Effect of Verbenone on Attraction of Predatory and Woodboring Beetles (Coleoptera) to Kairomones in Lodgepole Pine Forests

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ABSTRACT The response of bark beetle predators and woodboring beetles to the bark beetle anti-aggregation pheromone, verbenone, was tested in the field with multiple-funnel traps baited with attractant kairomones. Catches of the predators *Thanasimus undatulus* (Say), *Enoclerus sphegeus* (F.), *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae), and *Lasconotus complex* LeConte (Coleoptera: Colydiidae) declined significantly with increasing release rates of verbenone. *Lasconotus subcostulatus* Kraus, and *Corticeus praetermissus* (Fall) (Coleoptera: Tenebrionidae) (in two of three experiments), showed no significant response to verbenone. In a third experiment, catches of *C. praetermissus* increased with verbenone dose. Likewise, catches of the striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae), increased with verbenone dose in one experiment, but there was no effect in two other experiments. Verbenone had no effect on the response of *Spondylis upiformis* Mannerheim (Coleoptera: Cerambycidae). We hypothesize that predators specializing on early successional bark beetles are repelled by verbenone since this compound indicates a late stage attack. Generalist predators and woodborers either do not respond to verbenone at all, or they may be attracted by it.

KEY WORDS Kairomone, Scolytidae, *Trypodendron lineatum*, Cleridae, *Thanasimus undatulus*, *Enoclerus sphegeus*

THE CHEMICAL ATTRIBUTES of dead wood change in a rather characteristic manner with age. Flechtmann et al. (1999) showed that quantities of monoterpene volatiles emitted from screened billets of loblolly pine, *Pinus taeda* L., decreased rapidly within the first week of aging. Ethanol increased over the first 2 wk and then decreased, and various terpene alcohols, as well as the purported bark beetle anti-aggregation pheromone verbenone (4,6,6-trimethylbicyclo[3.1.1]-hept-3-en-2-one), increased slowly before declining. For example, verbenone emissions increased slowly until week 6, after which they declined.

Each stage of an aging ephemeral resource like dead wood is attractive to a relatively distinct community of insects that occupy the wood in succession (Price 1997). Early successional colonizers of aging wood, and other relatively ephemeral and patchy resources, tend to be specialists, whereas generalists and predatory insects dominate later stages (Hanski 1987). Thus, bark beetles and woodborers requiring relatively fresh phloem tissue are early succession species, while other woodborers arrive later. For example, Flechtmann et al. (1999) found that different species-complexes of scolytid beetles were attracted at specific stages of pine billet aging, i.e., bark beetles generally were attracted in the first 2–3 wk, and ambrosia beetles were attracted later. Similarly, predaceous beetles that specialize on adult bark beetles tend to arrive early attracted by the kairomones produced by their prey, whereas generalist or opportunist predators become abundant later. For example, checkered beetles (Cleridae) are attracted by the aggregation pheromones of their bark beetle prey (Dahlsten 1982), and are frequently seen on trees or logs during the bark beetle colonization phase (B.S.L., unpublished data). Erbilgin and Raffa (2001) showed that predators also respond to host volatiles, indicating that these insects use cues from the host tree, as well as pheromones emitted by the prey. Many other insects, such as small predatory beetles in the genera *Lasconotus* (Coleoptera: Colydiidae) and *Corticeus* (Coleoptera: Tenebrionidae), are associated with bark beetle galleries (Furniss and Carolin 1980, Parker and Davis 1971, Hackwell 1973, Dallara et al. 2000). At least some of these are known to feed on bark beetle eggs and larvae, which become available as bark beetles establish their brood galleries.

Verbenone has been identified from several species of tree-killing bark beetles: *Dendroctonus ponderosae* Hopkins (Pitmann et al. 1969), *D. frontalis* Zimmer-

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Table 1. Description of semiochemical-releasing devices used in verbenone dose experiments for bark beetle associates near Princeton, BC, 1990

Device	Chemical[a] (enantiomer ratio)	Description	Release rate (mg/d)[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 (250 μl)	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	Closed polyethylene screw-cap bottle (15 ml)	260
13	3-Carene + α-pinene	Closed polyethylene screw-cap bottle (15 ml)	210
14	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.

man (Renwick and Vité 1970), *D. brevicomis* LeConte (Byers et al. 1984), *D. adjunctus* Blandford (Hughes et al. 1976), and *I. typographus* (L.) (Bakke 1981). Mass attacks by these bark beetles are terminated in part by the production of verbenone by resident beetles (Borden 1982). Verbenone therefore has attracted considerable interest as a potential management tool for tree-killing bark beetles for at least 20 yr (see Amman 1994, Amman and Lindgren 1995 for review). In operational scale experiments, verbenone has shown considerable promise for reducing attack by *D. ponderosae* in high value stands (Amman et al. 1989, Lindgren et al. 1989, Lindgren and Borden 1993). Although much of the research on verbenone has been directed at demonstrating its anti-aggregation effect on aggressive bark beetles, verbenone also deters feeding by adults of the weevils *Hylobius pales* (Herbst) (Salom et al. 1994) in the United States, and *H. abietis* (L.) (Lindgren et al. 1996) in Sweden. Adults of these weevil species do their maturation and sustenance feeding on the fresh inner bark of conifers, although they oviposit on dead conifer roots. The species-specificity of verbenone has been questioned by Lindgren (1994), and Lindgren et al. (1996), who hypothesized that the compound may be linked to host quality, e.g., the level of microbial activity and aging of phloem tissue. In the mountain pine beetle, *D. ponderosae*, verbenone is produced from verbenols primarily by microorganisms (Hunt and Borden 1989), and to a lesser extent by autoxidation (Hunt et al. 1989).

Verbenone interrupts the attraction of two species sympatric with *D. ponderosae* associated with fresh phloem tissue in a dose-dependent fashion (Miller et al. 1995, Lindgren and Miller 2002), but has no effect on the attraction of two sympatric species, *Hylurgops porosus* (LeConte) and *Hylastes longicollis* Swaine, associated with older decayed phloem tissue (Lindgren and Miller 2002). Hayes and Strom (1994) found that catches of the bark beetle predator *Temnochila chlorodia* in traps baited with pheromones for *D. ponderosae* and *D. brevicomis*, respectively, were reduced by verbenone. To our knowledge, there is no other information on the effect of verbenone on bark beetle predators or commensals. We investigated the effects of five release rates of verbenone on catches of several species of predatory beetles and woodborers associated with lodgepole pine, *Pinus contorta* variety *latifolia* Engelmann infested by the mountain pine beetle, *D. ponderosae*, or the pine engraver, *Ips pini* (Say).

Materials and Methods

Semiochemical Release 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 quantitative analysis by capillary gas chromatography. Release rates for all remaining devices were determined by weight loss. Devices 6 and 7 (ipsenol and ipsdienol) were formulated in 1,3-butanediol at a concentration of 80 mg/ml.

Experiments. In 1990, seven experiments were conducted to evaluate dose effects of verbenone on the response of bark-beetle associated species to various attractants (Table 2). In each experiment, eight blocks 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 the ground.

In each experiment, treatments were assigned randomly to traps within each block including attractants alone or with release devices resulting in one of five verbenone release rates: 0.01, 0.2, 1.8, 3.1, and 12.4 mg/d (@ 22–24°C). The two lowest rates were obtained with devices 1 and 2. The second highest rate was achieved with device 4. The third lowest rate was obtained with three times device 3, whereas the high-

Table 2. Summary of verbenone dose experiments for bark beetle associates near Princeton, BC, 1990

Exp	Species collected	Dates	Attractants
1	*T. undatulus* *E. sphegeus*	30 June–3 Aug	Ipsenol Frontalin *exo*-Brevicomin *cis*-Verbenol
2	*E. lecontei* *L. complex* *C. praetermissus*	29 Aug–13 Sep	Ipsdienol 3-Carene + α-pinene
3	*L. complex* *L. subcostulatus* *C. praetermissus*	13–25 Sep	Frontalin Ipsdienol Ipsenol 3-Carene
4	*C. praetermissus*	3–29 Aug	Ipsdienol 3-Carene + β-pinene
5	*T. lineatum*	2–16 Aug	Verbenols *exo*-Brevicomin Myrcene
6	*T. lineatum*	21–30 June	Frontalin Verbenols *exo*-Brevicomin Ethanol 3-Carene + β-pinene
7	*S. upiformis*	7–21 June	Frontalin Ethanol Ipsdienol 3-Carene + β-pinene

est rate was obtained with four times 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, because 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). The kairomone blends used in experiments 1–3 targeted *Thanasimus undatulus* (Say), (Coleoptera: Cleridae), *Corticeus praetermissus* (Fall) (Coleoptera: Tenebrionidae), and *Lasconotus complex* LeConte (Coleoptera: Colydiidae), respectively. Catches in experiments 3–7 were nontarget species from experiments targeting the scolytid beetles *Ips pini* (Say), *D. ponderosae*, *Hylurgops porosus*, and *Hylastes longicollis*, respectively (Lindgren and Miller 2002).

Statistical Analyses. Linear regressions were fitted to data for traps with devices releasing verbenone. Residuals were examined to determine fit of a linear regression model and verify homoscedasticity. In some datasets, data for the lowest release rate of verbenone were not used in the regression model, since examination of the residuals clearly indicated that a linear model was inappropriate. Data for the control traps are represented as a 95% confidence interval in each figure. All data were subjected to two-way analyses of variance analysis of variance (ANOVA), using block and treatment as model factors, followed by Fisher least significant difference (LSD) multiple comparison test when $P < 0.05$, to examine potential effects of treatments other than linear dose responses. Log transformations were conducted on data, as required from examinations of residuals, to correct for heteroscedasticity and nonlinearity. All analyses were done using SYSTAT 9.0 statistical software (SPSS 1999).

Results

Verbenone significantly affected the responses of bark beetle predators. Catches of the checkered beetle, *Thanasimus undatulus*, were inversely proportional to the release rate of verbenone (Fig. 1A). Catches of this species at the two highest rates of verbenone were significantly lower than catches in control traps ($F = 2.41$; df = 5, 34; $P = 0.006$, LSD multiple comparison test, $P = 0.05$). Catches of *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) (Fig. 1B) in experiment 2, and *Enoclerus sphegeus* (F.) (Fig. 1C) in experiment 1, were also inversely proportional to the release rate of verbenone over the range of 0.2–10 mg/d. However, mean catches of *Enoclerus* spp. in control traps were not significantly different from any of those in verbenone-baited traps ($F = 2.00$; df = 5, 17; $P = 0.134$, LSD multiple comparison test, $P = 0.05$, and $F = 3.05$; df = 5, 42; $P = 0.20$, LSD multiple comparison test, $P = 0.05$, respectively).

Catches of *Lasconotus complex* were inversely proportional to the release rate of verbenone over the range of 0.2–10 mg/d in two experiments (Fig. 2 A and B), whereas catches of *L. subcostulatus* Kraus (Coleoptera: Colydiidae) were not related to the release rate of verbenone (Fig. 2C). Catches of *L. complex* in traps baited with the highest release rate of verbenone were significantly lower than those in control traps in experiment 2 ($F = 2.87$; df = 5, 35; $P = 0.028$, LSD multiple comparison test, $P = 0.05$) (Fig. 2B) and experiment 3 ($F = 16.61$; df = 5, 34; $P < 0.001$, LSD multiple comparison test, $P = 0.05$) (Fig. 2A). Catches of *L. subcostulatus* in control traps were not significantly different from those in verbenone-baited traps ($F = 1.32$; df = 5, 35; $P = 0.279$, LSD multiple comparison test, $P = 0.05$) (Fig. 2C).

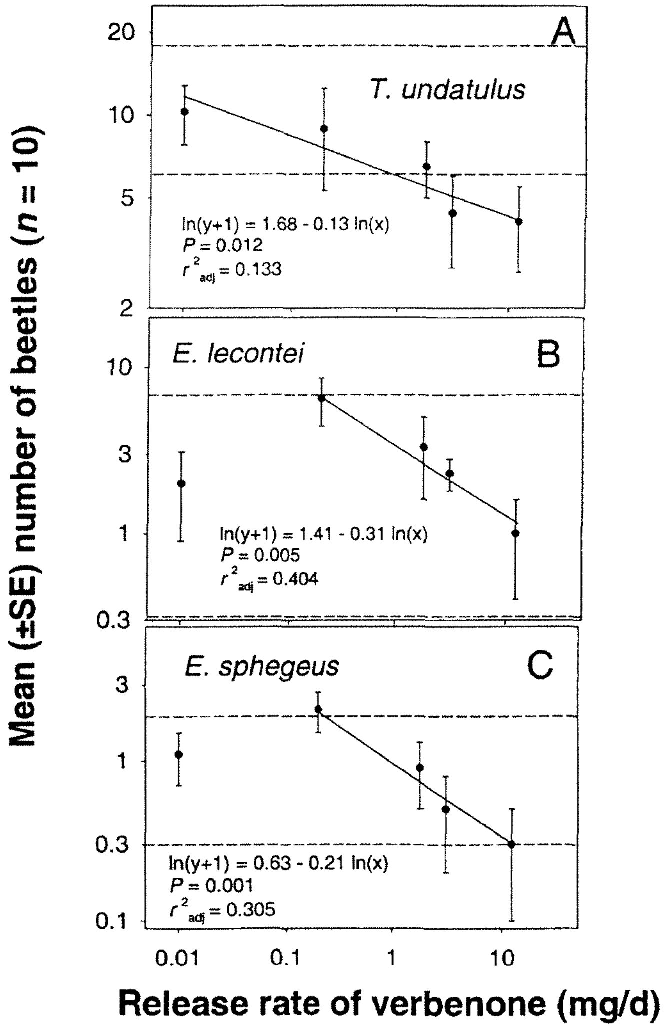

Fig. 1. Effect of verbenone, released at different rates, on the attraction to kairomones of *T. undatulus* in experiment 1 (A), *E. lecontei* in experiment 2 (B), and *E. sphegeus* in experiment 1 (C). See Table 2 for experimental details. Slopes of regression lines are significantly different from zero (*t*-test, $P < 0.05$). Dashed horizontal lines represent confidence limits (95%) for catches in control traps (attractants only).

Catches of *Corticeus praetermissus* were directly proportional to the release rate of verbenone over the range of 0.2–10 mg/d in experiment 4 (Fig. 2D) but not in experiments 2 and 3 (Fig. 2 E and F). Catches of *C. praetermissus* were significantly higher in traps baited with verbenone at the highest rate than those in control traps in experiment 4 ($F = 2.70$; df = 5, 34; $P = 0.037$, LSD multiple comparison test, $P = 0.05$) (Fig. 2D). There was no significant separation of means in experiment 2 ($F = 0.70$; df = 5, 34; $P = 0.629$, LSD multiple comparison test, $P = 0.05$) (Fig. 2E) and experiment 3 ($F = 0.56$; df = 5, 35; $P = 0.729$, LSD multiple comparison test, $P = 0.05$) (Fig. 2F).

Catches of the striped ambrosia beetle, *Trypodendron lineatum* (Oliv.) (Coleoptera: Scolytidae), exhibited a dose-dependent relationship in experiment 5 (Fig. 3B) but not in experiment 6 (Fig. 3A). However, there was no significant separation of mean trap catches in either experiment 5 ($F = 1.60$; df = 5, 40; $P = 0.183$, LSD multiple comparison test, $P = 0.05$) or experiment 6 ($F = 0.26$; df 5, 35; $P = 0.932$, LSD multiple comparison test, $P = 0.05$). In experiment 7, trap catches of the longhorn beetle, *Spondylis upiformis* Mannerheim (Coleoptera: Cerambycidae), did not show a significant response to verbenone dose (Fig. 3C) nor was there any significant separation of means ($F = 0.94$; df 5, 29; $P = 0.468$, LSD multiple comparison test, $P = 0.05$).

Discussion

Attraction to verbenone has been demonstrated for *Rhizophagus grandis* Gyll. (Coleoptera: Rhizophagidae) (Grégoire et al. 1992), a specialist predator of the Eurasian spruce beetle, *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae). Verbenone is one of many chemicals emitted from brood galleries of *D. micans* (Grégoire et al. 1991), and part of this mixture is used as a kairomone by the beetle. The only predatory species that was attracted to verbenone in our study

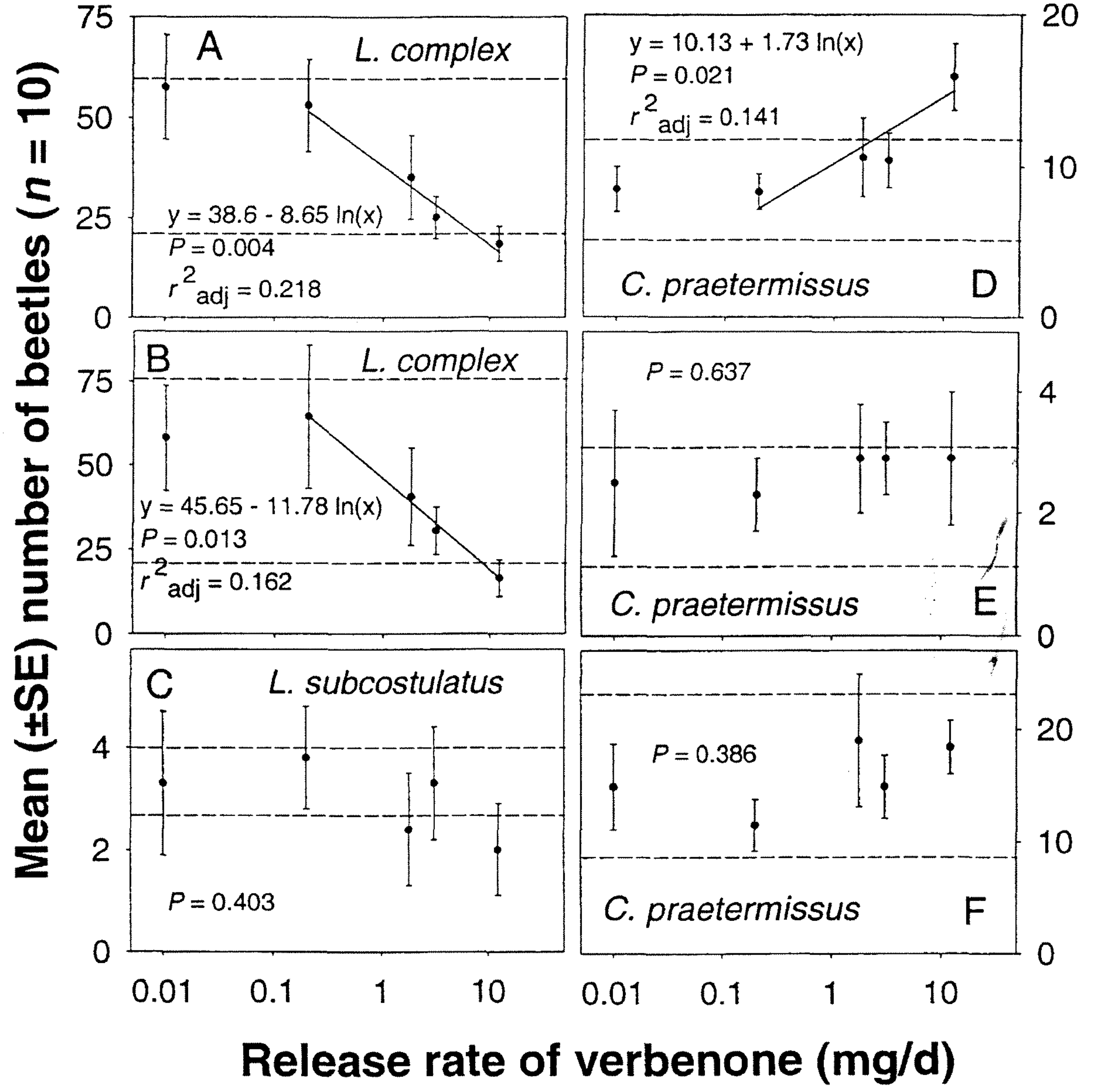

Fig. 2. Effect of verbenone, released at different rates, on the attraction to kairomones of *L. complex* in experiments 3 (A) and 2 (B), *L. subcostulatus* in experiment 3 (C), and *C. praetermissus* in experiments 3 (E), 2 (F), and 4 (D). See Table 2 for experimental details. Slopes of regression lines are significantly different from zero (t-test, $P < 0.05$). Dashed horizontal lines represent confidence limits (95%) for catches in control traps (attractants only).

was *Corticeus praetermissus*, but only in one of three experiments. In experiment 4, the significant regression only explained 14.1% of the variation. Thus, taken together with the nonsignificant regression in the second experiment, the results for this species should be interpreted with caution. However, the positive response to verbenone occurred in an experiment conducted earlier in the year than the other experiments, so the lack of response in the later experiments may be due to a seasonal change in search behavior. Seasonal effects on search behavior were found for the parasitic wasp, *Leptopilina heterotoma* (Thomson) (Hymenoptera: Eucoilidae) (Roitberg et al. 1992). Relatively little is known about the biology of *Corticeus* spp., but members of this genus have been implicated as facultative predators of bark beetle eggs and larvae (Parker and Davis 1971, Triplehorn 1990). A positive response to high doses of verbenone would imply that *C. praetermissus* arrives late in the succession of bark beetles, when the emission of verbenone peaks (Flechtmann et al. 1999). *Corticeus praetermissus* also responds to pheromones of *Ips* spp. (Miller and Borden 2000), which use weakened or recently dead trees, so a positive response to verbenone would be contrary to expectations.

Lasconotus subcostulatus adults enter and oviposit in galleries of *Ips* spp. shortly after the bark beetles attack trees (Hackwell 1973). However, Stephen and Dahl-

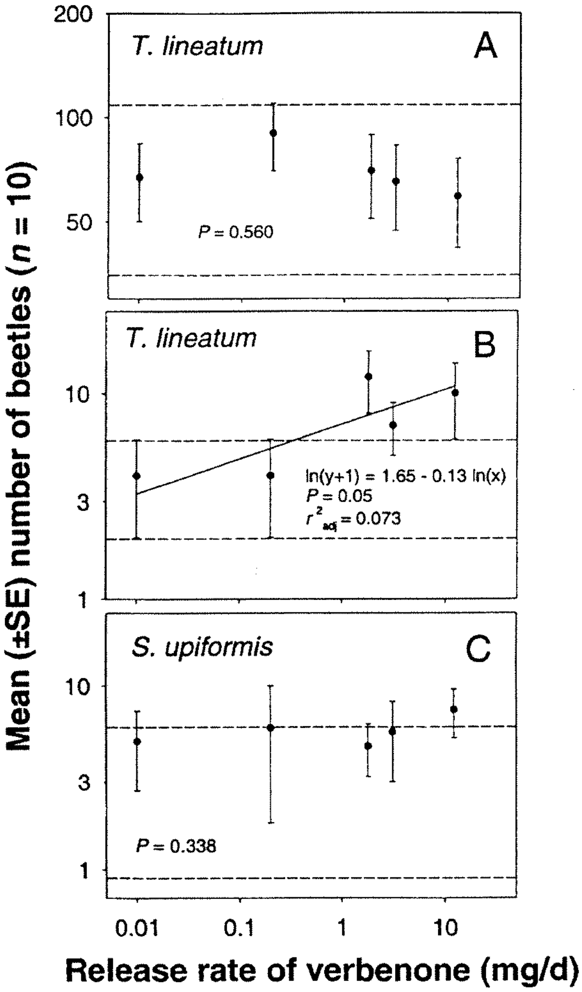

Fig. 3. Effect of verbenone, released at different rates, on the attraction to kairomones of *T. lineatum* in experiments 6 (A) and 5 (B), and *S. upiformis* in experiment 7 (C). See Table 2 for experimental details. Slopes of regression lines are significantly different from zero (*t*-test, $P < 0.05$). Dashed horizontal lines represent confidence limits (95%) for catches in control traps (attractants only).

sten (1976) found that *L. subcostulatus* arrived when western pine beetle larvae were in the latest instars, and concluded that the predator probably fed on larvae of other bark beetle associates. In our study, *L. subcostulatus* showed no significant response to verbenone (Fig. 2C), but we caught very few specimens, making the validity of this result uncertain. However, the result is consistent with a late arriving species. *L. complex*, however, responded negatively to verbenone in a dose-dependent fashion (Fig. 2 A and B) in two experiments. Both adults and larvae of *Lasconotus* spp. enter bark beetle galleries. Hackwell (1973) showed that only the third and fourth instars of the predator attack and feed on bark beetle larvae, while early instars feed on bark beetle larvae only if these are immobilized. Thus, oviposition must take place early enough to allow the *Lasconotus* spp. larvae to mature in time to take advantage of the bark beetle prey. When the prey consist of relatively slowly developing species like the mountain pine beetle, however, the timing of arrival may be less critical. If *L. complex* feeds largely on younger life stages, it would be advantageous to beetles to avoid high verbenone levels, which would be indicative of late stage bark beetle attacks (Flechtmann et al. 1999).

Clerid beetles that prey on adult bark beetles arrive almost simultaneously with attacking bark beetles (Dahlsten 1982). Adult clerids can frequently be seen feeding on adult bark beetles before they enter the bark (B.S.L., unpublished data). Late arriving clerids would be less likely to find adult bark beetles to prey on since the predators do not enter the bark, so there may be a selective advantage in arriving early. The life cycles of many species of clerid beetles are closely synchronized with their bark beetle prey (Furniss and Carolin 1980). For larvae of these species, bark beetle larvae and pupae are important prey. This would appear to favor early arrival and oviposition on attacked trees. A negative response to verbenone (Fig. 1 A and B) is consistent with a species arriving early after bark beetle attack. However, since bark beetles continue to oviposit as they expand their galleries over an extended period (Furniss and Carolin 1980), eggs and early instar prey would be available even for the larvae of later arriving clerids, so late arrival may not be disadvantageous. For example, *E. lecontei* continued to arrive at western pine beetle-infested trees well after the mass arrival of their prey (Stephen and Dahlsten 1976). Nevertheless, a stage-specific response to infested trees by clerids would be consistent with the findings by Sullivan et al. (1997) who found that two parasitoids, *Roptrocerus xylophagorum* and *Spathius pallidus* (Hymenoptera: Pteromalidae and Braconidae, respectively), responded most strongly to specific stages of southern pine beetle brood. For such predatory and parasitic species, verbenone may provide information on the condition of the breeding substrate of their prey.

While the larvae of some woodboring insects use fresh phloem during at least some part of their development, other species enter the sapwood immediately. Adults of the striped ambrosia beetle, *T. lineatum*, bore directly into the sapwood, where they establish their galleries (Borden 1988). Little is known about *Spondylis upiformis*, but if they use phloem, it is for a limited time only (Furniss and Carolin 1980). Since true woodborers have little interaction with phloeophagous species, verbenone would only be significant if it relayed information on the suitability of wood for breeding. Fettköther et al. (2000) found that old house borer, *Hylotrupes bajulus* (L.) (Coleoptera: Cerambycidae), females responded positively to verbenone, which was present in larval frass. In our study, neither *T. lineatum* nor *S. upiformis* responded significantly to an increasing dose of verbenone, except that *T. lineatum* responded positively in one experiment. Catches of *S. upiformis* were too low to make definitive conclusions, while the data for *T. lineatum* are ambiguous. Flechtmann et al. (1999) found that peak catches of the ambrosia beetles *Xyleborinus saxeseni*

(Ratzeburg) and *Xyleborus californicus* Wood in tent traps baited with aging loblolly pine billets occurred at about the same time as emissions of verbenone and some other oxygenated terpene alcohols peaked. The increasing catches with dose in our study occurred when populations of *T. lineatum* were low, so the significant regression could be spurious. However, this species is known to require aging of wood before attacking (Prebble and Graham 1957), so it is possible that it responds to verbenone under certain circumstances. Furthermore, the positive response occurred in an experiment conducted in August, when most of the *T. lineatum* flight is over (Lindgren and Borden 1983), and the majority of flying beetles are reemerging adults (Borden 1988). Thus, this response may be due to a seasonal effect, i.e., host selection may use different or additional cues than earlier in the year. In several other experiments conducted in different habitats, *T. lineatum* did not respond to verbenone (unpublished data).

The responses to verbenone by predators and woodborers in our experiments were measured relative to a kairomone attractant mix (Miller and Borden 2000), rather than specific pheromones. It is possible that the particular mixes of semiochemicals used as attractants in our experiments could have influenced the magnitude or nature of the responses of predators and woodborers. Thus, our results may not be reliable in cases where the kairomones we used did not attract sufficient numbers of insects to the traps. It is possible that different responses observed in different experiments, e.g., for *C. praetermissus* in experiment 3 versus 2 and 4, and for *T. lineatum* in experiment 5 versus 6, could be due to interactions between the kairomone attractant mix and verbenone. In both of these cases, experiments were also conducted at different times of year, which may have resulted in different responses due to seasonal shifts in behavior (Roitberg et al. 1992).

An advantage of our approach is that the attractant is held constant throughout the experiment, thus allowing us to conclude that significant differences in responses are due to verbenone, as opposed to changes in the attractants. However, Flechtmann et al. (1999) found that the arrival-sequence of insects to aging wood (screened loblolly pine billets) occurs in response to changes in both attractant and repellent compounds. For example, their paper demonstrated that verbenone increases over the initial 6 wk of aging of the screened billets. Thus, we would expect early successional species, i.e., those that require a fresh resource, to be repelled by verbenone. Our data show that this appears to be true even for species that are indirectly affected, i.e., predatory beetles. Later successional species, insects that do not use phloem, or species that do not depend on the early successional phloeophagous species as prey, either do not respond to verbenone, or they are attracted by it. The proportional response to verbenone dose by *C. praetermissus* in one experiment may indicate that this species arrives later than other predators, and may use food sources other than bark beetle eggs and larvae associated with the bark beetle galleries, e.g., fungi or mites. While our research demonstrates that verbenone does affect several species of beetles associated with bark beetle-infested lodgepole pine, additional research is required to fully understand the role of this compound.

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References Cited

Amman, G. D. 1994. Potential of verbenone for reducing lodgepole and ponderosa pine mortality caused by mountain pine beetle in high-value situations, pp. 33–37. *In* P. J. Shea (ed.), Proceedings of the symposium on the management of western bark beetles with pheromones: research and development. U.S. For. Serv. Gen. Tech. Rep. PSW-150.

Amman, G. D., and B. S. Lindgren. 1995. Semiochemicals for management of mountain pine beetle, *Dendroctonus ponderosae* Hopkins: current status of research and application, pp. 14–22. *In* S. M. Salom and K. R. Hobson (eds.), Application of Semiochemicals for Management of Bark Beetle Infestations. Proceedings of an Informal Conference. U.S. For. Serv. Gen. Tech. Rep. INT-GTR-318.

Amman, G. D., R. W. Thier, M. D. McGregor, and R. F. Schmitz. 1989. Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetles in Idaho. Can. J. For. Res. 19: 60–64.

Bakke, A. 1981. Inhibition of the response in *Ips typographus* to the aggregation pheromone; field evaluation of verbenone and ipsenol. Z. angew. Entomol. 92: 172–177.

Borden, J. H. 1982. Aggregation pheromones, pp. 74–139. *In* J. B. Mitton and K. B. Sturgeon (eds.), Bark beetles in North American forests. University of Texas Press, Austin, TX.

Borden, J. H. 1988. The striped ambrosia beetle, pp. 579–596. *In* A. A. Berryman (ed.), Dynamics of forest insect populations. Plenum, New York.

Byers, J. A., D. L. Wood, J. Craig, and L. B. Hendry. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: Regulation of inter- and intraspecific competition. J. Chem. Ecol. 10: 861–877.

Dahlsten, D. L. 1982. Relationships between bark beetles and their natural enemies, pp. 140–182. *In* J. B. Mitton and K. B. Sturgeon (eds.), Bark beetles in North American forests. University of Texas Press, Austin, TX.

Dallara, P. L., S. J. Seybold, H. Meyer, T. Tolasch, W. Francke, and D. L. Wood. 2000. Semiochemicals from three species of *Pityophthorus* (Coleoptera: Scolytidae): identification and field response. Can. Entomol. 132: 889–906.

Erbilgin, N., and K. F. Raffa. 2001. Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. Oecologia 127: 444–453.

Fettköther, R., G.V.P. Reddy, U. Noldt, and K. Dettner. 2000. Effect of host and larval frass volatiles on behavioural responses of the old house borer, *Hylotrupes bajulus* (L.) (Coleoptera: Cerambycidae), in a wind tunnel bioassay. Chemoecology 10: 1–10.

Flechtmann, C.A.H., M. J. Dalusky, and C. W. Berisford. 1999. Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. Environ. Entomol. 28: 638–648.

Furniss, R. L., and V. M. Carolin. 1980. Western forest insects. U.S. For. Serv. Misc. Publ. 1339.

Grégoire, J.-C., M. Baisier, A. Drumont, D. L. Dahlsten, H. Meyer, and W. Francke. 1991. Volatile compounds in the larval frass of *Dendroctonus valens* and *Dendroctonus micans* (Coleoptera: Scolytidae) in relation to oviposition by the predator, *Rhizophagus grandis* (Coleoptera: Rhizophagidae). J. Chem. Ecol. 17: 2003–2019.

Grégoire, J.-C., D. Couillien, R. Krebber, W. A. König, H. Meyer, and W. Francke. 1992. Orientation of *Rhizophagus grandis* (Coleoptera:Rhizophagidae) to oxygenated monoterpenes in a species-specific predator-prey relationship. Chemoecology 3: 14–18.

Hackwell, G. A. 1973. Biology of *Lasconotus subcostulatus* (Coleoptera: Colydiidae) with special reference to feeding behavior. Ann. Entomol. Soc. Am. 66: 62–65.

Hanski, I. 1987. Colonization of ephemeral habitats, pp. 155–186. *In* A. J. Gray, M. J. Crawley, and P. J. Edwards (eds.), Colonization, succession and stability. Blackwell, Oxford, England.

Hayes, J. L., and B. L. Strom. 1994. 4-Allylanisole as an inhibitor of bark beetle (Coleoptera: Scolytidae) aggregation. J. Econ. Entomol. 87: 1586–1594.

Hughes, P. R., J.A.A. Renwick, and J. P. Vité. 1976. The identification and field bioassay of chemical attractants in the roundheaded pine beetle. Environ. Entomol. 5: 1165–1168.

Hunt, D.W.A., and J. H. Borden. 1989. Terpene alcohol pheromone production by *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae) in the absence of readily culturable microorganisms. J. Chem. Ecol. 15: 1433–1463.

Hunt, D.W.A., J. H. Borden, B. S. Lindgren, and G. Gries. 1989. The role of autoxidation of α-pinene in the production of pheromones of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Can. J. For. Res. 19: 1275–1282.

Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299–302.

Lindgren, B. S. 1994. Res. needs for anti-aggregation pheromones of bark beetles, pp. 62–67. *In* Research, development and commercialization of semiochemicals in insect pest management in Canada. Canada Pest Management Alternatives Office and Pest Management Alternatives Program.

Lindgren, B. S., and J. H. Borden. 1983. Survey and mass trapping of ambrosia beetles in timber processing areas on Vancouver Island. Can. J. For. Res. 13: 481–493.

Lindgren, B. S., and J. H. Borden. 1993. Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in response to their antiaggregation and aggregation pheromones. Can. J. For. Res. 23: 286–290.

Lindgren, B. S., and D. R. Miller. 2002. Effect of verbenone on five species of bark beetles (Coleoptera: Scolytidae) in lodgepole pine forests. Environ. Entomol.

Lindgren, B. S., J. H. Borden, G. H. Cushon, L. J. Chong, and C. J. Higgins. 1989. Reduction of mountain pine beetle (Coleoptera: Scolytidae) attacks by verbenone in lodgepole pine stands in British Columbia. Can. J. For. Res. 19: 65–68.

Lindgren, B. S., G. Nordlander, and G. Birgersson. 1996. Feeding deterrence and acute toxicity of verbenone to the pine weevil, *Hylobius abietis*. J. Appl. Entomol. 120: 397–403.

Miller, D. R., and J. H. Borden. 2000. Dose-dependent and species-specific responses of pine bark beetles (Coleoptera: Scolytidae) to monoterpenes in association with pheromones. Can. Entomol. 132: 183–195.

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.

Parker, D. L., and D. W. Davis. 1971. Feeding habits of *Corticeus substriatus* (Coleoptera: Tenebrionidae) associated with the mountain pine beetle in lodgepole pine. Ann. Entomol. Soc. Am. 64: 293–294.

Pitman, G. B., J. P. Vité, G. W. Kinzer, and A. F. Fentiman, Jr. 1969. Specificity of population- aggregating pheromones in *Dendroctonus*. J. Insect Physiol. 15: 363–366.

Prebble, M. L., and K. Graham. 1957. Studies of attack by ambrosia beetles in softwood logs on Vancouver Island, British Columbia. For. Sci. 3: 90–112.

Price, P. W. 1997. Insect ecology, 3rd ed. Wiley, New York.

Renwick, J.A.A., and J. P. Vité. 1970. Systems of chemical communication in *Dendroctonus*. Contrib. Boyce Thompson Inst. 24: 283–292.

Roitberg, B., M. Mangel, R. Lalonde, C. Roitberg, J. van Alphen, and L. Vet. 1992. Seasonal dynamic shifts in patch exploitation by parasitic wasps. Behav. Ecol. 3: 156–65.

Salom, S. M., J. A. Carlson, B. N. Ang, D. M. Grossman, and E. R. Day. 1994. Laboratory evaluation of biologically-based compounds as antifeedants for the Pales weevil, *Hylobius pales* (Herbst) (Coleoptera: Curculionidae). J. Entomol. Sci. 29: 407–419.

SPSS. 1999. SYSTAT statistical package, version 9.0. SPSS, Chicago, IL.

Stephen, F. M., and D. L. Dahlsten. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. Can. Entomol. 108: 283–304.

Sullivan, B. T., C. W. Berisford, and M. J. Dalusky. 1997. Field response of southern pine beetle parasitoids to some natural attractants. J. Chem. Ecol. 23: 837–856.

Triplehorn, C. A. 1990. Rev. of the genus *Corticeus* (Coleoptera: Tenebrionidae). Ann. Entomol. Soc. Am. 83: 287–306.

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