

# Test of Nonhost Angiosperm Volatiles and Verbenone to Protect Trap Trees for *Sirex noctilio* (Hymenoptera: Siricidae) From Attacks by Bark Beetles (Coleoptera: Scolytidae) in the Northeastern United States

KEVIN J. DODDS<sup>1</sup> AND DANIEL R. MILLER<sup>2</sup>

J. Econ. Entomol. 103(6): 2094–2099 (2010); DOI: 10.1603/EC10225

**ABSTRACT** *Sirex noctilio* F. (Hymenoptera: Siricidae) is an invasive woodwasp, currently established in northeastern North America. In other regions of the world, stressed trap trees are used to monitor populations of *S. noctilio* and to provide inoculation points for the biological control nematode *Deladenus siricidicola* Bedding. However, the operational use of trap trees for *S. noctilio* in North America may be compromised by the large community of native organisms that inhabit stressed and dying pine trees. Common bark beetles such as *Ips pini* (Say) and *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) could potentially compete with *S. noctilio* and associates for resources on trap trees, possibly reducing the efficacy of trap trees as habitats for the woodwasp. In an attempt to develop a technology to mitigate this potential issue, three common semiochemical interruptants—conophthorin, green leaf volatile mix, and verbenone—were tested for effectiveness in reducing arrivals of *I. pini* and *I. grandicollis* on trap trees treated with herbicides in northeastern United States. In addition, the effects of these compounds were determined independently with pheromone-baited multiple-funnel traps. None of the interruptants reduced numbers of *I. pini* or *I. grandicollis* either arriving on trap trees or caught in pheromone-baited traps. However, verbenone increased catches of *I. grandicollis* in traps baited with its pheromone, ipsenol. The mix of green leaf volatiles reduced catches of a native ambrosia beetle, *Gnathotrichus materiarius* (Fitch), whereas verbenone reduced trap catches of an exotic ambrosia beetle, *Xylosandrus germanus* (Blandford). Catches of *X. germanus* in traps adjacent to trap trees were enhanced with conophthorin.

**KEY WORDS** *Ips pini*, *Ips grandicollis*, *Xylosandrus germanus*, *Gnathotrichus materiarius*, conophthorin

In 2004, the exotic and invasive woodwasp species *Sirex noctilio* F. (Hymenoptera: Siricidae) was detected in central New York (Hoebeker et al. 2005, Dodds and de Groot 2011). In the southern hemisphere, attacks by *S. noctilio* have caused extensive mortality of North American pine trees in plantations, resulting in significant economic losses (Borchert et al. 2007). Current populations in northeastern United States and southern Ontario, Canada, have not caused serious impacts in pine stands to date (Dodds et al. 2010). However, the behavior and impacts of *S. noctilio* in forest stands that contain a higher incidence of

susceptible hosts growing under more uniform conditions are unknown.

Detection efforts for *S. noctilio* in North America have primarily used semiochemical-baited traps, albeit with limited success (Dodds and de Groot 2011). Trap trees created by injecting live pine trees with herbicide are an effective detection component of integrated pest management programs for *S. noctilio* in other countries (Haugen et al. 1990). Moreover, trap trees can provide important release points for the nematode *Deladenus siricidicola* Bedding in biological control programs against *S. noctilio* (Bedding and Akhurst 1974, Neumann et al. 1982).

A deployment methodology for trap trees targeting *S. noctilio* has been developed for the northeastern United States (Zylstra et al. 2010). However, a potential obstacle to a trap tree program in North America is the abundance of native bark and wood-boring insects and their associated fungi that use stressed and recently dead trees as reproductive habitats (Ross 1967, Paine et al. 1981, Klepzig et al. 2001, Dodds and Stephen 2002). Specifically, >50 species of Cerambycidae and Scolytidae are attracted to *S. noctilio* trap

The use of trade names and identification of firms or corporations does not constitute an official endorsement or approval by the U.S. Government of any product or service to the exclusion of others that may be suitable. Funding for this research was provided by the USDA Forest Service, Northeastern Area State and Private Forestry and Southern Research Station. The USDA is an equal opportunity provider and employer.

<sup>1</sup> Corresponding author: USDA Forest Service, Northeastern Area State & Private Forestry, Durham Field Office, 271 Mast Rd., Durham, NH 03824 (e-mail: kdodds@fs.fed.us).

<sup>2</sup> USDA Forest Service, Southern Research Station, 320 Green St., Athens, GA 30602.

trees in New York (unpublished data). *Ips pini* (Say) and *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) are of particular concern as both species can respond in large numbers to weakened pine trees and create galleries directly in the phloem tissue (Wood 1982, Erbilgin et al. 2002). In British Columbia, *I. pini* quickly colonized lodgepole pines, *Pinus contorta* Dougl. ex Loud. variety *latifolia* Engelm., treated with the herbicide glyphosate (Bergvinson and Borden 1991).

The chemical ecology of bark beetles such as *I. grandicollis* and *I. pini* involves a complex array of decisions based on host odors and pheromones produced by conspecifics and competing species (Byers 1989). Attraction of individual beetles can be interrupted by inappropriate host odors, antiaggregation pheromones, or pheromones of competing species. The potential to use such interruptive phenomena in a control program against bark beetles has been explored with various levels of success (Borden 1997). For example, verbenone is an anti-aggregation pheromone produced by many species of *Dendroctonus* (Scolytidae) (Borden 1997). Borden and Lindgren (1988) and Shore et al. (1992) used verbenone to protect lodgepole pines, baited with the aggregation pheromone for *Dendroctonus ponderosae* Hopkins, from attacks by *D. ponderosae* in British Columbia. Similarly, Gillette et al. (2006) were able to protect individual lodgepole pines from attack by *D. ponderosae* and *Dendroctonus valens* LeConte by application of verbenone-releasing flakes directly on trees in California.

Nonhost angiosperm volatiles also can interrupt attraction of bark beetles, especially in combination with verbenone. The combination of two nonhost angiosperm volatiles, (*E*)-2-hexen-1-ol and (*Z*)-3-hexen-1-ol, significantly reduced attacks of *D. ponderosae* on pheromone-baited lodgepole pine (Wilson et al. 1996). Applications of verbenone with a blend of nonhost angiosperm volatiles protected individual ponderosa pines, *Pinus ponderosa* P. Laws. ex C. Laws., from attacks by *Dendroctonus brevicomis* LeConte and *D. valens* (Fettig et al. 2008, 2009). Similarly, the combination of verbenone and conophthorin, a nonhost angiosperm volatile, protected spruce trees from attacks by *Ips perturbatus* (Eichhoff) (Graves et al. 2008). In all these trials, the responses of beetles to interruptants were challenged with the use of species-specific pheromones.

We hypothesized that interruptants could reduce bark beetle attacks on trap trees prepared for *S. noctilio*. Our objective was to evaluate some common nonhost angiosperm volatiles, a two-component green leaf volatile blend and conophthorin alone, and verbenone alone for efficacy in reducing colonization of trap trees by *I. pini* and *I. grandicollis*. To help explain results with trap trees, we evaluated the interruptive effects of these compounds independently with pheromone-baited traps. In both experiments, we monitored the responses of the following bark beetles commonly associated with stressed and dying pines: *I. pini*,

*I. grandicollis*, *Gnathotrichus materiarius* (Fitch), and *Xylosandrus germanus* (Blandford) (Scolytidae).

## Materials and Methods

**Semiochemical Release Devices.** Synergy Inc. (New Westminster, BC, Canada) supplied bubble-cap release devices for ( $\pm$ )-ipsenol (=racemic ipsenol, 50:50 mix of the two enantiomers) and ( $\pm$ )-ipsdienol and lanierone (chemical purities >98%). At 22–24°C, the release rates for ipsenol and ipsdienol were 0.5–1 mg/d, whereas lanierone was released at 10–50  $\mu$ g/d. Pouch lures of green leaf volatile blend [50:50 mix of 1-hexanol and (*Z*)-3-hexenol; chemical purity >98%] were supplied by Synergy Inc. as well, releasing at a rate of 80–100 mg/d at 22–24°C. Contech Enterprises Inc. (Victoria, BC, Canada) supplied microcentrifuge tubes (250  $\mu$ l) of (*E*)-( $\pm$ )-conophthorin (isomeric purity >97%, chemical purity >98%) and pouches of (–)-verbenone (enantiomeric purity 78%, chemical purity >98%), releasing conophthorin and verbenone at rates of five and 40 mg/d, respectively, at 22–24°C.

**Experiments.** Two experiments were conducted in 2007 to determine the effects of common interruptants on the responses of *I. pini* and *I. grandicollis* in northeastern United States. The following interruptants were tested in each experiment against a control: 1) conophthorin, 2) green leaf volatiles, and 3) verbenone. The experiments differed by background odors and locality.

In experiment 1, treatments were applied directly to trap trees in a stand of red pine, *Pinus resinosa* Aiton, on the Finger Lakes National Forest (NF) (42.4442° N, –76.8107° W) near Hector, Schuyler County, NY. The stand had evidence of recent bark beetle activity as well as winter storm damage. *S. noctilio* was not known to be present in the Finger Lakes NF in early 2007, although Schuyler County was considered positive for *S. noctilio*. Twenty red pines were selected as trap trees. Selected trees were all from the intermediate crown class, with an average diameter ( $\pm$ SE) of 16.9  $\pm$  0.4 cm. Trap trees were created on 31 May 2007 by drilling two holes (diameter, 4.4 mm)  $\approx$  1.3 cm into the sapwood and 30 cm from the base of each tree. The position of the first hole was randomly selected with the second hole drilled on the opposite side of the tree. Into each hole, a Tree Tech microinjector containing 0.55 g of active ingredient (AI) of the herbicide Dicamba (3,6-dichloro-*o*-anisic acid, Tree Tech, Morriston, FL) was inserted. A randomized complete block design was implemented, with five replicate blocks of four trap trees per block. Within each block, trap trees were >15 m from one another and blocks were separated by >25 m. The following treatments were randomly assigned to each trap tree: 1) blank control, 2) conophthorin, 3) green leaf volatiles, and 4) verbenone. On each trap tree, two release devices containing the same semiochemical(s) were placed at breast height (1.5 m) on opposite sides of trees. Release devices were changed every 4 wk.

Intercept panel traps (APTIV Inc., Portland OR) were placed on each trap tree such that the bottom of

Table 1. Effect of conophthorin, green leaf volatile (GLV) blend, and verbenone on catches of some bark and ambrosia beetles to trap trees on the Finger Lakes National Forest, NY (exp. 1) and pheromone-baited traps in Oswego, NY (exp. 2), 2007

| Species                     | Mean ( $\pm$ SE) no. of beetles captured |                  |                  |                  |
|-----------------------------|--|------------------|------------------|------------------|
|                             | Control                                  | Conophthorin     | GLV              | Verbenone        |
| Exp. 1: Finger Lakes        |  |                  |                  |                  |
| <i>I. grandicollis</i> (NS) | 34.2 $\pm$ 11.5                          | 46.8 $\pm$ 15.7  | 45.8 $\pm$ 15.3  | 37.6 $\pm$ 12.6  |
| <i>I. pini</i> (NS)         | 7.6 $\pm$ 5.4                            | 4.6 $\pm$ 3.3    | 31.4 $\pm$ 21.9  | 37.2 $\pm$ 26.0  |
| <i>G. materiarius</i> (NS)  | 12.5 $\pm$ 7.7                           | 8.4 $\pm$ 3.8    | 4.0 $\pm$ 1.9    | 10.2 $\pm$ 4.7   |
| <i>X. germanus</i>          | 9.3 $\pm$ 2.0                            | 17.1 $\pm$ 3.3*  | 10.0 $\pm$ 2.2   | 1.6 $\pm$ 0.6*   |
| Exp. 2: Oswego              |  |                  |                  |                  |
| <i>I. grandicollis</i>      | 34.1 $\pm$ 11.1                          | 28.6 $\pm$ 9.3   | 33.8 $\pm$ 11.0  | 81.6 $\pm$ 26.0* |
| <i>G. materiarius</i>       | 10.4 $\pm$ 2.6                           | 8.3 $\pm$ 2.2    | 3.0 $\pm$ 1.0*   | 2.6 $\pm$ 0.9*   |
| <i>X. germanus</i>          | 128.0 $\pm$ 25.1                         | 187.5 $\pm$ 36.6 | 142.7 $\pm$ 28.0 | 41.9 $\pm$ 8.6*  |

Means followed by an asterisk (\*) are significantly different from the control mean within the same row ( $P = 0.05$ ; Dunnett's test). There was no significant treatment effect for species followed by NS (see text).

each trap was  $\approx 1.5$  m from the base of each trap tree and not blocking the lures attached to each tree. Traps were oriented vertically, parallel with tree boles and  $\approx 0.5$  m from the bark surface. Approximately 250 ml of propylene glycol (Prestone RV antifreeze) was used as the killing and preservation fluid. Aggregation pheromones were not used to attract *Ips* spp. to trap trees as we assumed that host volatiles released by stressed trap trees would be sufficient to ensure beetle pressure on trap trees. Trap catches were collected 6 June–10 September 2007 at 2-wk intervals. During each collection, the lower 3 m of each trap tree was examined for bark beetle attacks or oviposition beading created by *S. noctilio*. When possible, bark beetles were collected for identification. Presence and absence of beetle activity was recorded for each trap tree along with any indication of decline (e.g., bark slippage, crown color changes).

In experiment 2, treatments were applied to 12-unit multiple-funnel traps (Synergy Inc. New Westminster, BC, Canada) baited with bark beetle pheromones. The experiment was conducted in a red pine stand on the campus of the State University of New York at Oswego, in Oswego, NY (43.4465° N, -76.5504° W). The stand had evidence of *I. grandicollis* and had been previously infested by *S. noctilio*.

A randomized complete block design was used with replicate blocks of four funnel traps per block. Traps within blocks were set in a 2 by 2 grid pattern with a spacing of 10–15 m between traps; replicate blocks were spaced  $>25$  m apart. Traps were hung from conduit poles bent at 90° with the base of traps  $\approx 0.5$  m from the ground. Each collection cup contained 250 ml of a propylene glycol mixture. Twenty traps were set in five replicate blocks with each trap baited with ipsenol, a pheromone used by *I. grandicollis* (Vité et al. 1972, 1976). The following treatments were randomly assigned to each funnel trap: 1) blank control, 2) conophthorin; 3) green leaf volatiles, and 4) verbenone. The trapping period for experiment 2 was 9 July–10 September 2007 with collections occurring at 2-wk intervals.

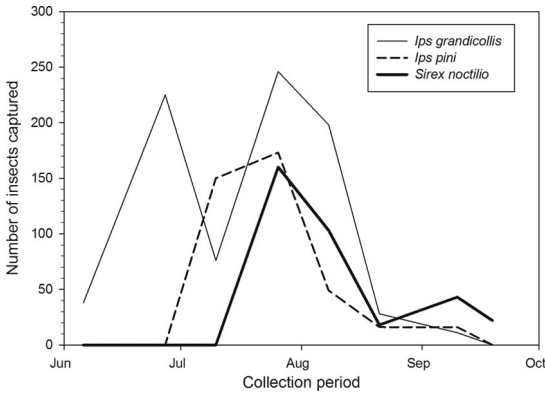
**Statistical Analyses.** Data were analyzed with SAS Statistical Package, version 9.2 (SAS Institute, Cary, NC). Trap catches were summed over the season and

analyzed using a generalized linear model (PROC GLIMMIX) via maximum likelihood estimation technique and the Laplace likelihood approximation method. Replicates were a random factor and treatment was a fixed factor. Data were modeled using the negative binomial distribution with log link function with one exception. *I. grandicollis* trap catches from experiment 2 were modeled using the normal distribution with the identity link function. Dunnett's multiple comparison test ( $\alpha = 0.05$ ) was used to compare mean trap catches for each treatment to controls traps.

## Results

**Experiment 1: Test of Trap Tree Protection.** There was no apparent tree protection from bark beetle attacks by any of the treatments. One month after treatment with herbicide, 75% of trap trees were colonized by bark beetles with the crown foliage of each tree beginning to fade. By the end of the summer, all trap trees were colonized and showed signs of dying crowns. Beetles attacking trap trees included *I. pini*, *I. grandicollis*, *D. valens*, and several species of ambrosia beetles. Trap trees were also colonized by numerous longhorn beetles (Cerambycidae), such as *Monochamus scutellatus* (Say), *Xylotrechus sagittatus* (Germar), and a *Tetropium* sp. Kirby. Signs of attack by *S. noctilio* (i.e., resin beads) were found on four trap trees, all of which also were colonized by *I. pini*, *I. grandicollis*, or both.

In experiment 1, totals of 822 *I. grandicollis* and 404 *I. pini* were captured in panel traps with both species present in the majority of traps. However, 30% of traps had *I. grandicollis* present but not *I. pini*. Treatments applied to trap trees had no effect on mean trap catches of *I. grandicollis* in traps hung from trap trees treated with conophthorin, green leaf volatiles, or verbenone ( $F_{3, 12} = 0.21$ ;  $P = 0.89$ ) (Table 1). Likewise, there was no treatment effect on mean catches of *I. pini* ( $F_{3, 12} = 2.12$ ;  $P = 0.15$ ) and the native ambrosia beetle *G. materiarius* ( $F_{3, 12} = 1.13$ ;  $P = 0.38$ ). However, trap catches of the exotic ambrosia beetle, *Xylosandrus germanus* (Blandford) were affected by treatments on trap trees ( $F_{3, 12} = 10.68$ ,  $P = 0.001$ ). Mean catches of *X. germanus* were lower in traps on

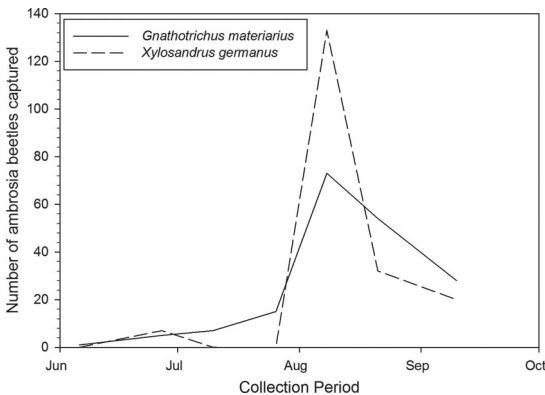


**Fig. 1.** Flight phenology of *Ips grandicollis* and *I. pini* arriving at trap trees in a red pine stand on the Finger Lakes National Forest, NY in 2007. Data on flight phenology of *Sirex noctilio* is from Zylstra (2010), a study conducted 120 km northeast of the Finger Lakes National Forest.

trap trees treated with verbenone compared with control trees (Table 1). Traps on trees treated with conophthorin captured more *X. germanus* than control trees.

*I. pini* and *I. grandicollis* exhibited long flight periods on the Finger Lakes NF that overlap significantly with that of *S. noctilio* (Fig. 1). *I. grandicollis* arrived at trap trees earlier in the season than *I. pini* and was active in early June. Both species were collected at trap trees throughout July and August and were still active at the last collection date (10 September). *G. materiaris* and *X. germanus* flight activity peaked in mid-August (Fig. 2).

**Experiment 2: Funnel Trap Test With Pheromones.** In 2007, 985 *I. grandicollis* in total were captured in pheromone-baited traps in experiment 2. There was a significant treatment effect on trap catches of *I. grandicollis* ( $F_{3, 12} = 5.18; P = 0.02$ ). Verbenone significantly increased captures of *I. grandicollis* to ipsenol-baited traps (Table 1). There were no significant differences among the other treatment means. Trap



**Fig. 2.** Flight phenology of *Gnathotrichus materiaris* and *Xylosandrus germanus* arriving at trap trees in a red pine stand on the Finger Lakes National Forest, NY in 2007.

catches of *G. materiaris* to ipsenol-baited traps were significantly reduced by green leaf volatiles and verbenone ( $F_{3, 12} = 6.68; P = 0.007$ ) (Table 1). As in experiment 1, *X. germanus* trap catches were lower in traps baited with verbenone compared with the control traps ( $F_{3, 12} = 22.47; P < 0.0001$ ). Only six *I. pini* were captured in experiment 2.

**Discussion**

We were unable to protect red pine trees treated with herbicide from attacks by bark beetles with applications of verbenone, conophthorin, or the green leaf volatile blend of 1-hexanol and (Z)-3-hexenol. The lack of protection against *I. grandicollis* and *I. pini* in attractants and host susceptibility. In all previous trials in western North America, attractants were placed on healthy trees. Successful attacks by bark beetles required a critical density of beetles to overcome tree defenses. In our study, tree defenses were removed through the use of herbicide. Attacks by single individuals could occur successfully anywhere along the entire bole. Once attacks were made, additional pheromones would have been released resulting in quick utilization of the entire tree bole. In British Columbia, application of herbicide into lodgepole pine resulted in full utilization of tree boles by *I. pini* (Bergvinson and Borden 1991). Moreover, interruptants in previous trials were placed generally in close proximity to attractants. In our study, attractants (kairomones and pheromones) probably emanated from the entire bole, and it is possible that the use of two interruptants at one location was simply insufficient to counter the host availability. The successful use of interruptants with trap trees treated with herbicide may require broad application of interruptants along the entire bole, as in Gillette et al. (2006).

Another factor in the lack of protection against bark beetle attacks may rest with the lack of any significant interruptant effect of the semiochemicals tested against *I. grandicollis* or *I. pini* in experiments using either trap trees or attractant-baited traps. The mean number of *I. grandicollis* and *I. pini* caught in traps on trap trees treated with conophthorin, green leaf volatiles, or verbenone was the same as those in traps on untreated trap trees (Table 1). Similarly, catches of *I. grandicollis* in pheromone-baited funnel traps were not reduced with the addition of conophthorin, green leaf volatiles, or verbenone. In fact, catches of *I. grandicollis* in Oswego, NY, were higher in traps baited with ipsenol and verbenone than in those baited with ipsenol alone.

The lack of any significant interruption by the green leaf volatile mix of 1-hexanol and (Z)-3-hexenol on the attraction of *I. pini* is consistent with results from western North America. Various combinations of non-host angiosperm volatiles, including 1-hexanol and (Z)-3-hexenol, did not interrupt attraction of *I. pini* to pheromone-baited traps in British Columbia (Huber et al. 2001). In contrast, the green leaf volatile blend of 1-hexanol and (Z)-3-hexenol did reduce trap



catches of *G. materiarius*. The responses of other species of *Gnathotrichus* found in western North America have been interrupted by a green leaf volatile blend containing (Z)-3-hexenol, 1-hexanol, (Z)-2-hexenol, and (E)-2-hexenol (Deglow and Borden 1998a,b).

Our results with *I. pini* and conophthorin in New York are inconsistent with those for *I. pini* in western North America. Huber et al. (2000) found that conophthorin interrupted the attraction of *I. pini* to traps baited with ipsdienol and lanierone in stands of lodgepole pine, whereas conophthorin had no effect in our studies. Inconsistencies also were noted with *X. germanus*. In Europe, Kohnle et al. (1992) found that conophthorin interrupted attraction of *X. germanus* to ethanol-baited traps. In contrast, we found that traps on trap trees baited with conophthorin caught significantly more *X. germanus* than traps on unbaited control trap trees.

Verbenone acts as an inhibitor for various species of bark beetles (Payne et al. 1978, Bedard et al. 1980, Devlin and Borden 1994, McPherson et al. 1997, Rappaport et al. 2001). The lack of any interruptive effect by verbenone on the attraction of *I. pini* and *I. grandicollis* is particularly surprising. Verbenone is interruptive to *I. pini* in British Columbia (Borden et al. 1992, Miller et al. 1995, Lindgren and Miller 2002a). Conversely, verbenone-baited traps in experiment 2 captured significantly more *I. grandicollis* than control traps. We know of only one other scolytid species that is attracted by verbenone. Lindgren and Miller (2002b) found that the striped ambrosia beetle, *Trypodendron lineatum* (Olivier), exhibited a dose-dependent attraction to verbenone. In our experiments, trap catches of *G. materiarius* and *X. germanus* were significantly reduced by the addition of verbenone. This is the first report of the genus *Gnathotrichus* responding negatively to verbenone. Verbenone is an inhibitor for other exotic ambrosia beetles, including *Xylosandrus compactus* (Eichhoff) (Dudley et al. 2006) and *Xylosandrus crassiusculus* (Motschulsky) (E. G. Burbano et al., unpublished data), and may be a promising management tool for this genus.

Although the concern for interactions occurring between bark beetles, their associated fungi, and *S. noctilio* is speculative at this point, there was considerable overlap in flight phenology of the two *Ips* spp., ambrosia beetles, and the woodwasp (Figs. 1 and 2). *S. noctilio* flight phenology determined from a study  $\approx$ 120 km northeast of the Finger Lakes NF (Zylstra et al. 2010) was overlaid onto the *Ips* data generated during this study to compare seasonal flight patterns. Captures of both species peaked concurrent with *S. noctilio* captures, suggesting these species would be searching for suitable hosts at the same time and potentially competing for trap tree resources. Attempts to use disruptants or interruptants to protect woodwasp trees should consider blends of various compounds. In addition, the interruptants should probably be applied over the full tree surface because engraver beetles can probably begin their attacks farther up the bole and then proceed downward to occupy the full bole.

## Acknowledgments

We thank Garret Dubois for assistance in the field and laboratory; Angela Hammond-Maddux for assistance in sorting insects, Mike Liu and Christopher Zimmer for assistance in locating a study site on the Finger Lakes National Forest, E. Richard Hoebeke for confirming species of Scolytidae, Steven J. Seybold for providing comments on study design, and Tree Tech Microinjection Systems for providing herbicide injectors.

## References Cited

- Bedard, W. D., P. E. Tilden, K. Q. Lindahl, D. L. Wood, and P. A. Rauch. 1980. Effects of verbenone and *trans*-verbenol on the response of *Dendroctonus brevicomis* (Coleoptera, Scolytidae) to natural and synthetic attractant in the field. *J. Chem. Ecol.* 6: 997–1013.
- Bedding, R. A., and R. J. Akhurst. 1974. Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. *J. Aust. Entomol. Soc.* 13: 129–135.
- Bergvinson, D. J., and J. H. Borden. 1991. Glyphosate-induced changes in the attack success and development of the mountain pine beetle and impact of its natural enemies. *Entomol. Exp. Appl.* 60: 203–212.
- Borchert, D., G. Fowler, and L. Jackson. 2007. Organism pest risk analysis: risk to the conterminous United States associated with the woodwasp, *Sirex noctilio* Fabricius, and the symbiotic fungus, *Amylostereum areolatum* (Fries: Fries) Bodin. *Pest Risk Analysis, U.S. Dep. Agric.-APHIS-PPQ-EDP*.
- Borden, J. H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles, pp. 421–438. *In* R. T. Cardé and A. K. Minks (eds.), *Pheromone research: new directions*. Chapman & Hall, New York.
- Borden, J. H., and B. S. Lindgren. 1988. The role of semiochemicals in IPM of the mountain pine beetle, pp. 247–255. *In* T. L. Payne and H. Saarenmaa (eds.), *Integrated control of scolytid bark beetles*. Virginia Polytechnic Institute and State University Press, Blacksburg, VA.
- Borden, J. H., D. R. Devlin, and D. R. Miller. 1992. Synomones of two sympatric species deter attack by the pine engraver, *Ips pini* (Coleoptera, Scolytidae). *Can. J. For. Res.* 22: 381–387.
- Byers, J. A. 1989. Chemical ecology of bark beetles. *Experientia* 45: 271–283.
- Deglow, E. K., and J. H. Borden. 1998a. Green leaf volatiles disrupt and enhance response to aggregation pheromones by the ambrosia beetle, *Gnathotrichus sulcatus* (Coleoptera: Scolytidae). *Can. J. For. Res.* 28: 1697–1705.
- Deglow, E. K., and J. H. Borden. 1998b. Green leaf volatiles disrupt and enhance response by the ambrosia beetle, *Gnathotrichus retusus* (Coleoptera: Scolytidae) to pheromone-baited traps. *J. Entomol. Soc. Br. Columbia* 95: 9–15.
- Devlin, D. R., and J. H. Borden. 1994. Efficacy of antiaggregants for the pine engraver, *Ips pini* (Coleoptera, Scolytidae). *Can. J. For. Res.* 24: 2469–2476.
- Dodds, K. J., and P. de Groot. 2011. *Sirex*, surveys, and management: challenges of having *Sirex noctilio* in North America. *In* B. Slippers, M. J. Wingfield, and P. de Groot (eds.), *The Sirex woodwasp: expanding frontiers*. Springer, Dordrecht, The Netherlands.
- Dodds, K. J., and F. M. Stephen. 2002. Arrival and species complex of Cerambycidae on pines attacked by southern pine beetle. *J. Entomol. Sci.* 37: 272–274.

- Dodds, K. J., P. de Groot, and D. A. Orwig. 2010. The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Can. J. For. Res.* 40: 212–223.
- Dudley, N., J. D. Stein, T. Jones, and N. E. Gillette. 2006. Semiochemicals provide a deterrent to the black twig borer, *Xylosandrus compactus* (Coleoptera: Curculionidae, Scolytinae), pp. 34. In K. W. Gottschalk (ed.), U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species. U.S. Dep. Agric. Forest Service, Northern Research Station, Annapolis, MD.
- Erbilgin, N., E. V. Nordheim, B. H. Aukema, and K. F. Raffa. 2002. Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: within- and between-year associations with predators, competitors, and habitat quality. *Environ. Entomol.* 31: 1043–1051.
- Fettig, C. J., C. P. Dabney, S. R. McKelvey, and D.P.W. Huber. 2008. Nonhost angiosperm volatiles and verbenone protect individual ponderosa pines from attack by western pine beetle and red turpentine beetle (Coleoptera: Curculionidae, Scolytinae). *West. J. Appl. For.* 23: 40–45.
- Fettig, C. J., S. R. McKelvey, C. P. Dabney, R. R. Borys, and D.P.W. Huber. 2009. Response of *Dendroctonus brevicomis* to different release rates of nonhost angiosperm volatiles and verbenone in trapping and tree protection studies. *J. Appl. Entomol.* 133: 143–154.
- Gillette, N. E., J. D. Stein, D. R. Owen, J. N. Webster, G. O. Fiddler, S. R. Mori, and D. L. Wood. 2006. Verbenone-releasing flakes protect individual *Pinus contorta* trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). *Agric. For. Entomol.* 8: 243–251.
- Graves, A. D., E. H. Holsten, M. E. Ascerno, K. P. Zogas, J. S. Hard, D.P.W. Huber, R. A. Blanchette, and S. J. Seybold. 2008. Protection of spruce from colonization by the bark beetle, *Ips perturbatus*, in Alaska. *For. Ecol. Manage.* 256: 1825–1839.
- Haugen, D. A., R. A. Bedding, M. G. Underdown, and F. G. Neumann. 1990. National strategy for control of *Sirex noctilio* in Australia. Australian Forest Grower, Special Liftout Section No. 13.
- Hoebeke, E. R., D. A. Haugen, and R. A. Haack. 2005. *Sirex noctilio*: discovery of a paleartic siricid woodwasp in New York. *Newsl. Mich. Entomol. Soc.* 50: 24–25.
- Huber, D.P.W., J. H. Borden, N. L. Jeans-Williams, and R. Gries. 2000. Differential bioactivity of conophthorin on four species of North American bark beetles (Coleoptera: Scolytidae). *Can. Entomol.* 132: 649–653.
- Huber, D.P.W., J. H. Borden, and M. Stastny. 2001. Response of the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), to conophthorin and other angiosperm bark volatiles in the avoidance of non-hosts. *Agric. For. Entomol.* 3: 225–232.
- Klepzig, K. D., J. C. Moser, M. J. Lombardero, R. W. Hofstetter, and M. P. Ayres. 2001. Symbiosis and competition: complex interactions among beetles, fungi and mites. *Symbiosis* 30: 83–96.
- Kohnle, U., S. Densborn, P. Kölsch, H. Meyer, and W. Francke. 1992. E-7-Methyl-1,6-dioxaspiro[4–5]decane in the chemical communication of European Scolytidae and Nitidulidae (Coleoptera). *J. Appl. Entomol.* 114: 187–192.
- Lindgren, B. S., and D. R. Miller. 2002a. Effect of verbenone on five species of bark beetles (Coleoptera: Scolytidae) in lodgepole pine forests. *Environ. Entomol.* 31: 759–765.
- Lindgren, B. S., and D. R. Miller. 2002b. Effect of verbenone on attraction of predatory and woodboring beetles (Coleoptera) to kairomones in lodgepole pine forests. *Environ. Entomol.* 31: 766–773.
- McPheron, L. J., S. J. Seybold, A. J. Storer, D. L. Wood, T. Ohtsuka, and I. Kubo. 1997. Effects of enantiomeric blend of verbenone on response of *Ips paraconfusus* to naturally produced aggregation pheromone in the laboratory. *J. Chem. Ecol.* 23: 2825–2839.
- Miller, D. R., J. H. Borden, and B. S. Lindgren. 1995. Verbenone: dose-dependent interruption of pheromone-based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). *Environ. Entomol.* 24: 692–696.
- Neumann, F. G., J. A. Harris, F. Y. Kassaby, and G. Minko. 1982. An improved technique for early detection and control of the *Sirex* wood wasp in radiata pine plantations. *Aust. For.* 45: 117–124.
- Paine, T. D., M. C. Birch, and P. Švihra. 1981. Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* 48: 1–6.
- Payne, T. L., J. E. Coster, J. V. Richerson, L. J. Edson, and E. R. Hart. 1978. Field response of southern pine beetle to behavioral chemicals (*Dendroctonus frontalis* Zimmerman) (Coleoptera: Scolytidae). *Environ. Entomol.* 7: 578–582.
- Rappaport, N. G., D. R. Owen, and J. D. Stein. 2001. Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. *Environ. Entomol.* 30: 837–841.
- Ross, D. A. 1967. Wood- and bark-feeding Coleoptera of felled western larch in British Columbia. *J. Entomol. Soc. Br. Columbia* 64: 23–24.
- Shore, T. L., L. Safranyik, and B. S. Lindgren. 1992. The response of mountain pine beetle (*Dendroctonus ponderosae*) to lodgepole pine trees baited with verbenone and *exo-brevicommin*. *J. Chem. Ecol.* 18: 533–541.
- Vité, J. P., A. Bakke, and J.A.A. Renwick. 1972. Pheromones in *Ips* (Coleoptera: Scolytidae): occurrence and production. *Can. Entomol.* 104: 1967–1975.
- Vité, J. P., R. Hedden, and K. Mori. 1976. *Ips grandicollis*: field response to the optically pure pheromone. *Naturwissenschaften* 63:43–44.
- Wilson, I. M., J. H. Borden, R. Gries, and G. Gries. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *J. Chem. Ecol.* 22: 1861–1875.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Mem. No. 6.
- Zylstra, K. E., K. J. Dodds, J. A. Francese, and V. C. Mastro. 2010. *Sirex noctilio* (Hymenoptera: Siricidae) in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees. *Agric. For. Entomol.* 12: 243–250.

Received 16 June 2010; accepted 27 July 2010.