Effect of Verbenone on Five Species of Bark Beetles (Coleoptera: Scolytidae) in Lodgepole Pine Forests

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ABSTRACT The response by five species of bark beetles to a range of verbenone doses were tested in bioassays using Lindgren funnel traps baited with attractant semiochemicals. The objective was to determine how these bark beetles respond to verbenone, a purported anti-aggregation pheromone of several economically significant bark beetle species. Catches of *Dendroctonus ponderosae* Hopkins, a species attacking live trees, were unaffected relative to a control trap (no verbenone) at release rates of 0.2 mg/24 h or less, but were significantly reduced at rates of 1.8 mg/24 h or more. Catches of *Ips pini* (Say) and *I. latidens* (LeConte), two opportunistic species normally attacking fresh, dead host material, were gradually reduced with increasing verbenone dose. Verbenone did not affect catches of *Hylurgops porosus* (LeConte) and *Hylastes longicollis* Swaine, two species normally associated with bark in contact with the ground, where saprophytic microorganisms quickly invade phloem tissue. The effect by verbenone on catches of the five species was consistent with differences in host-age preference. Catches of species requiring relatively fresh host tissue were reduced by verbenone, whereas catches of species accepting aged tissue were unaffected.

KEY WORDS *Dendroctonus ponderosae, Ips pini, Ips latidens, Hylurgops porosus, Hylastes longicollis, Pinus contorta*

VERBENONE (4,6,6-TRIMETHYLBICYCLO[3.1.1]-HEPT-3-EN-2-ONE) was identified first for *D. ponderosae* Hopkins (Pitman and Vité 1969) and *D. frontalis* Zimmerman (Renwick and Vité 1970), and later for other bark beetle species such as *D. brevicomis* LeConte (Byers et al. 1984), *D. adjunctus* Blandford (Livingston et al. 1983), and *I. typographus* (L.) (Bakke 1981). In the mountain pine beetle, it is produced by microorganisms associated with females and directly through autoxidation (Pitman et al. 1969, Rudinsky 1968, Libbey et al. 1985, Hunt and Borden, 1988, Hunt et al. 1989). Anti-aggregation pheromones, such as 3-methyl-2-cyclohexen-1-one (MCH) and verbenone, interrupt the attraction of bark beetles to their aggregation pheromones and likely serve an epideictic role (Borden 1982). Over the past 20 yr, verbenone has attracted considerable interest as a potential management tool in mitigating the impact of tree-killing bark beetles (see Amman 1994, Amman and Lindgren 1995 for reviews). In operational experiments, verbenone showed considerable promise in reducing attack by the mountain pine beetle in high value lodgepole pine stands (Amman et al. 1989, Lindgren et al. 1989). However, results in subsequent experiments have been inconsistent (Amman 1994, Amman and Lindgren 1995).

Verbenone also affects other species, either in an interspecific context with those species that produce it or in relation to natural degradation of host material. For example, verbenone inhibits feeding by adults of the weevils *Hylobius pales* (Herbst) (Salom et al. 1994), and *H. abietis* (L.) (Lindgren et al. 1996). Both of these species feed on live plants, even though they oviposit on dead host material. Thus, verbenone appears to have a general inhibitory effect, at least on phloeophagous insects that use relatively fresh phloem.

Miller et al. (1995) showed that the pheromone-based attraction of the bark beetles *Dendroctonus ponderosae, Ips latidens* (LeConte) and *Ips pini* (Say) was interrupted by verbenone in a dose-dependent fashion. All of these species require relatively fresh phloem for successful brood production. *Dendroctonus ponderosae* uses living trees as a breeding resource, while both *Ips pini* and *I. latidens* are capable of killing weakened trees, but normally prefer recently dead trees (Furniss and Carolin 1980). The objective of this study was to compare the verbenone response of these three species to the responses of two species, *Hylurgops porosus* (LeConte) and *Hylastes longicollis* Swaine, that typically feed on aged phloem tissue, below or at ground level (Wood 1982). We hypoth-

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Table 1. Description of semiochemical-releasing devices

Device	Chemical[a]	Description	Release rate (mg/24 h)[b]
1	Verbenone (+17/−83)	Closed polyethylene centrifuge tube (250 μl)	0.01
2	Verbenone (+17/−83)	Closed polyethylene centrifuge tube (400 μl)	0.2
3	Verbenone (+17/−83)	Polyethylene/nylon bubble cap	0.6
4	Verbenone (+17/−83)	Polyethylene bubble cap	3.1
5	*exo*-Brevicomin (+50/−50)	Flex lure	0.05
6	Ipsenol (+50/−50)	Polyvinyl bubble cap	0.2
7	Ipsdienol (+50/−50)	Polyvinyl bubble cap	0.2
8	Frontalin	Closed polyethylene centrifuge tube (250μl)	0.6
9	Verbenols (+17/−83)[c]	Polyethylene bubble cap	1.8
10	*cis*-Verbenol (+17/−83)	Polyethylene bubble cap	2.1
11	Myrcene	Closed polyethylene screw-cap bottle (15 ml)	280
12	3-Carene + β-pinene	Closed polyethylene screw-cap bottle (15 ml)	200

[a] All chemical purities >98%.
[b] At 22–24 °C.
[c] 13:87 mixture of *cis*- and *trans*-verbenol.

esized that these two species would be less sensitive to the presence of verbenone than *D. ponderosae*, *I. pini* and *I. latidens*.

Materials and Methods

Semiochemical-Releasing Devices. All release devices were obtained from Phero Tech (Delta, BC) (Table 1). Release rates for devices 5–7 were determined by collection of volatiles on Porapak-Q and analysis by capillary gas chromatography. Release rates for all remaining devices were determined by weight loss. Devices 6 and 7 consisted of ipsenol and ipsdienol, formulated in 1,3-butanediol at a concentration of 80 mg/ml.

Experiments. Six separate experiments were conducted to evaluate dose effects of verbenone on the response of five bark beetle species to various attractants (Table 2). In each experiment, eight blocks (replicates) of six 12-unit Lindgren multiple funnel traps (Lindgren 1983, Phero Tech) were set at least 100 m apart in stands of mature lodgepole pine near Princeton, BC. Traps were spaced 10–15 m apart in grids of 2 × 3 within each block. Each trap was at least 2 m from any tree and suspended by rope such that the bottom of each trap was 0.2–0.5 m above ground level.

Table 2. Parameters for verbenone dose experiments near Princeton, BC, in 1990.

Experiment	Species collected	Dates	Attractants
1	*H. porosus* *H. longicollis* *I. pini*	7–21 June	Ethanol Frontalin Ipsdienol 3-Carene + β-pinene
2	*H. porosus* *H. longicollis*	21–30 June	Ethanol Frontalin Verbenols[a] *exo*-Brevicomin 3-Carene + β-pinene
3	*H. longicollis* *I. latidens*	30 June–3 Aug	Frontalin *exo*-Brevicomin Ipsenol *cis*-Verbenol
4	*I. latidens*	1–30 July	Ipsenol
5	*I. pini*	29 Aug–13 Sept	Ipsdienol 3-Carene + β-pinene
6	*D. ponderosae*	2–16 Aug	Verbenols[a] *exo*-Brevicomin Myrcene

All chemical purities >98%.
[a] 13:87 mix of *cis*- and *trans*-verbenol.

In each experiment, treatments were assigned randomly to traps within each block as follows: attractants alone or with devices resulting in one of five verbenone release rates: 0.01, 0.2, 1.8, 3.1, and 12.3 mg/24 h (at 22–24°C). The two lowest rates were obtained with devices 1 and 2 (see Table 1 for description of devices). The second highest rate was obtained with device 4. The third lowest rate was obtained with three device 3, whereas the highest rate was obtained with four device 4. The control trap in each experiment was a trap baited only with attractants. Whenever possible, known pheromone and kairomone blends were used as attractants. However, since attractants for several of the species tested were unknown, we used semiochemical mixes that had yielded significant catches of the target species in previous research (D.R.M., unpublished data). Voucher specimens have been deposited at the Entomology Collection at Simon Fraser University, Burnaby, BC, Canada.

Statistical Analyses. Data were analyzed by regression using SYSTAT 9.0 statistical software (SPSS 1999). For *D. ponderosae*, the data were analyzed by analysis of variance (ANOVA), because this species exhibited a clear threshold response to verbenone. Means in this experiment were separated by Tukey's procedure. Log transformations were conducted on data, as required from examinations of residuals, to correct for heteroscedasticity and nonlinearity.

Results

Verbenone significantly interrupted the attraction of *D. ponderosae* to attractant-baited multiple-funnel traps ($F = 12.07$; df = 5, 41; $P < 0.001$). However, responses of *D. ponderosae* did not exhibit a log-log dose-dependent relationship as in Miller et al. (1995)

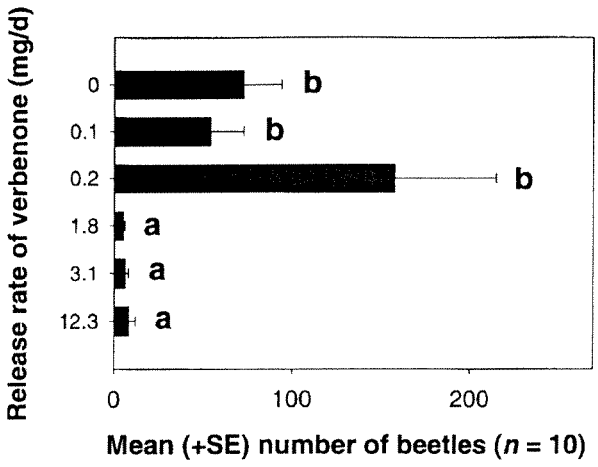

Fig. 1. Effect of verbenone, released at five rates, on the attraction of *D. ponderosae* to multiple-funnel traps baited with myrcene, *exo*-brevicomin, and *cis*- and *trans*-verbenol (experiment 6). See Table 1 for experimental details. Means followed by different letters are significantly different at $P = 0.05$ (Tukey's multiple comparison test).

(Fig. 1). Catches of beetles in traps releasing verbenone at the two lowest rates were not significantly different from those in control traps but significantly different from those in traps releasing verbenone at the three highest rates. There was no significant difference in trap catches among traps baited with verbenone released at the three highest rates. The data suggest a threshold-type of response, occurring at rates between 0.2 and 1.8 mg/24 h (at 22–24°C).

As in Miller et al. (1995), verbenone significantly reduced catches of *Ips pini* and *I. latidens* in a dose-dependent fashion (Fig. 2). The relationship between catches of beetles and dose of verbenone was log-log for *I. latidens* as in Miller et al. (1995) but log-linear for *I. pini* unlike Miller et al. (1995). Only ipsdienol was used as an attractant for *I. pini* in Miller et al. (1995), whereas our experiments used ipsdienol in combination with host compounds.

Verbenone had no significant effect on catches of *Hylastes longicollis* (experiment 1: $F = 0.07$; df = 5, 42; $P = 0.996$, experiment 2: $F = 0.33$; df = 5,42; $P = 0.891$, and experiment 3: $F = 1.47$; df = 5, 42; $P = 0.221$) or *Hylurgops porosus* (experiment 1: $F = 0.56$; df = 5, 42; $P = 0.729$, experiment 2: $F = 0.27$; df = 5, 42; $P = 0.929$). Nor were there any significant regressions between catches of beetles and dose of verbenone (Fig. 3). Catches of *H. longicollis* and *H. porosus* were unaffected by verbenone regardless of the attractants used, or total number of responding beetles.

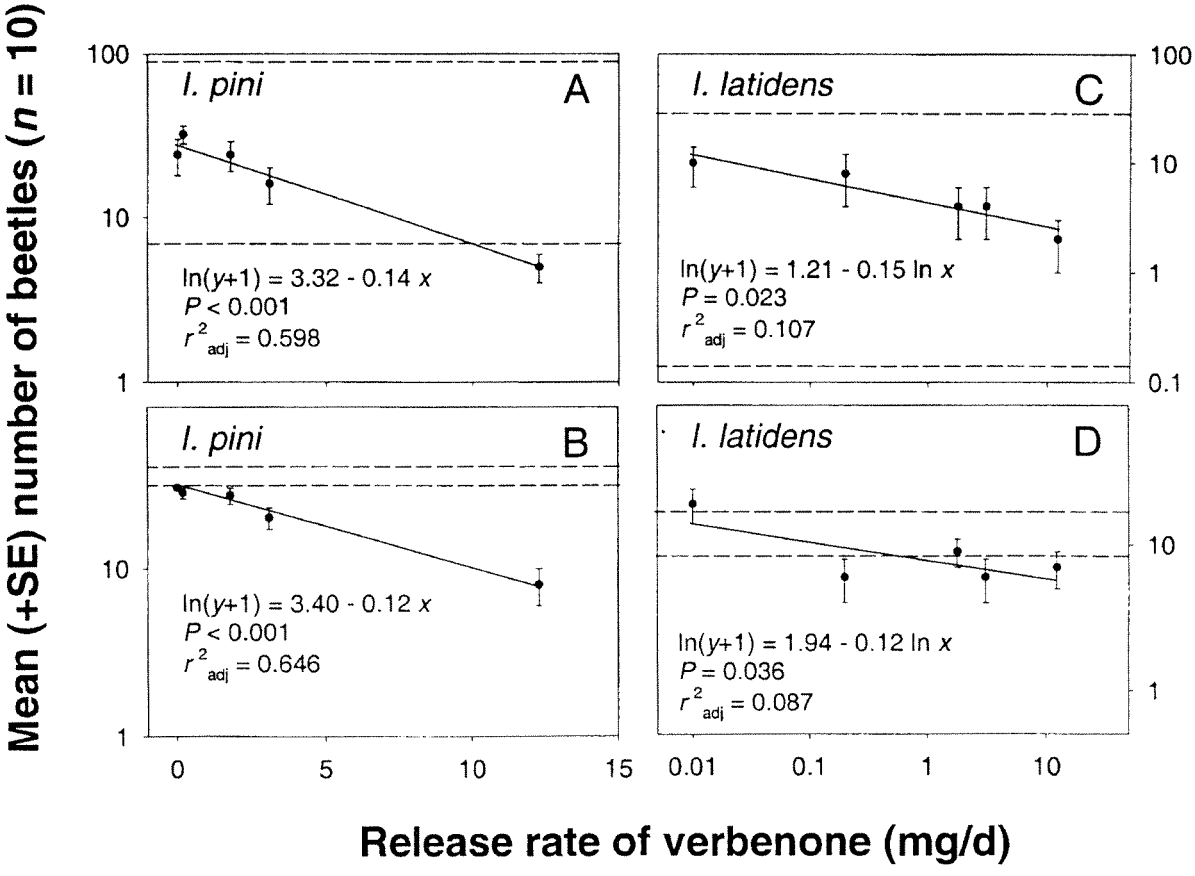

Fig. 2. Effect of verbenone, released at five rates, on the attraction of *I. pini* in experiments 1 (A) and 5 (B), and *I. latidens* in experiments 3 (D) and 4 (C). See Table 1 for experimental details. Slopes of regression lines are significantly different from zero (t-test, $P < 0.05$). Dashed horizontal lines represent confidence limits (95%) for catches in control traps.

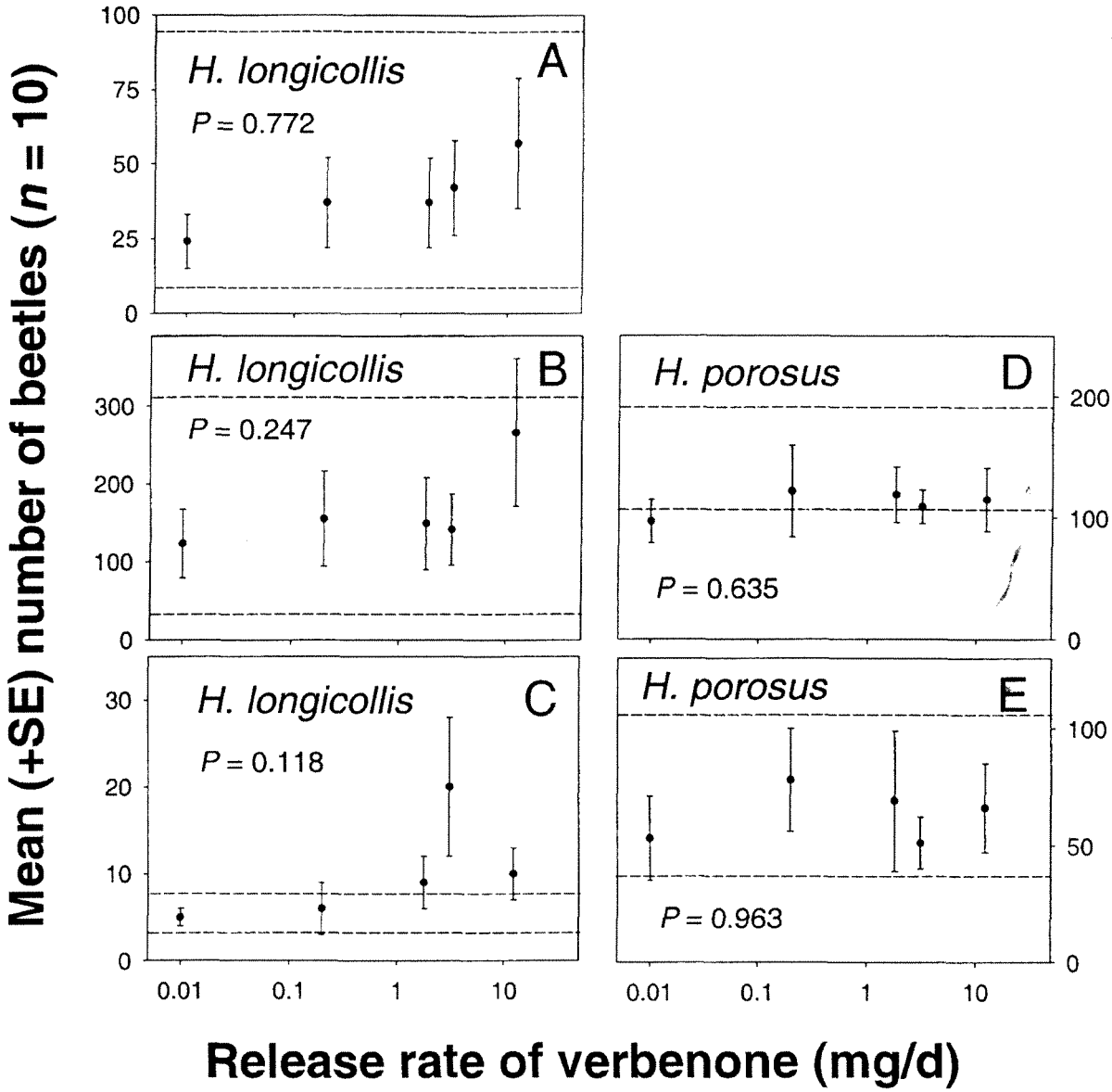

Fig. 3. Effect of verbenone, released at five rates, on the attraction of *Hylastes longicollis* in experiments 1 (A), 2 (B), and 3 (C) and *Hylurgops porosus* in experiments 1 (D) and 2 (E). See Table 1 for experimental details. Slopes of regression lines are significantly different from zero (*t*-test, $P < 0.05$). Dashed horizontal lines represent confidence limits (95%) for catches in control traps.

Discussion

Verbenone is a simple oxidation product of verbenol, which in turn is an oxidation product of α-pinene (Birgersson and Leufvén 1988), one of the most ubiquitous of all monoterpenes in the Pineaceae. It is likely that most phloeo- and xylophagous insects attacking this group of conifers would be exposed to relatively high levels of α-pinene or the oxidation products, verbenol or verbenone. α-Pinene is quite toxic to a number of coniferophagous insects (Cook and Hain 1988, Werner 1995, Lindgren et al. 1996), whereas verbenol and verbenone appear to be less toxic, possibly in part due to lower vapor pressure (Werner 1995, Lindgren et al. 1996).

Insects inhabiting environments high in toxic compounds could be expected to have either a high tolerance for the compound or an effective detoxification system. Many of these insects use α-pinene as a kairomone (Montgomery and Wargo 1983). The mountain pine beetle uses various host compounds, including α-pinene, as kairomones (Borden 1982). Both *cis*- and *trans*-verbenol are used as pheromones by *D. ponderosae* (Pitman and Vité 1969, Conn et al. 1983, Miller and Lafontaine 1991).

Because verbenol is relatively nontoxic compared with α-pinene, its conversion to verbenone does not appear to have a direct adaptive benefit to a phloeophagous insect in terms of increasing host tissue

suitability. *Hylobius abietis* fed equally on verbenone-contaminated pine pieces and on noncontaminated controls if they were previously starved (Lindgren et al. 1996). Mountain pine beetles attacked verbenone-treated trees immediately under the release device (Lindgren et al. 1989, Lindgren and Borden 1993), indicating that beetles may ignore high local verbenone concentrations when phagosensory cues indicate that host tissues are fresh.

The term "pheromone" was defined by Nordlund (1981) as "a compound emitted by a member of one species, that when perceived by another member of the same species alters the behavior of the receiver to the benefit of both emitter and receiver." Given the ubiquitous presence of verbenone in nature, it would seem unlikely that it is simply an anti-aggregation pheromone. If verbenone levels are generally associated with microbial degradation of host tissue, it should be functionally labeled as a kairomone, or perhaps even an "apneumone," i.e., kairomones emitted from dead tissue (Nordlund 1981).

A characteristic of most species of scolytids that use fresh host tissue is their association with mycangial fungi and other microorganisms (Paine et al. 1997). The role of these microorganisms, which are primarily fungi and yeasts, range from an interaction with the beetle in overcoming tree defenses to serving as a food source for the insect. Leufvén et al. (1984) showed that yeasts associated with *Ips typographus* can convert verbenols to verbenone. Using axenically reared insects, Hunt and Borden (1989) demonstrated that the mountain pine beetle is unable to oxidize verbenols to verbenone in the absence of readily culturable microorganisms. After the successful colonization of the phloem by a bark beetle, microorganisms would invade the tissue at least locally, and this may lead to the production of significant quantities of verbenone. Verbenone would then be a general kairomone, signifying the microbial deterioration of plant tissues, which would logically be avoided by early succession scolytids. The phloem tissues in lodgepole pine stumps, as well as phloem tissues under bark in contact with the ground, deteriorate rapidly relative to parts of the tree not in contact with the ground. Such areas are usually attacked primarily by late succession species, e.g., *Hylastes* spp. and *Hylurgops* spp., but avoided or attacked to a lesser extent by the early succession species, e.g., *Ips* spp. Verbenone may play a role both in intra- and inter-specific density regulation, but also in niche partitioning. At least in some cases, the "anti-aggregative" effect of verbenone may be a function of host tissue quality, as opposed to avoidance of intra- or interspecific competition.

Lindgren (1994) and Lindgren et al. (1996) proposed the alternate hypothesis that verbenone is a host tissue quality indicator, i.e., verbenone quantity is a function of microbial degradation of tissue. Theoretical support for this hypothesis includes evidence that verbenone is produced naturally from verbenols by microorganisms (Leufvén et al. 1984) and by autoxidation of verbenols (Hunt et al. 1989), and not necessarily by the insects themselves (Hunt and Borden 1989). If this hypothesis is valid, one would expect verbenone to have an inhibitory effect primarily on species which require fresh host tissue. Furthermore, such species should respond to verbenone at relatively low doses, whereas species that use aged tissue should not respond to verbenone, respond only to high doses, or even be attracted depending on where they occur in the succession of insect colonization. Based on this hypothesis, one would expect the following ordering in verbenone dose sensitivity by the five species we studied: *D. ponderosae* > *I. pini* ≥ *I. latidens* > *H. porosus* ≥ *H. longicollis*. Furthermore, species that are poor interspecific competitors would be expected to respond strongly to any indicator that competitors have occupied the breeding resource, hence they would be expected to be completely repelled at some threshold dose.

Our data show an apparent agreement with the hypothesis proposed by Lindgren (1994) and Lindgren et al. (1996). *Dendroctonus ponderosae*, a poor interspecific competitor (Safranyik et al. 1999), shows a threshold response to verbenone at some release rate above 0.2 mg/24 h (Fig. 1), resulting in an almost complete shutdown of attractiveness of the aggregation pheromone. This is consistent with the results from Borden and Lindgren (1988), who found that a release rate of 1 mg/24 h reduced catches to levels not significantly different from unbaited control traps. The two *Ips* species, which are somewhat better competitors, but still require relatively fresh phloem, respond proportionately to verbenone dose. Finally, *H. porosus* and *H. longicollis*, two species often found in high numbers on stumps or logs in contact with the ground, did not respond significantly to verbenone dose. Thus, the magnitude of response by these species appears to be related to their preference for fresh host tissue and perhaps to their ability to tolerate interspecific competition. However, additional research is required to test the hypothesis more explicitly.

Flechtmann et al. (1999) did chemical analyses of volatiles in screened loblolly pine billets at different ages, and found that verbenone, along with several terpene alcohols, increased with age while terpenes decreased. The changes also coincided with the succession of insect species arriving at traps baited with billets, but because the billets were screened, the verbenone was not insect-produced. Thus, their study indicated that verbenone may play a role in normal succession processes in aging wood, even in the absence of insect attack. Similar studies are needed with lodgepole pine, as are behavioral studies on the response to verbenone by the insect species we studied to further test the alternative hypotheses of verbenone function.

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