# Kairomonal Response of *Thanasimus undatulus*, *Enoclerus sphegeus* (Coleoptera: Cleridae), and *Temnochila chlorodia* (Coleoptera: Trogositidae) to Bark Beetle Semiochemicals in Eastern Oregon

JIANLIN ZHOU, DARRELL W. ROSS,<sup>1</sup> AND CHRISTINE G. NIWA<sup>2</sup>

Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752

**ABSTRACT** The kairomonal responses of *Thanasimus undatulus* (Say), *Enoclerus sphegeus* F., and *Temnochila chlorodia* (Mannerheim) to semiochemicals used by *Dendroctonus pseudotsugae* Hopkins, *D. rufipennis* Kirby, *D. brevicomis* LeConte, *D. ponderosae* Hopkins, and *Ips pini* (Say) to locate hosts were quantified in the field during the period of *D. pseudotsugae* dispersal in the spring and early summer. Traps baited with frontalin plus seudenol caught significantly more *T. undatulus* than traps baited with any other lure. Only a few *E. sphegeus* were collected during the study, suggesting that it might use semiochemicals other than those tested in this study to locate its prey. All of the traps baited with lures containing *exo*-brevicomin caught significantly more *T. chlorodia* than traps baited with other lures. These results suggest that *T. undatulus* uses seudenol primarily to locate its prey habitat, and *T. chlorodia* uses *exo*-brevicomin for the same purpose. These predators likely feed upon bark beetles that produce these compounds or other bark beetles that are found in the same habitats. A secondary pest of ponderosa pine, *Pityogenes carinulatus* (LeConte), was attracted in significant numbers to the traps baited with *I. pini* pheromone components. Traps baited with ipsdienol and lanierone caught significantly more *P. carinulatus* than traps baited with ipsdienol and lanierone caught significantly more *P. carinulatus* than traps baited with ipsdienol

**KEY WORDS** Thanasimus undatulus, Enoclerus sphegeus, Temnochila chlorodia, kairomone, Pityogenes carinulatus, bark beetles

SCOLYTID BEETLE AGGREGATION pheromones have been used effectively in a number of tactics to help meet forest management objectives (Borden 1989, Shea 1994, Salom and Hobson 1995). Pheromones have been used to attract beetles to baited trees that are either treated with insecticides before baiting thus killing arriving insects (Smith 1986) or harvested after attack to destroy the developing brood (Knopf and Pitman 1972, Pitman 1973, Borden 1989, Thier and Weatherby 1991). Another tactic employing aggregation pheromones is mass trapping of bark and ambrosia beetles (DeMars et al. 1980; Bedard and Wood 1981; Borden and McLean 1981; Bakke 1983, 1989). An early attempt by Pitman (1973) to mass trap Dendroctonus pseudotsugae Hopkins was unsuccessful with the trapping technology available at that time. Subsequently, a more efficient trap for scolytid beetles was developed (Lindgren 1983) and more attractive semiochemicals for D. pseudotsugae were identified (Rudinsky et al. 1974, Libbey et al. 1983). With the new technology, Ross and Daterman (1997) demonstrated

that large numbers of dispersing beetles could be removed from the forest, and the distribution of tree mortality could be controlled, by using pheromonebaited traps. However, they also trapped large numbers of a clerid predator, *Thanasimus undatulus* (Say), and much smaller numbers of two other predators, a clerid, *Enoclerus sphegeus* F., and a trogositid, *Temnochila chlorodia* (Mannerheim). Capturing these predators could potentially negate some of the benefits of removing *D. pseudotsugae* from the environment.

These predators are attracted to several bark beetle aggregation pheromones. T. undatulus, reported to be associated with D. pseudotsugae (Kline and Rudinsky 1964, Cowan and Nagel 1965), Dendroctonus ponderosae Hopkins (Amman 1972), Dendroctonus rufipennis Kirby (Knight 1961), Ips spp. (Reid 1957), Scolytus spp., and Pseudohylesinus spp. (Furniss and Carolin 1977), has been found to be attracted to frontalin (Pitman and Vité 1970, Pitman 1973, Schmitz 1978, Chatelain and Schenk 1984), seudenol (Dyer and Hall 1980, Ross and Daterman 1995), cis-verbenol (Miller et al. 1991), and ipsdienol (Miller and Borden 1990). E. sphegeus, reported to be associated with D. pseudotsugae (Kline and Rudinsky 1964, Cowan and Nagel 1965) and *D. ponderosae* (Struble 1942, Amman 1972), has been found to be attracted to *trans*-verbenol (Schmitz 1978) and ipsdienol (Miller and Borden

Environ. Entomol. 30(6): 993-998 (2001)

This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or recommendation by the USDA for its use.

<sup>&</sup>lt;sup>1</sup> To whom correspondence and reprint requests should be addressed: (e-mail: darrell.ross@orst.edu).

<sup>&</sup>lt;sup>2</sup> USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331.

| Treatment | Lure<br>components | Formulation       | Release rate<br>per day at 23°C | Chemical<br>purity, % | Enantiomertic composition $[\%(+)/\%(-)]$ |
|-----------|--------------------|-------------------|---------------------------------|-----------------------|---|
| 1         | Frontalin          | Vial              | 2.6 mg                          | >99                   | 50/50                                     |
| 2         | Frontalin          | Vial              | 2.6 mg                          | > 99                  | 50/50                                     |
|           | $\alpha$ -pinene   | Vial              | $1.5 \text{ mg}^a$              | > 99                  | 10/90                                     |
| 3         | Frontalin          | Polyvinylchloride | $2.5 \text{ mg}^b$              | 82                    | 50/50                                     |
|           | Seudenol           | Polyvinylchloride | $1.6 \text{ mg}^b$              | 99                    | 50/50                                     |
| 4         | exo-brevicomin     | Vial              | 1.7 mg                          | 98                    | 50/50                                     |
|           | Myrcene            | Vial              | 6.5 mg                          | 90                    | 50/50                                     |
| 5         | exo-brevicomin     | Vial              | 1.7 mg                          | 98                    | 50/50                                     |
|           | Myrcene            | Vial              | 6.5 mg                          | 90                    | 50/50                                     |
|           | Frontalin          | Vial              | 2.6 mg                          | > 99                  | 50/50                                     |
| 6         | exo-brevicomin     | Flex lure         | $280.0 \ \mu g^a$               | 98                    | 50/50                                     |
|           | Myrcene            | Bottle            | $95.0 \text{ mg}^b$             | 90                    | 50/50                                     |
|           | trans-verbenol     | Bubble cap        | $1.5 \text{ mg}^a$              | 86                    | 25/75                                     |
| 7         | Ipsdienol          | Bubble cap        | $110.0 \ \mu g^b$               | 97                    | 50/50                                     |
| 8         | Ipsdienol          | Bubble cap        | $110.0 \ \mu g^b$               | 97                    | 50/50                                     |
|           | Lanierone          | Bubble cap        | $10.0 \ \mu g^b$                | > 99                  | 50/50                                     |

Table 1. Technical description of bark beetle lures

All information on pheromone lures except those for treatment 3 was provided by Phero Tech, Delta, BC, Canada.  $^{a}$  At 20°C.

<sup>b</sup> At 25°C.

1990). Similarly, significant numbers of *T. chlorodia*, a predator of *D. pseudotsugae* (Kline and Rudinsky 1964), and *Dendroctonus brevicomis* LeConte (Stephen and Dahlsten 1976), have been collected in traps baited with *exo*-brevicomin (Pitman and Vité 1971, Bedard et al. 1980).

The information on kairomonal responses of T. undatulus, E. sphegeus, and T. chlorodia is fragmented. Past studies were conducted in different regions often with a single pheromone component or the pheromones of one bark beetle species. Most of the data demonstrating kairomonal responses of these predators were derived from studies designed to meet other objectives. Only one study has compared the attraction of these predators to a variety of bark beetle pheromones in the same location at the same time. Schmitz (1978) studied their attraction to a variety of bark beetle pheromones in northern Idaho, and concluded that T. undatulus used frontalin to locate prey while E. sphegeus used trans-verbenol for the same purpose. Because responses to semiochemicals may vary geographically, there is a need to study further the extent to which the predators are attracted to different bark beetle semiochemicals. Our objective was to assess the relative attractiveness of the pheromone components of different bark beetle species, which are commonly present in the same region, to the predators during the period of D. pseudotsugae dispersal. The results of such a study could indicate the degree to which the predators specialize on particular bark beetle species or the habitat where those species are found.

## Materials and Methods

This study was conducted on the La Grande Ranger District of the Wallowa-Whitman National Forest,  $\approx 17$  km west of La Grande, OR. Elevations across all replications ranged from 1,040–1,280 m. The most common tree species in the area were Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco; ponderosa pine, *Pinus ponderosa* Douglas ex Lawson; western larch, *Larix occidentalis* Nuttall; grand fir, *Abies grandis* (Douglas) Lindley; and lodgepole pine, *Pinus contorta* Douglas ex Loudon. At the time of the study, these forests supported high populations of *D. pseudotsugae* and *Scolytus ventralis* Leconte as a result of an extended drought and defoliation by the western spruce budworm, *Choristoneura fumiferana* (Clemens) (USDA Forest Service 1996).

Eight replicates of eight treatments were installed in a randomized complete block design between 13 April and 4 May 1995. Each replicate was established in an open grassland at least 50 m from the nearest tree. Experimental units consisted of single baited, 16-unit multiple-funnel traps (Lindgren 1983). Traps were hung from metal poles with their bases  $\approx$ 50 cm above the ground. A piece of dichlorvos-impregnated plastic was placed in each collection container to kill trapped insects and prevent predation. All traps within a replication were located in a line at least 25 m from adjacent traps. All replications were between 0.3 and 7 km from each other.

Treatments consisted of eight different combinations of aggregation pheromones and host tree terpenes commonly used to attract bark beetle species found in the western United States. The formulation, release rate, chemical purity, and enantiomertic composition of attractants used in each treatment lure are listed in Table 1. All semiochemical formulations were purchased from Phero Tech, Delta, BC, Canada, except frontalin and seudenol used in treatment 3 that were formulated in our laboratory. The lures used in the study are known to be attractive to *D. rufipennis* (treatment 2), *D. pseudotsugae* (treatment 3), *D. brevicomis* (treatments 4 and 5), *D. ponderosae* (treatment 6), and *Ips pini* (Say) (treatments 7 and 8).

| Treatment    | D. pseudotsugae |                          | D. brevicomis |                           | I. pini   |                           | P. carinulatus |                           |
|--------------|-----------------|--------------------------|---------------|---------------------------|-----------|---------------------------|----------------|---------------------------|
|              | Total no.       | No./trap/day             | Total no.     | No./trap/day              | Total no. | No./trap/day              | Total no.      | No./trap/day              |
| F            | 122             | $0.27\pm0.074\mathrm{b}$ | 24            | $0.05 \pm 0.193 d$        | 3         | $0.007\pm0.004\mathrm{c}$ | 3              | $0.007 \pm 0.005c$        |
| $F + \alpha$ | 161             | $0.38\pm0.167\mathrm{b}$ | 35            | $0.07 \pm 0.022 d$        | 3         | $0.007\pm0.005c$          | 4              | $0.009\pm0.004c$          |
| F + S        | 9203            | $20.61 \pm 4.043a$       | 15            | $0.03\pm0.017\mathrm{d}$  | 4         | $0.009\pm0.003c$          | 6              | $0.011\pm0.006c$          |
| E + M        | 7               | $0.02\pm0.006c$          | 415           | $0.78\pm0.148\mathrm{b}$  | 3         | $0.006\pm0.004c$          | 7              | $0.013\pm0.008c$          |
| E + M + F    | 118             | $0.28\pm0.087\mathrm{b}$ | 1651          | $2.29 \pm 0.408a$         | 0         | $0.000\pm0.000\mathrm{c}$ | 4              | $0.009\pm0.004c$          |
| E + M + T    | 6               | $0.01\pm0.008c$          | 144           | $0.25\pm0.044\mathrm{c}$  | 3         | $0.006\pm0.004c$          | 1              | $0.002\pm0.002c$          |
| Ι            | 8               | $0.02\pm0.007\mathrm{c}$ | 0             | $0.00\pm0.000e$           | 115       | $0.180\pm0.054b$          | 91             | $0.020\pm0.080\mathrm{b}$ |
| I + L        | 5               | $0.12\pm0.010\mathrm{c}$ | 1             | $0.001\pm0.001\mathrm{e}$ | 355       | $0.513 \pm 0.187a$        | 218            | $0.408 \pm 0.167a$        |
| Total        | 9,630           |                          | 2,285         |                           | 486       |                           | 334            |                           |

Table 2. Numbers of Dendroctonus pseudotsugae, Dendroctonus brevicomis, Ips pini, and Pityogenes carinulatus caught in traps baited with different semiochemicals in eastern Oregon, 1995

*F*, frontalin;  $\alpha$ ,  $\alpha$ -pinene; S, seudenol; *E*, *exo*-brevicomin; *M*, myrcene; *T*, *trans*-verbenol; *I*, ipsdienol; *L*, lanierone. Means  $\pm$  SE followed by different letters within a species are significantly different by Fisher's protected LSD test (*P* < 0.05).

Traps were emptied on 16 May, 24 May, 31 May, 7 June, 15 June, 24 June, 30 June, and 1 August. To account for positional effects, treatments were rerandomized within replicates following each collection. For each sample, the total numbers of all abundant bark beetle species, and three predacious associates, *T. undatulus*, *E. sphegeus*, and *T. chlorodia*, were counted.

Due to a large number of zero counts, the data for the eight collections of each species were pooled for each treatment within a block to provide numbers sufficient for statistical analyses. The numbers of each insect species were subjected to analysis of variance (ANOVA) with the model of a randomized complete block design. Before ANOVA, each variable was tested for homogeneity of variance by examining the residuals. If the variances were nonhomogeneous, the data were transformed by the formula,  $\log (x + 0.01)$ . Means were compared and separated by Fisher protected least significant difference (LSD) test (Ott 1988) when appropriate. The nontransformed means and their associated standard errors are reported. For variables that, even with transformation, did not have homogeneous variances, the data were subjected to Friedman's rank test (Conover 1980). The means were compared by the method described by Conover (1980) when the Friedman's test resulted in rejection of the null hypothesis. All data analyses were performed with SAS computer software (SAS Institute 1990).

### Results

Only four bark beetle species were collected in sufficient numbers to perform statistical analyses (Table 2). *D. pseudotsugae* was the most abundant bark beetle collected in the traps. The ANOVA indicated that the treatment effect on *D. pseudotsugae* trap catch was highly significant (F = 67.04; df = 7, 49; P = 0.0001). All of the traps with lures that contained frontalin caught significantly more *D. pseudotsugae* than those without frontalin, and traps baited with the combination of frontalin and seudenol caught significantly more than any other traps (Table 2).

*Dendroctonus brevicomis* was the second most abundant bark beetle collected in the traps (Table 2). The

treatment effect on *D. brevicomis* trap catch was highly significant (F = 84.86; df = 7, 49; P = 0.0001). All of the traps with lures that contained *exo*-brevicomin caught significantly more *D. brevicomis* than those traps without *exo*-brevicomin. Traps baited with the combination of *exo*-brevicomin, myrcene, and frontalin caught the most *D. brevicomis* followed by those baited with *exo*-brevicomin plus myrcene, and *exo*-brevicomin, myrcene, and *trans*-verbenol. Traps baited with frontalin alone and in combination with  $\alpha$ -pinene or seudenol caught significantly more *D. brevicomis* than those baited with ipsdienol or ipsdienol plus lanierone (Table 2).

The treatment effect on catches of *I. pini* and *Pityogenes carinulatus* (LeConte) were highly significant (F = 67.04; df = 7, 49; P = 0.0001 and F = 10.22; df = 7, 49; P = 0.0001, respectively). These two species responded similarly to the different treatments. Significantly more beetles of both species were collected in traps with lures containing ipsdienol compared with traps without ipsdienol in the lure (Table 2). Traps baited with the combination of ipsdienol and lanierone caught significantly more beetles of both species than ipsdienol alone.

Among the predators, only T. undatulus and T. chlorodia were captured in sufficient numbers for statistical analyses. The rank test followed by ANOVA indicated that the treatment effect on T. undatulus trap catch was highly significant (F = 24.49; df = 7, 49; P =0.0001). Significantly more T. undatulus were collected in traps baited with frontalin plus seudenol than in traps with any other lures (Table 3). There were no significant differences in T. undatulus collected in traps with the other lures. Significantly more T. chlorodia were caught in traps baited with exo-brevicomin and myrcene than those without these attractants (F = 8.26; df = 7, 49; P = 0.0001), and there were no differences among the three lures that contained these compounds (Table 3). Few T. chlorodia adults were collected in traps baited with other lures and there were no significant differences among them.

The numbers of *E. sphegeus* caught in the traps were too small to perform statistical analyses on that data.

| Treatment    | T. undatulus |                              | E. sphegeus |                           | T. chlorodia |                     |
|--------------|--------------|------------------------------|-------------|---------------------------|--------------|---------------------|
|              | Total no.    | No./trap/day                 | Total no.   | No./trap/day <sup>a</sup> | Total no.    | No./trap/day        |
| F            | 3            | $0.007\pm0.004\mathrm{b}$    | 0           | $0 \pm 0.000$             | 1            | $0.002 \pm 0.002 b$ |
| $F + \alpha$ | 1            | $0.002 \pm 0.002 \mathrm{b}$ | 1           | $0.002 \pm 0.002$         | 2            | $0.004 \pm 0.003 b$ |
| F + S        | 62           | $0.141 \pm 0.048a$           | 0           | $0\pm 0.000$              | 2            | $0.004 \pm 0.003 b$ |
| E + M        | 0            | $0\pm0.000\mathrm{b}$        | 2           | $0.004 \pm 0.003$         | 27           | $0.058 \pm 0.024a$  |
| E + M + F    | 0            | $0\pm0.000\mathrm{b}$        | 0           | $0 \pm 0.000$             | 40           | $0.087 \pm 0.011a$  |
| E + M + T    | 0            | $0\pm0.000\mathrm{b}$        | 1           | $0.002 \pm 0.002$         | 30           | $0.065 \pm 0.019a$  |
| Ι            | 0            | $0 \pm 0.000 \mathrm{b}$     | 0           | $0 \pm 0.000$             | 1            | $0 \pm 0.000 b$     |
| I + L        | 2            | $0.004 \pm 0.003 b$          | 4           | $0.008 \pm 0.005$         | 5            | $0.015 \pm 0.007 b$ |
| Total        | 68           |                              | 8           |                           | 108          |                     |

Table 3. Numbers of Thanasimus undatulus, Enoclerus sphegeus, and Temnochila chlorodia caught in traps baited with different semiochemicals in eastern Oregon, 1995

*F*, frontalin;  $\alpha$ ,  $\alpha$ -pinene; *S*, seudenol; *E*, *exo*-brevicomin; *M*, myrcene; *T*, *trans*-verbenol; *I*, ipsdienol; *L*, lanierone. Means  $\pm$  SE followed by different letters within a species are significantly different by Fisher's protected LSD test. (*P* < 0.05).

<sup>*a*</sup> No statistical analysis was performed on these data due to low numbers.

#### Discussion

Dendroctonus pseudotsugae, D. brevicomis, and I. pini responded as expected to the different lures based on previous research (Silverstein et al. 1968; Bedard et al. 1969, 1970; Pitman and Vité 1970; Rudinsky et al. 1974; Birch et al. 1980; Teale et al. 1991; Ross and Daterman 1995). P. carinulatus is a secondary pest associated primarily with ponderosa pine. It attacks the tops and limbs of weakened, dying, and newly felled trees, occasionally causing economic damage (Wood 1982). Unlike I. pini, the pheromone system of P. carinulatus is unknown. Our results indicate that P. carinulatus responds to the aggregation pheromone of I. pini, especially when lanierone is present along with ipsdienol.

Among the bark beetle semiochemicals used in this study, T. undatulus showed a significant response only to traps containing frontalin and seudenol in 5% polyvinylchloride formulations. Although the release rate of frontalin in the vials measured at a temperature 2°C lower was slightly higher than that of the PVC-formulated frontalin, catches of T. undatulus in traps baited with lures containing the frontalin vials were not different from those of traps that did not contain frontalin. These results are inconsistent with earlier reports that frontalin was attractive to T. undatulus (Pitman and Vité 1970, Furniss and Schmitz 1971, Rudinsky et al. 1972, Schmitz 1978, Chatelain and Schenk 1984, Miller et al. 1987, McGregor and Miller 1989). Our results suggest that seudenol is a key attractant, contributing to the response of both D. pseudotsugae and T. undatulus. However, Dyer and Lawko (1978) reported that seudenol did not enhance the attractiveness of frontalin plus alpha-pinene to T. undatulus in British Columbia, Canada, and Dyer and Hall (1980) found that frontalin was significantly more attractive to T. undatulus than seudenol. In contrast, Ross and Daterman (1995) found that seudenol significantly increased the attractiveness of frontalin to this clerid, which was confirmed by our results. These conflicting results may reflect geographic differences in the responsiveness of T. undatulus to various semiochemicals. In support of the existence of geographic races of T. undatulus, Schmitz (1978) observed morphologically distinct forms in different regions. Hence, further experiments need to be conducted to determine if there are variations in response to semiochemicals by *T. undatulus* populations in different geographic regions.

The experiment carried out by Miller and Borden (1990) in lodgepole pine in British Columbia, Canada, showed that E. sphegeus and T. undatulus were attracted to ipsdienol-baited traps in significantly higher numbers than to other treatments. In Idaho, Schmitz (1978) found that *E. sphegeus* preferred lures containing trans-verbenol to others tested. Only a few E. sphegeus adults were trapped in our experiment and these showed no preference to any attractant used in the study. However, both E. sphegeus and T. undatulus were caught in similar numbers on unbaited sticky traps which were used to monitor the landing patterns of D. pseudotsugae and its predacious associates in another experiment conducted in 1995 in the same general area. Also, larval E. sphegeus and T. undatulus were abundantly present in D. pseudotsugae larval galleries under the bark of the baited trees in that study (unpublished data). This evidence suggests that E. sphegeus utilizes semiochemicals other than frontalin and seudenol emanating from D. pseudotsugae attacked trees to locate its prey.

For the kairomonal response of *T. chlorodia*, our results are consistent with earlier studies in which *exo*-brevicomin was shown to be attractive (Pitman and Vité 1971, Bedard et al. 1980, Tilden et al. 1983, DeMars et al. 1986). Bedard et al. (1980) suggested that *trans*-verbenol might interfere with the response of *T. chlorodia* to *exo*-brevicomin. However, our results showed no negative effect when *trans*-verbenol was present in a lure containing *exo*-brevicomin and myrcene, compared with lures containing only *exo*-brevicomin and myrcene. This was true even though the lure containing *trans*-verbenol released *exo*-brevicomin at a much lower rate than the lure without *trans*-verbenol.

*Temnochila chlorodia* has been reported to be an important natural enemy of *D. pseudotsugae*, especially in the Intermountain Region (Kline and Rudinsky 1964, Marsden et al. 1981). However, it did not

appear to be closely associated with *D. pseudotsugae* in our study area. Not only did it not respond to the *D. pseudotsugae* lure (treatment 3, frontalin plus seudenol), but also no larval *T. chlorodia* were found in *D. pseudotsugae* galleries in a companion study in the same area (unpublished data).

Our results suggest that *T. undatulus* relies primarily on seudenol to locate its prev, whereas T. chlorodia relies similarly on exo-brevicomin. Apparently, these predators feed on bark beetle species that produce those pheromones or other species that are found in the same habitat. For example, trees attacked by D. *pseudotsugae* may also be infested by *Scolytus* spp. and *Pseudohylesinus* spp. in the upper bole and branches (Furniss and Carolin 1977). Under laboratory conditions, T. undatulus has been shown to prefer these smaller scolytids over D. pseudotsugae when given a choice (Schmitz 1978). Consequently, T. undatulus attracted by seudenol released by D. pseudotsugae may prey not only on that species but also on other associated scolytids. Neither predator showed any response to pheromones produced by sympatric bark beetle species indicating that they are to some extent specialized on one to a few species. A better understanding of bark beetle and predator responses to semiochemicals could be used to develop management techniques that are effective against the target insect and minimize negative impacts on the natural enemies.

# Acknowledgments

Thanks are given to Robert Peck for field assistance and to Steve Burke (Phero Tech, Incorporated) for providing the technical description of the pheromone lures. Thanks are extended also to Lisa Ganio, Department of Forest Science (Oregon State University) for statistical consulting. The authors thank the staff of the La Grande Ranger District, Wallowa-Whitman National Forest, for providing maps and access to the research sites. This research was supported by funds provided by the United States Department of Agriculture, Forest Service, Pacific Northwest Research Station.

#### **References Cited**

- Amman, G. D. 1972. Prey consumption and development of *Thanasimus undatulus*, a predator of the mountain pine beetle. Environ. Entomol. 1: 528–530.
- Bakke, A. 1983. Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. Z. Angew. Entomol. 96: 118–125.
- Bakke, A. 1989. The recent *Ips typographus* outbreaks in Norway – experiences from a control program. Holarct. Ecol. 12: 515–519.
- Bedard, W. D., and D. L. Wood. 1981. Suppression of *Den*droctonus brevicomis by using a mass-trapping tactic, pp. 103–114. In E. R. Mitchell [ed.], Management of insect pests with semiochemicals. Plenum, New York
- Bedard, W. D., P. E. Tilden, D. L. Wood, R. M. Silverstein, R. G. Brownlee, and J. O. Rodin. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science 164: 1284–1285.
- Bedard, W. D., R. M. Silverstein, and D. L. Wood. 1970. Bark beetle pheromones. Science 167: 1638–1639.

- Bedard, W. D., P. E. Tilden, D. L. Wood, K. Q. Lindahl, Jr., R. W. Silverstein, and J. O. Rodin. 1980. Field responses of the western pine beetle and one of its predators to hostbeetle-produced compounds. J. Chem. Ecol. 6: 625–641.
- Birch, M. C., D. M. Light, D. L. Wood, L. E. Browne, R. M. Silverstein, B. J. Bergot, G. Ohloff, J. R. West, and J. C. Young. 1980. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. J. Chem. Ecol. 6: 703–717.
- Borden, J. H. 1989. Semiochemicals and bark beetle populations: Exploitation of natural phenomena by pest management strategists. Holarct. Ecol. 12: 501–510.
- Borden, J. H., and J. A. McLean. 1981. Pheromone-based suppression of ambrosia beetles in industrial timber processing areas, pp. 133–154. *In E. R. Mitchell*, [ed.], Management of insect pests with semiochemicals. Plenum, New York
- Chatelain, M. P., and J. A. Schenk. 1984. Evaluation of frontalin and *exo*-brevicomin as kairomones to control mountain pine beetle (Coleoptera: Scolytidae) in lodgepole pine. Environ. Entomol. 13: 1666–1674.
- Conover, W. J. 1980. Practical nonparametric statistics, 2nd ed. Wiley, New York
- Cowan, B. F., and W. P. Nagel. 1965. Predators of the Douglas-fir beetle in western Oregon. Oregon State University, Corvallis, OR. Agric. Exp. Stn. Tech. Bull. 86.
- DeMars, C. J., G. W. Slaughter, W. D. Bedard, N. X. Norick, and B. Roettgering. 1980. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. J. Chem. Ecol. 6: 853–866.
- DeMars, C. J. Jr., D. L. Dahlsten, N. X. Sharpnack, and D. L. Rowney. 1986. Tree utilization and density of attacking and emerging populations of the western pine beetle (Coleoptera: Scolytidae) and its natural enemies, Bass Lake, California, 1970–1971. Can. Entomol. 118: 881–900.
- Dyer, E.D.A., and P. M. Hall. 1980. Effect of the living host tree (*Picea*) on the response of *Dendroctonus rufipennis* (Coleoptera: Scolytidae) and a predator *Thanasimus undatulus* (Coleoptera: Cleridae) to frontalin and seudenol. Can. Entomol. 112: 167–171.
- Dyer, E.D.A., and C. M. Lawko. 1978. Effect of seudenol on spruce beetle and Douglas-fir beetle aggregation. Environ. Can. Bi-Mon. Res. Notes 34: 30–32.
- Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. U.S. Dep. Agric. For. Serv. Misc. Publ. 1339.
- Furniss, M. M., and R. F. Schmitz. 1971. Comparative attraction of Douglas-fir beetles to frontalin and tree volatiles. USDA For. Serv. Res. Pap. INT-96.
- Kline, L. N., and J. A. Rudinsky. 1964. Predators and parasites of the Douglas-fir beetle: description and identification of the immature stages. Oregon State University, Corvallis, OR. Agric. Exp. Stn. Tech. Bull. 79.
- Knight, F. B. 1961. Variations in the life history of the Engelmann spruce beetle. Ann. Entomol. Soc. Am. 54: 209– 214.
- Knopf, J.A.E., and G. B. Pitman. 1972. Aggregation pheromone for manipulation of the Douglas-fir beetle. J. Econ. Entomol. 65: 723–726.
- Libbey, L. M., A. C. Ochlschlager, and L. C. Ryker. 1983. 1-Methylcyclohex-2-en-1-ol as an aggregation pheromone of *Dendroctonus pseudotsugae*. J. Chem. Ecol. 9: 1533–1541.
- Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299–302.
- Marsden, M. A., M. M. Furniss, and L. N. Kline. 1981. Modeling seasonal abundance of Douglas-fir beetle in relation to entomophagous insects and location in trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-111.

- McGregor, M. D., and M. C. Miller. 1989. Cross-attraction surveys for insect enemies of southern pine beetle, pp. 201–212. In D. L. Kulhavy and M. C. Miller [eds.], Potential for biological control of *Dendroctonus* and *Ips* bark beetles. Center for Applied Studies, School of Forestry, Stephen F. Austin State University, Nacogdoches, TX.
- Miller, D. R., and J. H. Borden. 1990. β-phellandrene: kairomone for pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). J. Chem. Ecol. 16: 2519–2531.
- Miller, D. R., J. H. Borden, G.G.S. King, and K. N. Slessor. 1991. Ipsenol: an aggregation pheromone for *Ips latidens* (Leconte) (Coleoptera: Scolytidae). J. Chem. Ecol. 17: 1517–1527.
- Miller, M. C., J. C. Moser, M. McGregor, J. C. Gregoire, M. Baisier, D. L. Dahlsten, and R. A. Werner. 1987. Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 80: 417–428.
- Ott, L. 1988. An introduction to statistical methods and data analysis, 3rd ed. PWS-KENT, Boston, MA.
- Pitman, G. B. 1973. Further observations on douglure in a Dendroctonus pseudotsugae management system. Environ. Entomol. 2: 109–112.
- Pitman, G. B., and J. P. Vité. 1970. Field response of Dendroctonus pseudotsugae (Coleoptera: Scolytidae) to synthetic frontalin. Ann. Entomol. Soc. Am. 63:661-664.
- Pitman, G. B., and J. P. Vité. 1971. Predator-prey response to western pine beetle attractants. J. Econ. Entomol. 64: 403–404.
- Reid, R. W. 1957. The bark beetle complex associated with lodgepole pine slash in Alberta. Part III—notes on the biologies of several predators with special reference to *Enoclerus sphegeus* Fab. (Coleoptera: Cleridae) and two species of mites. Can. Entomol. 89: 111–120.
- Ross, D. W., and G. E. Daterman. 1995. Response of *Den*droctonus pseudotsugae (Coleoptera: Scolytidae) and *Thanasimus undatulus* (Coleoptera: Cleridae) to traps with different semiochemicals. J. Econ. Entomol. 88: 106– 111.
- Ross, D. W., and G. E. Daterman. 1997. Using pheromonebaited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. For. Sci. 43: 65–70.
- Rudinsky, J. A., M. M. Furniss, L. N. Kline, and R. F. Schmitz. 1972. Attraction and repression of *Dendroctonus pseudot-sugae* (Coleoptera: Scolytidae) by three synthetic pheromone traps in Oregon and Idaho. Can. Entomol. 104: 815–822.
- Rudinsky, J. A., M. E. Morgan, L. M. Libbey, and T. B. Putnam. 1974. Additional components of the Douglasfir beetle (Coleoptera: Scolytidae) aggregative pheromone and their possible utility in pest control. Z. Agnew. Entomol. 76: 65–77.

- Salom, S. M., and K. R. Hobson (eds.). 1995. Application of Semiochemicals for Management of Bark Beetle Infestations–Proceedings of an informal conference, Annual Meeting of the Entomological Society of America, 12–16 December 1993. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-GTR-318.
- SAS Institute. 1990. SAS/STAT user's guide for personal computers, version 6, 3rd ed. SAS Institute, Cary, NC.
- Schmitz, R. F. 1978. Taxonomy and bionomics of the North American species of *Thanasimus* Latreille (Coleoptera: Cleridae). Ph.D. dissertation, University of Idaho, Moscow.
- Shea, P. J. 1994. Proceedings of the Symposium on Management of Western Bark Beetles with Pheromones: Research and Development, 22–25 June 1992, Kailua-Kona, Hawaii. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PSW-GTR-150.
- Silverstein, R. M., R. G. Brownlee, T. E. Bellas, D. L. Wood, and L. E. Browne. 1968. Brevicomin: principal sex attractant in the frass of the female western pine beetle. Science 159: 889–891.
- Smith, R. H. 1986. Trapping western pine beetles with baited toxic trees. USDA For. Serv. Res. Note PSW-382.
- Stephen, F. M., and D. L. Dalhsten. 1976. The temporal and spatial arrival pattern of *Dendroctonus brevicomis* in ponderosa pine. Can. Entomol. 108: 217–282.
- Struble, G. R. 1942. Biology of two native coleopterous predators of the mountain pine beetle in sugar pine. Pan.-Pac. Entomol. 18: 97–107.
- Teale, S. A., F. X. Webster, A. Zhang, and G. N. Lanier. 1991. Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York. J. Chem. Ecol. 17: 1159–1176.
- Thier, R. W., and J. C. Weatherby. 1991. Mortality of Douglas-fir after two semiochemical baiting treatments for Douglas-fir beetle (Coleoptera: Scolytidae). J. Econ. Entomol. 84: 962–964.
- Tilden, P. E., W. D. Bebard, K. Q. Lindahl, Jr., and D. L. Wood. 1983. Trapping *Dendroctonus brevicomis:* changes in attractant release rate, dispersion of attractant, and silhouette. J. Chem. Ecol. 9: 321–331.
- USDA Forest Service. 1996. Forest insect and disease conditions in the United States 1995. USDA Forest Service, Forest Health Protection, Washington, DC.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs No. 6. Brigham Young University, Provo, UT.

Received for publication 19 January 2001; accepted 23 July 2001.