at higher rates than 105 mg/d (at 23–25°C) resulted in a decrease in attraction of *C. coniperda* to pinyol-baited traps (Miller et al. 2003). Cone beetle flight at the Beech Creek Seed Orchard generally starts in mid-March and ends in late May with only one generation per year (D.R.M., unpublished data).

#### Experiment 1

This experiment was a broad survey on the attractiveness of six monoterpenes typically released from cones of eastern white pine (Miller et al. 2003). The trapping period was 28 March–30 May 2002. Each of 75 traps was randomly assigned one of the following treatments: 1) unbaited control; 2) (−)-α-pinene; 3) (−)-β-pinene; 4) (−)-3-carene; 5) myrcene; 6) (−)-limonene; and 7) (−)-limonene, respectively. These experiments examined the interaction of (−)-limonene at higher rates than 105 mg/d (at 23–25°C) resulted in a decrease in attraction of *C. coniferda* to pinyol-baited traps (Miller et al. 2003).

#### Experiment 2

This experiment examined the interaction between (−)- and (−)-limonene on the attraction of cone beetles. Thirty-two two traps were set in eight replicate blocks of four traps per block. The trapping period was 1 March–30 May 2003. The following treatments were randomly assigned to traps within each block: 1) unbaited control; 2) (−)-limonene; 3) (−)-limonene; and 4) (−)-limonene and (−)-limonene. For treatment 4, traps were baited with two release devices; one device for each enan-
tiomer of limonene.

#### Experiments 3 and 4

These experiments examined the interaction of (−)- and (−)-limonene, respec-
tively, with α-pinene and pityol in attracting cone beetles to traps. In both experiments, traps were set in replicate blocks of eight traps per block with five blocks per experiment. The trapping period for experiment 3 was 1 March–30 May 2003, whereas the trapping period for experiment 4 was reduced to 1 March–30 April 2003 due to vandalism and loss of seven traps in early May. In experiment 3, the following treatments were randomly assigned to traps within each block: 1) unbaited control; 2) (+)-limonene; 3) (-)-α-pinene; 4) pityol; 5) (+)-limonene and (-)-α-pinene; 6) (+)-limonene and pityol; 7) (-)-α-pinene and pityol; and 8) (+)-limonene, (-)-α-pinene, and pityol. In experiment 4, the following treatments were randomly assigned to traps within each block: 1) unbaited control; 2) (-)-limonene; 3) (-)-α-pinene; 4) pityol; 5) (-)-limonene and (-)-α-pinene; 6) (-)-limonene and pityol; 7) (-)-α-pinene and pityol; and 8) (-)-limonene, (-)-α-pinene, and pityol.

**Experiment 5.** This experiment determined the effect of the release rate of (-)-limonene in attracting cone beetles to traps. Fifty traps were set in 10 replicate blocks of five traps per block. The trapping period was 27 March–10 May 2004. All traps were baited with devices releasing (-)-limonene with treatments differing by release rate. The following release rate treatments were randomly assigned to traps within each block: 50, 150, 295, 610, and 1,830 mg/d (at 23–25°C in still air). The highest release rate was obtained with three of device 2 and the lowest release rate was obtained with five of device 4. The three intermediate release rates were obtained with a single device 3, 1 and 4, respectively.

**Statistical Analyses.** The data were analyzed with the SYSTAT version 11.00.01 and the SigmaStat version 3.1 statistical packages (Systat Software, Inc., Point Richmond, CA). All analyses were conducted on total trap catches over the trapping periods. Trap catch data were transformed by ln(y + 1) or ln(y), as required, to remove heteroscedasticity (Pepper et al. 1997). Data in experiments 1–4 were subjected to one-way analysis of variance (ANOVA) followed by the Holm–Sidak multiple comparison test when P ≤ 0.05. Because of significant differences in release rates for the different monoterpenes, treatment means in experiment 1 were compared only with those of controls, whereas all pairwise comparisons were examined in experiments 2–4. In addition, data in experiment 2 were subjected to full factorial two-way ANOVA by using replicate, (+)-limonene, (-)-limonene, and the interaction between (+)- and (-)-limonene as model factors, whereas those in experiments 3 and 4 were subjected to full factorial three-way ANOVA by using replicate, (-)-α-pinene, pityol, limonene, and the interactions between each pair as well as the three-way interaction as model factors. Data from experiment 5 was subjected to regression analysis. Sex ratio data (using proportion of males in catches as the test variable) for treatments with sufficient numbers (>10 beetles) were subjected to one-way ANOVA.

**Results**

**Experiment 1.** The total number of white pine cone beetles caught in experiment 1 was 4,565 with 90% of beetles captured in traps baited with either (+)- or (-)-limonene. There was a significant treatment effect in the experiment (F = 26.652; df = 6, 68; P < 0.001). Catches in traps baited with (-)-α-pinene, myrcene, (-)-limonene, and (+)-limonene were greater than those in blank controls (Fig. 1). There was no significant effect of these four treatments on sex ratio of captured beetles (F = 0.122; df = 3, 22; P = 0.946). Fourteen samples were not included in the sex ratio analysis due to low trap catches (<10 beetles). The mean ± SE proportions of males in catches for traps baited with (-)-α-pinene, myrcene, and (-)- and (+)-limonene were 0.83 ± 0.01 (n = 4), 0.83 ± 0.07 (n = 3), 0.85 ± 0.04 (n = 10), and 0.83 ± 0.04 (n = 9), respectively.

**Experiment 2.** The traps caught 727 white pine cone beetles in total in experiment 2 with catches significantly affected by both (+)-limonene (F = 4.247; df = 1, 21; P = 0.052) and (-)-limonene (F = 16.218; df = 1, 21; P = 0.001). Catches of beetles in traps baited with either enantiomer of limonene were significantly higher than those in blank control traps (Fig. 2). However, the effect of the two enantiomers was not additive (F = 8.556; df = 1, 21; P = 0.008). Catches in traps baited with both enantiomers of limonene were not significantly different from those baited with either enantiomer alone (Fig. 2). There was no effect of the three limonene treatments on the sex ratio of cone beetles in trap catches (F = 0.185; df = 2, 14; P = 0.833). Seven samples were not included in the sex ratio analysis due to low trap catches (<10 beetles). The mean ± SE proportions of males in catches for traps baited with (-)-limonene, (+)-limonene, and both (+)- and (-)-limonene were 0.96 ± 0.03 (n = 4), 0.93 ± 0.05 (n = 7), and 0.92 ± 0.03 (n = 6), respectively.
Fig. 2. Effects of (−)- and (+)-limonene on mean + SE total catches of C. coniperda in Japanese beetle traps in experiment 2 (n = 8). Means followed by the same letter are not significantly different at α = 0.05 (Holm–Sidak multiple comparison test).

Experiments 3 and 4. Traps captured 4,007 and 8,657 white pine cone beetles in experiments 3 and 4, respectively. The responses of cone beetles in the two experiments were significantly affected by pityol, (−)-α-pinene, and limonene (Table 1). Catches in traps baited with either limonene or pityol were significantly greater than those in blank control traps (Fig. 3A and B). Traps baited with limonene or the combination of limonene and (−)-α-pinene were as attractive as those baited solely with pityol in both experiments. Catches in traps baited with pityol and the addition of limonene, (−)-α-pinene, or both limonene and (−)-α-pinene were significantly greater than those in traps baited with only pityol.

In experiments 3 and 4, the interaction between pityol and (−)-α-pinene was additive (P = 0.576 and P = 0.055, respectively) (Table 1). In both experiments, trap catches in traps baited with both compounds were greater than those in traps baited with each compound separately (Fig. 3A and B). The interaction between (−)-α-pinene and limonene was not additive in the two experiments (P = 0.029 and P = 0.042, respectively). The interaction between pityol and limonene was additive for (+)-limonene in experiment 3 (P = 0.062), but not for (−)-limonene in experiment 4 (P = 0.001) (Table 1). In both experiments, catches of cone beetles in traps baited with pityol and limonene were significantly greater than those in traps baited with either compound alone (Fig. 3A and B). The only significant difference between the two experiments was that catches in traps baited with the three-component lure were greater than those in traps baited solely with pityol or the combination of limonene with (−)-α-pinene in experiment 4 (Fig. 3B) but not in experiment 3 (Fig. 3A).

I found no evidence of female-bias in any of the limonene treatments in experiments 3 and 4 (F = 0.572; df = 5, 16; P = 0.687, F = 1.873; df = 5, 21; P = 0.142, respectively). Data for control traps and traps baited with (−)-α-pinene alone were not used in the analyses due to insufficient numbers of beetles (<10) for determining sex ratios. The mean ± SE proportions of males in trap catches for the experiments 3 and 4 were 0.95 ± 0.01 (n = 22) and 0.90 ± 0.01 (n = 27), respectively.

Experiment 5. Trap catches of white pine cone beetles were directly proportional to the release rate of (−)-limonene, although the regression equation explained only 12% of the variation in trap catches (Fig. 4). Trap catches of cone beetles were significantly lower in 2004 (total catch of 2,526 C. coniperda) than in 2002–2003 (experiments 1, 3, and 4). It is likely that populations of cone beetles at the Beech Creek Seed Orchard were reduced significantly before the establishment of experiment 5. Unlike the previous 2 yr, a prescribed burn was conducted throughout the orchard in early March 2004 in an attempt to reduce cone beetle populations by direct consumption of beetles while still in fallen cones. Prescribed fire is an effective tool in controlling cone beetles (Wade et al. 1989). There was no effect of limonene release rate on the sex ratio of captured cone beetles (F = 0.100; df = 1, 24; P = 0.754) with a mean ± SE proportion of males in trap catches of 0.97 ± 0.01 (n = 26).

Responses of E. nigripes. The total catch of E. nigripes in experiment 1 was 81 beetles, which was sufficient to discern a treatment effect (F = 2.386; df = 6, 68; P = 0.038). Catches of beetles in traps baited with

Table 1. Analyses of variance of effects of pityol and (−)-α-pinene with (+)- and (−)-limonene on catches of C. coniperda

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>(+)-α-pinene (exp. 3)</th>
<th>(−)-limonene (exp. 4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replicate</td>
<td>4</td>
<td>0.014</td>
<td>0.569</td>
</tr>
<tr>
<td>(−)-α-Pinene (A)</td>
<td>1</td>
<td>4.980</td>
<td>0.057</td>
</tr>
<tr>
<td>Limonene (L)</td>
<td>1</td>
<td>34.343</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pityol (P)</td>
<td>1</td>
<td>57.345</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>A × L</td>
<td>1</td>
<td>5.311</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>A × P</td>
<td>1</td>
<td>0.322</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>L × P</td>
<td>1</td>
<td>3.759</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>A × L × P</td>
<td>1</td>
<td>2.960</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>28</td>
<td>0.097</td>
<td>0.051</td>
</tr>
</tbody>
</table>
(-)-alpha-pinene were significantly greater than those in control traps (Fig. 5). Because only 24 E. nigripes were caught in experiment 2, the data could not be analyzed with sufficient statistical power. In experiment 5 (total catch of 147 beetles), catches of E. nigripes were unaffected by the release rate of (-)-limonene ($F = 0.650; df = 1, 48; P = 0.424$).

In experiments 3 and 4, trap catches of E. nigripes were significantly affected by pityol and both enantiomers of limonene (Table 2). In experiment 3, catches of beetles in traps baited with pityol alone, or in combination with (-)-alpha-pinene, were greater than those in traps with most of the other treatments (Fig. 6A). In experiment 4, catches of beetles in traps baited with pityol and (-)-alpha-pinene were greater than those in traps with five of the remaining treatments (Fig. 6B). There was no evidence of an increase in attraction of E. nigripes by limonene in either experiment (Fig. 6A and B). The principal effect of (+)-limonene in experiment 3 seemed to be an interruption of the attraction of beetles to pityol-baited traps (Fig. 6A). Catches of beetles in traps baited with pityol alone were significantly greater than those in traps baited with pityol and (+)-limonene. Similarly, catches of beetles in traps baited with pityol and (-)-alpha-pinene were significantly greater than those baited with all three compounds.

**Discussion**

Limonene is an attractive, host-produced kairomone for the white pine cone beetle, C. coniperda, in western North Carolina. Limonene is abundant in cones of eastern white pines in March when beetles are attacking cones and less abundant in cones in May when beetles cease attacks (Miller et al. 2003). White pine cone beetles were attracted in large numbers to traps baited simply with limonene, irrespective of enantiomeric composition (Figs. 1 and 2). The response of C. coniperda was dependent on the release rate of (-)-limonene (Fig. 4).

**Table 2. Analyses of variance of effects of pityol and (-)-alpha-pinene with (+)- and (-)-limonene on catches of E. nigripes**

<table>
<thead>
<tr>
<th>Source</th>
<th>(+)-Limonene (exp. 3)</th>
<th>(-)-Limonene (exp. 4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Replicate</td>
<td>4</td>
<td>0.184</td>
</tr>
<tr>
<td>(-)-alpha-Pinene (A)</td>
<td>1</td>
<td>2.808</td>
</tr>
<tr>
<td>Limonene (L)</td>
<td>1</td>
<td>21.575</td>
</tr>
<tr>
<td>Pityol (P)</td>
<td>1</td>
<td>40.184</td>
</tr>
<tr>
<td>A × L</td>
<td>1</td>
<td>1.409</td>
</tr>
<tr>
<td>A × P</td>
<td>1</td>
<td>0.943</td>
</tr>
<tr>
<td>L × P</td>
<td>1</td>
<td>10.249</td>
</tr>
<tr>
<td>A × L × P</td>
<td>1</td>
<td>0.066</td>
</tr>
<tr>
<td>Error</td>
<td>28</td>
<td>30</td>
</tr>
</tbody>
</table>

**Fig. 4.** Effect of release rate of (-)-limonene on mean ± SE total catches of C. coniperda in Japanese beetle traps in experiment 5. Slope of regression line is significantly different from zero ($P = 0.007$).

**Fig. 5.** Effects of six common pine monoterpenes on mean ± SE total catches of E. nigripes in Japanese beetle traps in experiment 1 ($n = 9–12$). Treatment means followed by an asterisk are significantly different from the control at $\alpha = 0.05$ (Holm–Sidak multiple comparison test).

**Fig. 6.** Effects of interactions between (-)-alpha-pinene and pityol with (+)-limonene (A) and (-)-limonene (B), separately, on mean (+SE) total catches of E. nigripes in Japanese beetle traps in experiments 3 and 4, respectively ($n = 5, 6$). Means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm–Sidak multiple comparison test).
synergy between limonene and \((-\alpha\)-pinene in at-
traction of \textit{C. coniperda} (Fig. 3A and B).

Catches of both male and female \textit{C. coniperda} were
enhanced by limonene, although catches of cone bee-
tles were male biased in all experiments. The mean ±
SE proportion of males in trap catches of \textit{C. coniperda}
ranged from 0.839 ± 0.109 in experiment 1 to 0.968 ±
0.005 in experiment 5. There was no significant effect
of treatment on sex ratio of captured beetles in any of
the five experiments. It is possible that the right com-
ponents (or blend of compounds) to attract female \textit{C.
coniperda} in high numbers have yet to be tested. In
laboratory and field assays, female \textit{C. coniperda} were
attracted to volatiles extracted from uninfested and
infested eastern white pine cones, with some prefer-
ence for those containing male beetles (de Groot et al.

Alternatively, the low proportion of females in trap
catches of \textit{C. coniperda} may reflect a lower proba-
bility of capture. It is possible that female cone beetles spend
less time than males in choosing cones. Females must
first initiate attacks on uninfested cones before males
can choose among cones attacked by females. Al-
though production of pinyol by female cone beetles
likely helps males to find female-infested cones, males
likely fly between trees and branches before choosing
the right cones. In addition, females may be choosy in
accepting males, resulting in an increase in searching
time by males as they fly off to other cones when
rejected. Once mated, females need to spend time in
cones laying eggs, whereas males may be free to leave
cones to find other female-attacked cones. Godwin
and ODell (1965) found that the sex ratio of \textit{C.
coniperda} in infested cones of eastern white pine was
female biased at a sex ratio of \(\approx 2:1\), whereas the sex
ratio of overwintering \textit{C. coniperda} in cones on the
ground was 1:1. Considerable research is still needed
to understand the basic behavioral ecology of cone
beetles.

Geographic variation in the use of semiochemicals
is an important issue with many species of bark beetles
(Byers 1989), and it may be an important consider-
ation for \textit{C. coniperda} with respect to limonene as all
of my studies were conducted in western North Caro-
olina. The range of \textit{C. coniperda} mirrors that of eastern
white pine, ranging from eastern Canada down to the
Southern Appalachians (Wood 1982). In studies con-
ducted in 2004, Brauner and de Groot (2006) found
that limonene, irrespective of enantiomeric composi-
tion, significantly increased attraction of \textit{C. coniperda}
to pinyol-baited traps in two eastern white pine seed
orchards in southern Ontario. Moreover, catches of
both male and female cone beetles in traps baited with
pinyol and \((-\alpha\)-limonene were directly proportional
to the release rate of \((-\alpha\)-limonene. As in this study,
Brauner and de Groot (2006) did not find any evi-
dence of synergy between limonene and \((-\alpha\)-pinene in attracting cone beetles. The addition of
\((-\alpha\)-pinene interrupted attraction of female \textit{C.
coniperda}, but not male \textit{C. coniperda}, to traps baited
with pinyol and \((-\alpha\)-limonene. Unlike the present results
(Figs. 1 and 2), the data of Brauner and de Groot
(2006) did not indicate significant attraction of beetles
to traps baited simply with limonene. My results and
those of Brauner and de Groot (2006) provide solid
evidence that limonene is a kairomone for \textit{C. coniperda}
in the southern and northern parts of its range. More
information on the responses of white pine cone bee-
tles in the middle of its range should be obtained to
verify the general responses to limonene.

The complete role of host volatiles in the chemical
ecology of white pine cone beetles is still unclear,
although limonene and \((-\alpha\)-pinene are evidently
important. Numerous other monoterpens are present
in cones of eastern white pine (Miller et al. 2003). In
the current study, myrcene released at a rate of \(\sim 170\
mg/d\) (at 23–25°C) was attractive to cone beetles (Fig.
1). The lack of response to the other compounds may
be due to differences in release rates. Attraction of
cone beetles to \((-\alpha\)-pinene is dose dependent with
attraction increasing as release rates increase and then
decreasing when rates get high (Miller et al. 2003).
At present, there is little, if any, information regarding
in situ release rates of host volatiles from cones and
branches of eastern white pine. Previous studies on
the chemical ecology of \textit{C. coniperda} focused on com-
position of volatiles rather than rates of emission (Bir-
gersson et al. 1995, Miller et al. 2003, Brauner and de
Groot 2006). There is a distinct need to evaluate the
composition and rates of host volatile emissions by
cones on eastern white pines to better understand the
role of monoterpens in the chemical ecology of \textit{C.
coniperda}.

Variation in chemical composition between cones,
conelets, and shoot tips also may be important in
understanding the chemical ecology of cone beetles.
Cone beetle biology has been generalized as follows:
beetles overwinter in cones, emerge, and attack sec-
ond-year cones that then fall to the ground. The cycle
repeats the following year (ODell and Godwin 1964).
However, attacks on twigs and first-year conelets have
been noted for several species of cone beetles, includ-
ing \textit{Conophthorus lambertianae} Hopkins (= \textit{C.
ponderosa} Wood) and \textit{C. resinosae} and \textit{C. coniperda}
(Struble 1947, Lyons 1956, Godwin and ODell 1965).
Mattson (1980) found significant damage to cones,
conelets, and shoots by \textit{C. resinosae} in red pine stands
over a period of 11 yr. In stands of jack pine, \textit{P. bank-
-siana} Lamb, an ecovariant of \textit{C. resinosae} (= \textit{C.
banksiana}) feeds primarily on shoots, overwintering in
downed shoot tips on the forest floor, and it rarely
attacks cones (McPherson et al. 1970, de Groot and
Borden 1991). Attacks by \textit{C. resinosae} on jack pine
shoots may be classified as feeding, breeding, ovipo-
sitioning, or overwintering attacks (Mattson 1989).

Presumably, white pine cone beetles attack shoot
tips and conelets during periods of low abundance of
second-year cones or when population levels of bee-
tles are high (Godwin and ODell 1965). Godwin and
ODell (1965) note that, whereas most \textit{C. coniperda}
overwinter in cones on the ground, a considerable
number of beetles emerge in late summer and early fall
and attack first-year conelets with males initiating as
many attacks as females. Some beetles leave cones on
the ground and move to other damaged cones on the ground. Shoots of red pine are often attacked in the fall by *C. resinosae*, possibly improving overwintering survivorship of the beetles (Lyons 1956).

Godwin and ODell (1965) found that white pine cone beetles formed small aggregations before attacking conelets in the fall with as many as eight beetles clustered around the conelet-petiole junction. Mattson (1980) generalized that cone beetles aggregate in small feeding groups before attacking cones for oviposition in the spring as well. Morgan and Mailu (1976) found aggregative feeding attacks by overwintered *C. coniperda* on both white pine twigs and cones in the spring with up to 12 beetles per site. Thigmotropic aggregative behaviors in *C. coniperda* are related to temperature and humidity, possibly serving a role in ensuring overwintering survivorship and maximal cone attack success in the spring (Henson 1961, 1964).

My results demonstrate that limonene interrupts the attraction of *E. nigripes* to the cone beetle pheromone pityol (Fig. 6A), even though limonene increases the attraction of *C. coniperda* to traps baited with pinyol. Similarly, Miller et al. (2003) found that *E. nigripes* (misreported as *T. dubius*) preferred pinyol-baited traps with lures releasing (−)-α-pinene at the highest rate tested (579 mg/d at 23°C), whereas *C. coniperda* preferred traps with lures releasing (−)-α-pinene at lower rates (107 mg/d at 23°C). In eastern North America, *E. nigripes* preys on numerous species of bark and wood boring beetles (USDA Forest Service 1985). It is possible that generalist predator species, such as *E. nigripes*, that feed on a broad array of prey use a broad olfactory search image as opposed to a narrow search image associated with only one prey species. A similar relationship was apparent in California where the pine engraver, *Ips pini* (Say), preferred ipsdienol-baited traps with lures releasing the pheromone lanierone at lower rates (0.1–100 μg/d under field conditions) than those preferred by the generalist bark beetle predator *Enoclerus lecontei* (Wolcott) (2 mg/d under field conditions) (Seybold et al. 1992).

Alternatively, the responses of *E. nigripes* in my experiments may relate to maximizing survivorship of larvae rather than adults. Generally, adult clerids feed on adult scolytid beetles, whereas larval clerids feed on larval scolytids (USDA Forest Service 1985). Cones attacked by cone beetles in late April and early May are apt to be larger than those attacked in March. It is possible that larger cones can sustain more cone beetle larvae than smaller cones. Adult clerids may be selecting attacked cones on the basis of suitability for survivorship of larval clerids. Because *E. nigripes* are attracted to pinyol, especially when combined with α-pinene (de Groot and DeBarr 2000, Miller et al. 2003), attraction to traps releasing high rates of α-pinene and low rates of limonene may be indicative of responses to larger cones.

Because most studies on the chemical ecology of white pine cone beetles have been conducted in seed orchards, further studies should consider the unique nature of eastern white pine seed orchards in contrast to natural stands of eastern white pine. Trees within an orchard are typically widely spaced to encourage open crowns and greater cone production. The understory vegetation in seed orchards is generally controlled by mowing, herbicides or prescribed burns. It is possible that the patterns seen in orchards may differ substantially from those in natural stands. Moreover, the patterns in the use of semiochemicals observed in orchards may be derived from selection pressures occurring within natural stands but not within seed orchards.

My work and that of Brauner and de Groot (2006) with limonene suggest that host volatiles other than α-pinene may play a significant role in the chemical ecology of both male and female white pine cone beetles in eastern white pine seed orchards. Studies on the volatiles associated with feeding and oviposition attacks on cones, conelets, and shoots (in spring and fall) may provide insights into potential attractants for female cone beetles. Such work should be tied to analyses of volatiles produced by cones relative to genetic composition and across various spatial and temporal scales.

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