

Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests

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Five principal semiochemicals were field tested in multiple funnel traps for behavioral activity against *Dendroctonus ponderosae* infesting lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, in British Columbia. The basic experimental design was to test each compound by adding it in varying concentration or enantiomeric composition to a blend of other semiochemicals. (–)-*trans*-Verbenol was attractive to both sexes. (±)-*exo*-Brevicomin and (±)-frontalin (in one of two experiments) were attractive with other semiochemicals to females at a release rate of 0.05 mg/24 h. At higher release rates (±)-*exo*-brevicomin was inhibitory to males, and frontalin was inhibitory to both sexes. Thus both serve as multifunctional pheromones. For neither *exo*-brevicomin nor frontalin were the separate enantiomers attractive at the low release rate, suggesting that they had an additive effect. However, at the high release rate both enantiomers mimicked the inhibitory effect of the racemates. Verbenone acted as an antiaggregation pheromone for both sexes. Increasing the release rate of myrcene from 18 to 150 mg/24 h to approximate the release rate from a newly attacked tree had the effect of doubling the catch of responding beetles. A conceptual model is proposed for the sequential interaction of these semiochemicals in the mass attack of a tree. Pioneer females release *trans*-verbenol, which acts in combination with myrcene from the host tree to attract mainly males. The responding males release *exo*-brevicomin and later frontalin, which in combination with *trans*-verbenol and myrcene attract mainly females. Meanwhile autoxidation of α -pinene in the host resin results first in the production of predominately *trans*-verbenol, which supplements that produced by the beetles. Later, autoxidation of α -pinene and microbial conversion of *cis*- and *trans*-verbenol result in the production of the antiaggregation pheromone verbenone. This compound, in combination with large amounts of *exo*-brevicomin and frontalin as the tree becomes fully occupied, results in the close-range redirection of responding beetles toward nearby trees.

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Cinq substances allélopathiques parmi les plus importantes ont été testées au champs avec des pièges à contenants multiples dans le but de déterminer leur effet sur le comportement de *Dendroctonus ponderosae* qui attaque le pin de Murray, *Pinus contorta* var. *latifolia* Engelmann, en Colombie britannique. Le dispositif expérimental consistait à tester chaque substance en ajoutant différentes concentrations de ces substances ou différentes proportions de leurs énantiomères à un mélange d'autres substances allélopathiques. Le (–)-*trans*-verbénol attire les deux sexes. L'(±)-*exo*-brévicomine et la (±)-frontaline mêlées à d'autres substances allélopathiques ont attiré les femelles une fois sur deux à un taux de 0,05 mg/24 h. À des taux plus élevés l'(±)-*exo*-brévicomine inhibait l'activité des mâles et la frontaline celle des deux sexes. Ces deux substances agissent donc comme des phéromones à fonctions multiples. Séparément, les énantiomères de l'*exo*-brévicomine et de la frontaline sont inactifs à faible dose suggérant que leur effet est additif. À forte dose cependant, les deux énantiomères ont un effet inhibiteur semblable à celui des composés racémiques. La verbénone agit comme une phéromone qui empêche l'agglomération chez les deux sexes. Deux fois plus d'insectes sont capturés lorsque le taux de myrcène passe de 18 à 150 mg/24 h, ce qui correspond approximativement à la quantité émise par un arbre en début d'attaque. Les auteurs proposent un modèle théorique pour expliquer l'action séquentielle de ces substances lors de l'attaque massive d'un arbre. Les femelles qui initient l'attaque produisent le *trans*-verbénol. Celui-ci, en se combinant à la myrcène provenant de l'arbre attaqué, attire surtout les mâles. Les mâles à leur tour produisent l'*exo*-brévicomine puis la frontaline qui, combinées au *trans*-verbénol et à la myrcène, attirent surtout les femelles. Pendant ce temps, l'auto-oxidation de l' α -pinène dans la résine de l'hôte entraîne, surtout au début, la production de *trans*-verbénol qui s'ajoute à celui produit par les insectes. Plus tard, l'auto-oxidation de l' α -pinène et la conversion du *cis*- et du *trans*-verbénol par les microorganismes amène la production de la verbénone, la phéromone anti-agglomération.

[Traduit par la revue]

Introduction

Three semiochemicals (message-bearing chemicals)² are utilized by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, to promote host selection and mass attack on its principal host, lodgepole pine, *Pinus contorta* var. *latifolia*

Engelmann, in British Columbia. These are the female-produced aggregation pheromone *trans*-verbenol (Pitman et al. 1968; Pitman 1971; Conn et al. 1983; Borden et al. 1983a), the male-produced pheromone *exo*-brevicomin (Rudinsky et al. 1974; Conn et al. 1983; Borden et al. 1983a), and the host tree kairomone myrcene, which synergises the response of both sexes to the other two semiochemicals (Conn et al. 1983; Borden et al. 1983a).

On the basis of trapping experiments, five semiochemicals are reported to have antiaggregative functions for *D. ponder-*

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²See Table 1, footnote a, for chemical names of the five semiochemicals tested experimentally.

sae: *exo*-brevicommin and *endo*-brevicommin released by attacking males (Rudinsky et al. 1974; Ryker and Rudinsky 1982; Libbey et al. 1985), verbenone produced by feeding beetles of both sexes (Ryker and Yandell 1983), frontalin produced by feeding males (Ryker and Libbey 1982; Libbey et al. 1985), and pinocarvone produced by feeding beetles of both sexes (Libbey et al. 1985).

In contrast to the results of Rudinsky et al. (1974) and Ryker and Rudinsky (1982), our experiments with *endo*-brevicommin at low and high release rates have failed to disclose any attractive or antiaggregative effect in lodgepole pine forests in British Columbia (unpublished results). There are numerous other examples of regional or host-related inconsistencies.

exo-Brevicommin was hypothesized to be a concentration-dependent, multifunctional pheromone (Rudinsky et al. 1974). Libbey et al. (1985) were able to confirm the antiaggregative effects at high release rates in trapping experiments in Oregon lodgepole pine stands, but they were unable to demonstrate attractive effects at low release rates. Moreover, *exo*-brevicommin apparently has a host-specific effect when used as a tree bait. On western white pines, *Pinus monticola* Dougl. ex. D. Don, it inhibited attack (McKnight 1979; Pitman et al. 1978), but on lodgepole pines it promoted attack (McKnight 1979; Borden et al. 1983a). Frontalin presents a similar enigma. In trapping experiments in lodgepole pine stands in Oregon, it had an antiaggregative effect at high concentration and no effect at low concentration (Libbey et al. 1985). However, the induced attack on 11 of 16 lodgepole pines baited with frontalin in Idaho (Chatelain and Schenk 1984) suggests that it too could be a multifunctional pheromone for *D. ponderosae*.

In both British Columbia (Conn et al. 1983) and Oregon (Libbey et al. 1985) 3-carene-10-ol produced by feeding females altered the sex ratio of beetles responding to other attractants in favor of males. Several other beetle-produced volatiles had little or no effect in lodgepole pine forests when tested alone or in combination with known attractants. These include acetophenone, myrcenol and 2-*p*-menthen-7-ol tested in British Columbia (Conn et al. 1983), diacetone alcohol tested in British Columbia (the authors, unpublished results), and linalool, piperitone and *trans*-pinocarveol tested in Oregon (Libbey et al. 1985). Two low molecular weight host volatiles, ethanol and acetone, also had no effect (Libbey et al. 1985). However, ipsdienol, a male-produced volatile (Hunt et al. 1986), had a significant antiaggregative effect (Hunt and Borden 1987).

Several of the major semiochemicals in *D. ponderosae* are chiral. Males from both Oregon and British Columbia produce >98% (+)-*exo*-brevicommin and >82% (+)-*endo*-brevicommin (Schurig et al. 1983). Beetles in white pine stands in Idaho and lodgepole pine stands in Oregon responded preferentially to (-)-*trans*-verbenol (McKnight 1979; Libbey et al. 1985). In lodgepole pine stands (-)-verbenone at a high release rate inhibited responses of both sexes to attractive volatiles, but in stands of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., both enantiomers were active (Ryker and Yandell 1983).

Myrcene was 12.5 times more effective than α -pinene as a synergist for male response in lodgepole pine stands in British Columbia (Conn et al. 1983). In lodgepole pine stands in Oregon, it was less than twice as effective as α -pinene (Libbey et al. 1985). Terpinolene was as effective as myrcene in a ponderosa pine stand in Washington (Billings et al. 1976). In white pine stands in Idaho, α -pinene was two times more effective as a synergist than myrcene (Pitman 1971). Comparing beetles in different host tree stands, McKnight (1979) found that myrcene and (+)- α -pinene were effective synergists in

stands of western white pine, whereas (-)- α -pinene was not. In lodgepole pine stands, the beetles did not discriminate between (+)- and (-)- α -pinene (myrcene not tested), but in ponderosa pine stands (+)- α -pinene and myrcene were superior to (-)- α -pinene. Finally, results from research on the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Billings 1985), and the western pine beetle, *D. brevicomis* LeConte (Tilden and Bedard 1985), indicate that attraction of beetles in the field can be increased by releasing monoterpene synergists at higher rates than previously used, suggesting that a similar response may occur in *D. ponderosae*.

The great geographic and host-related variation in activity of various semiochemicals for *D. ponderosae* suggests that detailed host- and site-specific studies should be made. In the interior of British Columbia, baits composed of *trans*-verbenol, *exo*-brevicommin, and myrcene have been proven effective in manipulating mountain pine beetle populations by inducing attack on baited lodgepole pines (Borden et al. 1983b, 1983c, 1986a). These baits are now used routinely on an operational basis (Borden and Lacey 1985). However, the precise roles of most of these semiochemicals in various combinations in inducing and inhibiting orientation by mountain pine beetles have not been investigated intensively.

We report the results of field-trapping experiments in which five of the major semiochemicals were tested in stands of lodgepole pine in the interior of British Columbia for verification of activity, effect of concentration, and role of either or both enantiomers in inducing or inhibiting positive orientation by both sexes of *D. ponderosae*.

Materials and methods

Field-trapping experiments, rather than tree-baiting experiments, were conducted to eliminate the confounding effects of volatiles released by host trees and attacking beetles therein. The basic experimental approach was to test each compound by adding it in varying concentration or composition to an essential or attractive blend of other semiochemicals. Ten experiments were conducted from 1982 to 1985, with specific objectives, experimental design, and semiochemicals tested as outlined in Table 1. The experiments were set up along Osprey Lake Road in active infestations ranging from 24 to 35 km northeast of Princeton, B.C. All experiments utilized multiple-funnel traps (Lindgren 1983). Eight-funnel traps were used in 1982, but most experiments in 1983-1985 used 16-funnel traps. Our unpublished results have shown that doubling the height (numbers of funnels) of the vertical silhouette, but not doubling the width (by attaching side panels), doubled the number of beetles caught.

The experiments employed complete, randomized blocks with traps placed at ≥ 25 -m intervals on lines that were at least 25 m apart. Captured beetles were removed from the traps at the end of each replicate. If the experiment was replicated over time, the placement of baits was rerandomized for subsequent replicates. All counts of captured beetles were transformed by $\log_{10}(x+1)$ and analyzed by ANOVA and the Newman-Keuls test.³

Results and discussion⁴

Role of individual semiochemicals influencing positive orientation

When tested with myrcene and *exo*-brevicommin, both (\pm)- and (-)-*trans*-verbenol induced significant attraction of *D. ponderosae* of both sexes, whereas (+)-*trans*-verbenol did not

³M. Greig and D. Osterlin. Analysis of variance and covariance. University of British Columbia, Vancouver. 1971, revised 1978. (Adapted from Brigham Young University documentation.)

⁴Unless otherwise stated, chiral compounds in the text not preceded by an indication of chirality are racemic.

TABLE 1. Descriptions of 10 randomized-block experiments testing concentrations and enantiomeric composition of various semiochemicals^a that attract or repel the mountain pine beetle

Expt. No.	Objective	Experimental setup	Semiochemical, ^a release devices, and rates			Cross-reference to results
			Compound	Device	Rate ^b	
1	To determine active enantiomer(s) of tV	(±)-tV and both enantiomers tested in combination with M and (±)eB; 8-funnel traps; 10 replicates, 20–26 Aug. 1982	M	Open glass vial (6 mL)	40–70 mg/24 h	Fig. 1
			(±)tV	4 open polyethylene microcentrifuge tubes (400 µL)	0.4 mg/24 h	
			(+) or (-)tV	2 open polyethylene microcentrifuge tube (400 µL)	0.2 mg/24 h	
2	To retest role of eB as multifunctional pheromone	(±)eB tested at 3 release rates in combination with M and tV; 8-funnel traps; 9 replicates, 24–28 July 1982	M	Open glass vial (6 mL)	40–70 mg/24 h	Fig. 2
			tV	2 open glass vials (2 mL)	1.0 mg/24 h	
			eB	Conrel fibre ^c (0.2 mm i.d.)	0.05 mg/24 h	
3	To determine active enantiomers of eB at low release rate	(±)eB and enantiomers tested in combination with M and tV; 16-funnel traps; 6 replicates for all treatments except 3 for (±)eB and 4 for (-)eB, 6–21 Aug. 1985	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Fig. 3
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Conrel fibre (0.2 mm i.d.)	0.05 mg/24 h	
4	To determine active enantiomer(s) of eB at high release rates	(±)eB and enantiomers tested in combination with M and tV; 16-funnel traps; 12 replicates, 6 on 10 Aug. and 6 on 11 Aug. 1984	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Table 2
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	1 or 2 polyethylene bubble caps ^d	5.0 or 10 mg/24 h	
5	To determine active enantiomers of eB at high release rate	(±)eB and enantiomers tested in combination with M and tV; 16-funnel traps; 18 replicates, 6 each on 29, 30, and 31 July 1984	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Table 2
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Polyethylene bubble cap	5.0 mg/24 h	
6	To test activity of F at different stimulus levels	(±)F tested at 3 release rates in combination with M, tV and eB; 8-funnel traps; 9 replicates, 28 July–9 Aug. 1982	M	Open glass vial (6 mL)	40–70 mg/24 h	Fig. 4
			tV	2 open glass vials (2 mL)	1.0 mg/24 h	
			eB	Glass capillary tube (1.0 mm i.d.)	0.5 mg/24 h	
			F	Conrel fibre (0.2 mm i.d.)	0.05 mg/24 h	
			F	Glass capillary tube (1.0 mm i.d.)	0.5 mg/24 h	
				10 glass capillary tubes (1.0 mm i.d.)	5.0 mg/24 h	

TABLE 1. (concluded)

Expt. No.	Objective	Experimental setup	Semiochemical, ^a release devices, and rates			Cross-reference to results
			Compound	Device	Rate ^b	
7	To determine active enantiomers of F at low release rate	(±)F and enantiomers tested in combination with M, tV, and eB; 16-funnel traps; 7 replicates for M, tV, eB and M, tV, eB, (-)F; 8 for M, tV, eB, (±)F; 9 for M, tV, eB, (+)F; 13 for unbaited control; 6-21 Aug. 1985	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Fig. 5
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Conrel fibre (0.2 mm i.d.)	0.05 mg/24 h	
			F	Conrel fibre (0.2 mm i.d.)	0.05 mg/24 h	
8	To determine active enantiomer(s) of F at high release rate	(±)F and enantiomers tested in combination with M, tV, and eB; 16-funnel traps; 18 replicates, 6 each on 3-8, 9 and 12-15 Aug. 1984	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Table 2
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Polyethylene bubble cap	~0.1 mg/24 h	
			F	5 polyethylene bubble caps	5.0 mg/24 h	
9	To test antiaggregative activity of V at 2 release rates	V tested in combination with M, tV, and eB; 16-funnel traps; 12 replicates, 16-18 Aug. 1984	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Fig. 5
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Polyethylene bubble cap	~1.0 mg/24 h	
			V	1 or 5 polyethylene bubble caps	~1.0 or 5.0 mg/24 h	
10	To determine effect of different release rates on synergistic activity of M	M tested in combination with tV and eB; 12-funnel traps; 7 replicates, 6-21 Aug. 1985	M	2 closed polyethylene microcentrifuge tubes (1.9 mL)	18 mg/24 h	Fig. 7
			tV	Plastic vial	150 mg/24 h	
			tV	Open polyethylene microcentrifuge tube (1.9 mL)	1.0 mg/24 h	
			eB	Conrel fibre (0.2 mm i.d.) Glass capillary tube (1.0 mm i.d.)	0.05 mg/24 h 0.5 mg/24 h	

^aAbbreviations, trivial names, chemical names, sources, and purity of semiochemicals are as follows. M, myrcene: 2-methyl-6-methylene-octa-2,7-diene; from Sigma Chemical Co., St. Louis, MO, U.S.A.; >98% pure. tV, *trans*-verbenol: *trans*-4,6,4-trimethylbicyclo[3.1.1]hept-3-en-2-ol., from Albany Int'l Co., Columbus, OH, for expts. 1, 2, 6, 68.9%(+) and 31.1%(-), 93.6% pure; from Phero Tech Inc., Vancouver, B.C., for expts. 3, 7, 10, 25%(+) and 75%(-), >88% pure; synthesized at Simon Fraser University for expts. 4, 5, 8, 9, 50%(+) and 50%(-), 98.2% pure; (+)tV synthesized at Simon Fraser University, 96.5%(+) and 3.5%(-), 99.0% pure. (-)tV synthesized at Simon Fraser University, 2.7%(+) and 96.3%(-), 97.5% pure. eB, *exo*-brevicomine: *exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane; (±)eB from Albany Int'l Co., Columbus, OH, >99.7% pure; (+)eB synthesized at Simon Fraser University, 97.5%(+) and 2.5%(-), >99% pure; (-)eB synthesized at Simon Fraser University 5%(+) and 95%(-), >98% pure. F, frontalinal: 1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane; (±)F from BASF, Ludwigshafen, Federal Republic of Germany, >99% pure; (+)F synthesized at Simon Fraser University, 96.5%(+) and 3.5%(-), >98% pure; (-)F synthesized at Simon Fraser University, 1.5%(+) and 98.5%(-), >98% pure. V, verbenone: 4,6,6-trimethylbicyclo[3.1.1]hept-3-en-one; from Aldrich Chemical Co., Milwaukee, WI; 23.5%(+) and 76.5%(-), 94% pure.

^bDetermined at 20°C in the laboratory.

^cAlbany Int'l Co., Needham, MA.

^dA bubble cap is a device from which a volatile is released through a plastic film covering an impervious, plastic reservoir; A. Meisen, Department of Chemical Engineering, University of British Columbia, Vancouver, B.C.

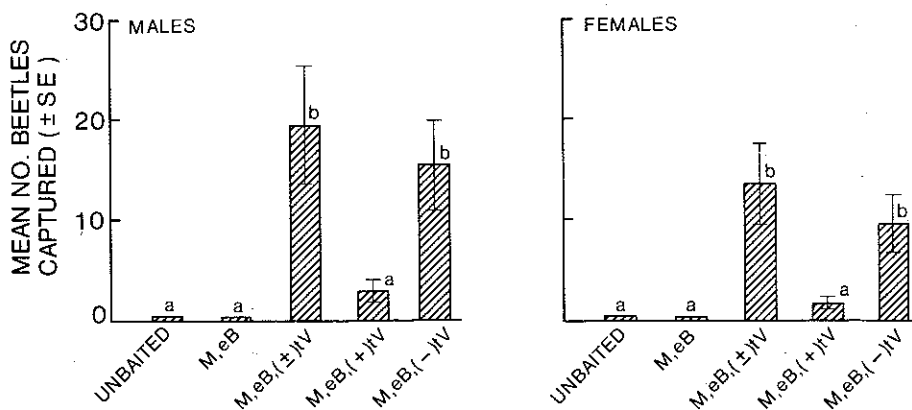


FIG. 1. Response of *D. ponderosae* in expt. 1 to multiple funnel traps baited with (+)-, (-)-, or (±)-*trans*-verbenol (tV) in combination with myrcene (M) and (±)-*exo*-brevicomin (eB). See Table 1 for experimental details. Note that (±)tV is actually 68.9% (+) and 31.1% (-). ANOVA values are $F=16.053$ for males and 19.738 for females, $df=4,35$. Bars with the same letter above are not significantly different, Newman-Keuls test, $P < 0.05$.

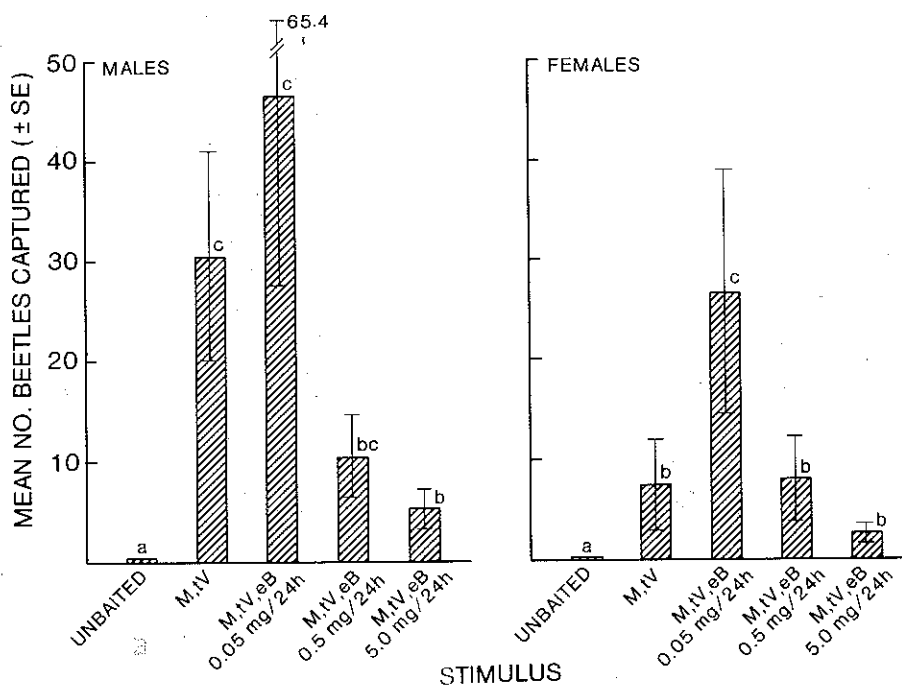


FIG. 2. Response of *D. ponderosae* in expt. 2 to multiple funnel traps baited with (±)-*exo*-brevicomin (eB) at three release rates in combination with myrcene (M) and (±)-*trans*-verbenol (tV). See Table 1 for experimental details. ANOVA values are $F=10.730$ for males and 10.070 for females, $df=4,32$. Bars with the same letter above are not significantly different, Newman-Keuls test, $P < 0.05$.

(Fig. 1). The *trans*-verbenol produced by four individual female *D. ponderosae* from the interior of British Columbia was found by gas chromatographic analysis of a diastereomeric derivative (Slessor et al. 1985) to consist of 65–87% (-)-*trans*-verbenol ($\bar{x} = 78.5\%$).⁵ This finding is consistent with the predominance of (-)- α -pinene in lodgepole pine (exact enantiomeric ratio unspecified) (Mirov 1961). The response is in agreement with that of beetles in white pine in Idaho (McKnight 1979) and lodgepole pine in Oregon (Libbey et al. 1985), which also responded preferentially to (-)-*trans*-verbenol.

exo-Brevicomin released at 0.05 mg/24 h induced a significant increase in the response of females compared with that induced by myrcene plus *trans*-verbenol, but it had no signifi-

cant effect on males (Fig. 2). This result confirms the conclusion of Rudinsky et al. (1974) that at low release rates, *exo*-brevicomin can be an attractant and corroborates evidence that it is female specific (Conn et al. 1983). However, the response of female *D. ponderosae* in British Columbia is different from that of Oregon beetles, which do not respond at all to *exo*-brevicomin at low release rates (Libbey et al. 1985). At the highest release rate of *exo*-brevicomin (5.0 mg/24 h) there was a significant inhibition of the response of males, while at 0.5 mg/24 h the inhibitory effect was only partial (Fig. 2). Thus the hypothesis that *exo*-brevicomin is a multifunctional pheromone (Rudinsky et al. 1974) is upheld for British Columbia populations of *D. ponderosae*.

When (+)-, (-)-, and (±)-*exo*-brevicomin were tested at a low release rate of 0.05 mg/24 h (Fig. 3), the synergistic effect on the response of females to myrcene plus *trans*-verbenol was

⁵Analysis by G. G. S. King, Department of Chemistry, Simon Fraser University, Burnaby, B.C. V5A 1S6.

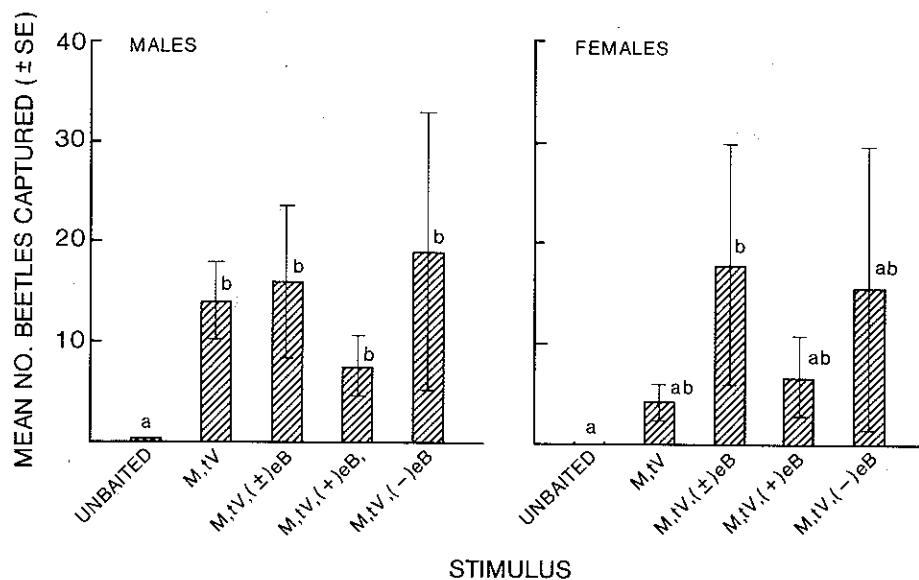


FIG. 3. Response of *D. ponderosae* in expt. 3 to multiple funnel traps baited with (+), (-), or (±)-*exo*-brevicomin (eB) in combination with myrcene (M) and (±)-*trans*-verbenol (tV). See Table 1 for experimental details. ANOVA values are $F=6.629$ for males and 3.125 for females, $df=4,15$. Bars with the same letter above are not significantly different, Newman-Keuls test, $P < 0.05$.

TABLE 2. Response of mountain pine beetles in three experiments to multiple funnel traps baited with myrcene (M) and *trans*-verbenol (tV) in combination with racemic *exo*-brevicomin (eB) or its enantiomers at high release rates (expts. 4 and 5), or M, tV, and eB in combination with racemic frontalin (F) or its enantiomers at a high release rate (expt. 8)

Expt. No.	No. of replicates	Stimulus (release rate of eB or F)	No. of beetles captured per trap ($\bar{x} \pm SE$) ^a	
			Males	Females
4	12	Unbaited trap	1.3±0.5a	3.1±1.4a
		M, tV	4.6±0.9c	4.1±0.9b
		M, tV, (±)eB (10.0 mg/24 h)	1.1±0.4ab	4.3±1.9b
		M, tV, (+)eB (5.0 mg/24 h)	2.0±0.7ab	7.6±2.2b
		M, tV, (-)eB (5.0 mg/24 h)	1.3±0.2b	4.5±1.7b
		5	18	Unbaited trap
M, tV	6.2±1.3c	5.1±1.3b		
M, tV, (±)eB (5.0 mg/24 h)	0.5±0.2ab	3.7±1.3b		
M, tV, (+)eB (5.0 mg/24 h)	0.9±0.3ab	4.4±1.0b		
M, tV, (-)eB (5.0 mg/24 h)	1.7±0.5b	5.7±1.0b		
8	18	Unbaited trap		1.6±0.8a
		M, tV, eB	11.9±4.2b	27.7±12.8b
		M, tV, eB, (±)F (5.0 mg/24 h)	0.9±0.5a	3.4±1.5a
		M, tV, eB, (+)F (5.0 mg/24 h)	1.8±0.5a	5.8±1.2a
		M, tV, eB, (-)F (5.0 mg/24 h)	1.3±0.5a	2.9±1.3a

^a*F* values and degrees of freedom by experiment and sex are as follows: expt. 4, males $F=5.189$, females $F=1.426$, $df=4,49$; expt. 5, males $F=2.882$, females $F=2.765$, $df=4,77$; expt. 8, males $F=10.815$, females $F=5.905$, $df=4,78$. Means within a column for each experiment followed by the same letter are not significantly different, Neuman-Keuls test, $P < 0.05$.

not as clear as in Fig. 2. This lack of clarity was in part due to low numbers of beetles captured and great variability between catches. Nonetheless, the response of females to the ternary bait with (±)-*exo*-brevicomin was the only one that stood alone as significantly different from that to the unbaited control (Fig. 3). Neither enantiomer had a significant effect on females and as in Fig. 2, the racemic compound also had no effect on males (Fig. 3). Possibly as in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Dickens et al. 1985), there is an additive effect of enantio-specific acceptors on the same sensory cells, which

results in only the racemic compound at low release rates eliciting a significant behavioral response.

At high release rates, (±)-, (+)-, and (-)-*exo*-brevicomin inhibited the response of males to myrcene plus *trans*-verbenol (Table 2), indicating that both enantiomers have independent antiaggregative properties. As in Fig. 2, (±)-*exo*-brevicomin released at 5.0 or 10.0 mg/24 h had no significant inhibitory effect on female response; moreover, neither enantiomer affected the behavior of females (Table 2).

When frontalin was added in experiment 6 to an attractive

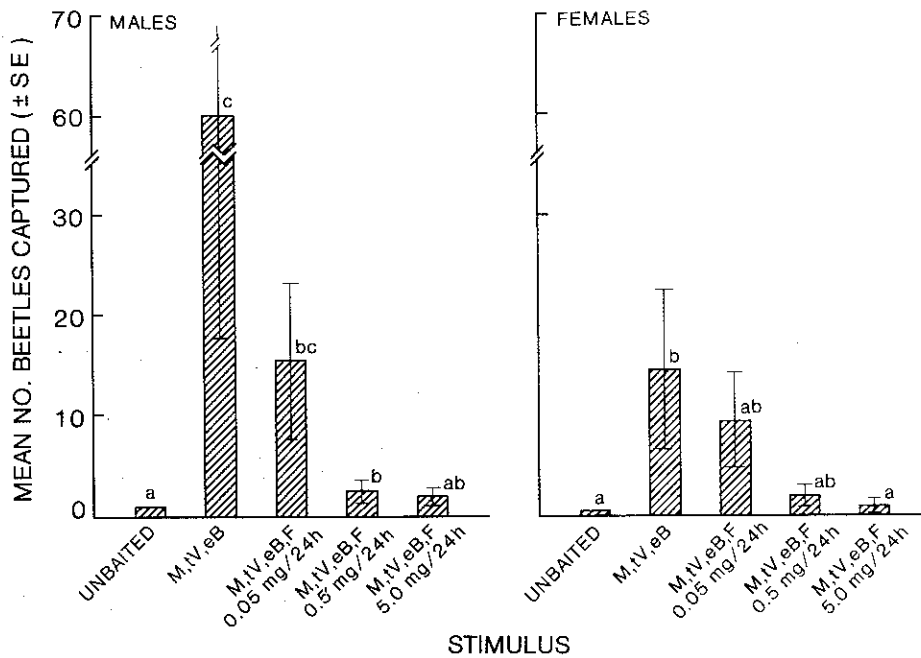


FIG. 4. Response of *D. ponderosae* in expt. 6 to multiple funnel traps baited with (\pm)-frontalin (F) at three release rates in combination with myrcene (M), (\pm)-*trans*-verbenol (tv), and (\pm)-*exo*-brevicomin (eB). See Table 1 for experimental details. ANOVA values are $F=8.645$ for males and 4.383 for females, $df=4,32$. Bars with the same letter above are not significantly different, Newman-Keuls test, $P < 0.05$.

ternary mixture of myrcene, *trans*-verbenol, and *exo*-brevicomin, it strongly inhibited the response of males at release rates of 0.5 and 5.0 mg/24 h and females at 5.0 mg/24 h (Fig. 4). However, in experiment 7, (\pm)-frontalin at 0.05 mg/24 h significantly enhanced the response of females to the ternary bait and appeared to have a similar, but not significant, effect on males (Fig. 5). The expression of this enhancement effect could have been promoted by the low release of *exo*-brevicomin, while in experiment 6 the 10-fold higher release rate of *exo*-brevicomin could have partially inhibited the response. Neither enantiomer duplicated this enhancement, and in fact each caused a slight, but significant, inhibition of female response, again suggesting an additive effect of both enantiomers (Dickens et al. 1985) to achieve a positive effect on orientation. The antiaggregative effect of frontalin at a high release rate of 5.0 mg/24 h (Fig. 4) was duplicated in experiment 8, in which both enantiomers were also highly inhibitory to beetles of both sexes at a release rate of 5.0 mg/24 h (Table 2).

Previously frontalin has been considered primarily an antiaggregation pheromone for *D. ponderosae* (Ryker and Libbey 1982; Libbey et al. 1985). However, Chatelain and Schenk (1984) demonstrated that frontalin at a release rate of 1.0 mg/24 h (high enough to cause inhibition in traps; Fig. 4), induced attack on lodgepole pines by the mountain pine beetle. This effect has been confirmed by J. H. Borden and L. J. Chong (unpublished data). These results, coupled with those from trapping experiments indicating an aggregative effect of frontalin on females at a low release rate (Fig. 5) and an antiaggregative effect on both males and females at higher release rates (Fig. 4, Table 2), demonstrate that frontalin is truly a multifunctional pheromone for *D. ponderosae* in lodgepole pine.

Verbenone was inhibitory to males at two release rates (0.1 and 5.0 mg/24 h) (Fig. 6). A similar trend in female response approached significance (ANOVA, $P < 0.09$). These results confirm Ryker and Yandell's (1983) report that verbenone is an antiaggregation pheromone of the mountain pine beetle. Moreover, they lend strength to the emerging realization that

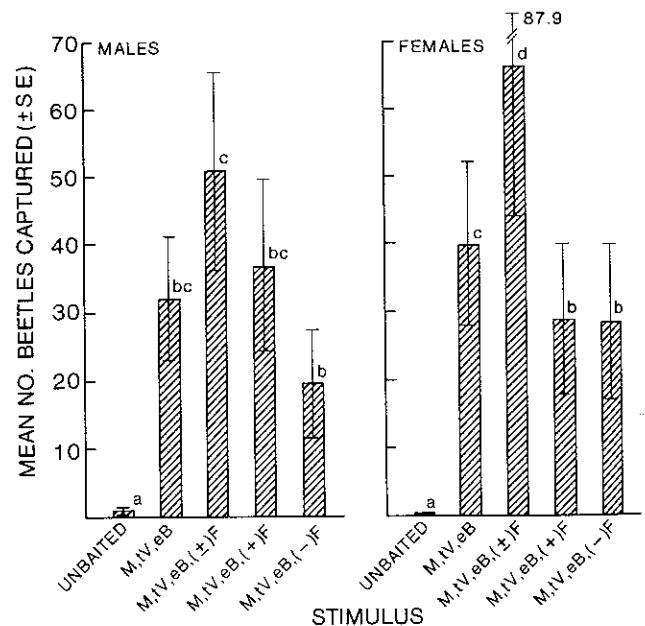


FIG. 5. Response of *D. ponderosae* in expt. 7 to multiple funnel traps baited with (+), (-), or (\pm)-frontalin (F) in combination with myrcene (M), (\pm)-*trans*-verbenol (tv), and (\pm)-*exo*-brevicomin (eB). See Table 1 for experimental details. ANOVA values are $F=26.833$ for males and 247.032 for females, $df=4,30$. Bars with the same letter above are not significantly different, Newman-Keuls test, $P < 0.05$.

verbenone is a broad spectrum inhibitor of olfactory response in bark beetles (Borden 1982), which is produced not only by the beetles themselves but also by autoxidation of α -pinene (Borden et al. 1986b) and by metabolism of *cis*- and *trans*-verbenol by symbiotic microorganisms associated with bark beetles such as *Ips typographus* (Leufven et al. 1984) and *D. ponderosae* (D. W. A. Hunt,⁶ personal communication).

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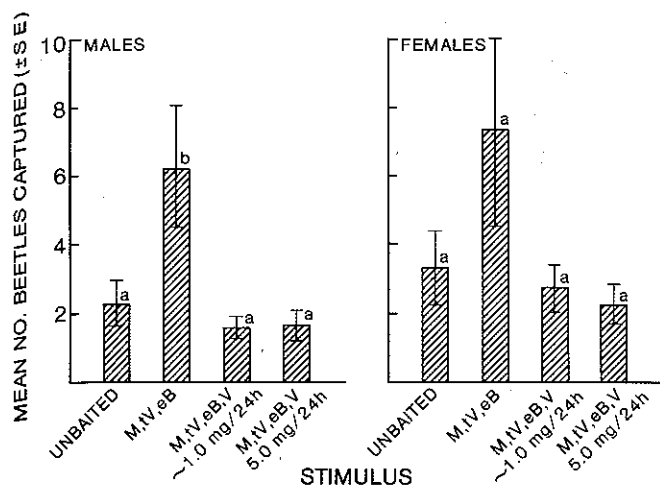


FIG. 6. Response of *D. ponderosae* in expt. 9 to multiple funnel traps baited with (–)-verbenone (V) at two release rates in combination with myrcene (M), (±)-*trans*-verbenol (tV), and (±)-*exo*-brevicomin (eB). See Table 1 for experimental details. ANOVA values are $F=8.645$ for males and 4.383 for females, $df=4,32$. Bars with the same letter above are not significantly different, Newman–Keuls test, $P < 0.05$.

In experiment 10, the release rate of *exo*-brevicomin had no significant effect on the expression of myrcene at two release rates (ANOVA, $P > 0.47$ and $P > 0.53$ for males and females, respectively). Therefore, the data were analyzed to compare the effect of low and high myrcene release rates. An 8.3-fold increase in the rate of myrcene release resulted in over twice as many *D. ponderosae* of both sexes responding to the ternary bait mixture (Fig. 7). These data suggest that the release rates for myrcene previously used for the mountain pine beetle are far below optimal. They support Billings' (1985) observation that releasing monoterpenes at high rates greatly increased the attraction of the southern pine beetle to other attractants, but in only a doubling of the response they more closely approximate results with the western pine beetle (Tilden and Bedard 1985). Evidently, the copious amounts of pheromone precursor and synergistic volatiles from an initially resistant, vigorous, newly attacked tree would have a very significant effect on attraction of host-seeking beetles. As noted by Raffa and Berryman (1983) such trees remain attractive for long periods of time and ultimately sustain the highest attack densities, provided that the initial attack is successful.

Model for semiochemical-mediated attack

Renwick and Vité (1970) developed a prototype conceptual model to describe the role of semiochemicals in mediating aggregation, mass attack, and cessation of attack on host trees by the mountain pine beetle. This model described the hypothesized roles of α -pinene and *trans*-verbenol, the only known semiochemicals for *D. ponderosae* at that time. Termination of attraction and mass attack was hypothesized to follow cessation of production of fresh resin by the attacked tree. Later Gieszler and Gara (1978) and Geiszler et al. (1980) embraced the concept of antiaggregation pheromones that mediated attack cessation and switching of attack to uninfested trees.

It is now possible to construct a far more detailed model for *D. ponderosae* (Fig. 8). Although it is based on data such as those in Figs. 1–7 and Table 2, the sequence of events, various roles of individual semiochemicals, and relative contributions of beetles, trees, and microorganisms are at least partially speculative. Refinement of the model will undoubtedly occur as additional data accrue on such phenomena as the autoxidation of

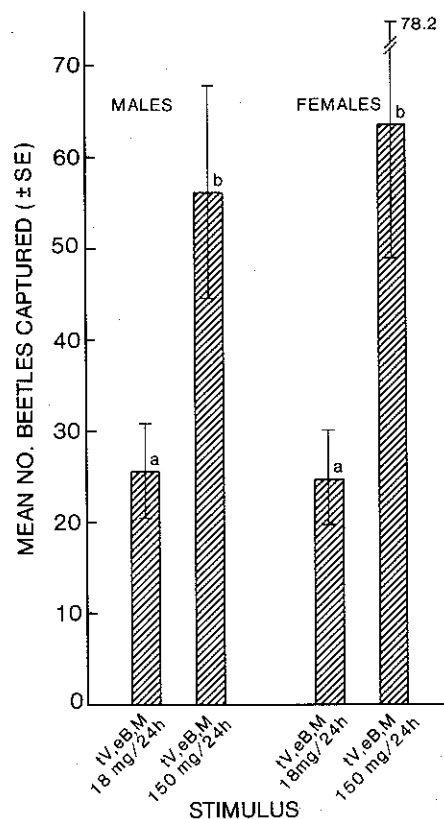


FIG. 7. Response of *D. ponderosae* in expt. 10 to multiple funnel traps baited with myrcene (M) at two release rates in combination with (±)-*trans*-verbenol (tV), and (±)-*exo*-brevicomin (eB). See Table 1 for experimental details. ANOVA values are $F=4.730$ for males and 4.268 for females, $df=1,17$. Bars with the same letter above are not significantly different, Newman–Keuls test, $P < 0.05$.

α -pinene, the role of microorganisms in producing semiochemicals such as verbenone, and the role of ipsdienol and other semiochemicals not yet included in the model.

Within hours of finding and beginning to bore into a new host, a pioneer female *D. ponderosae* will produce and release *trans*-verbenol (Fig. 8, phase 1). There is evidence for two modes of production by female *D. ponderosae*: (i) juvenile hormone-mediated conversion (Conn et al. 1984) of sequestered, derivatized α -pinene to *trans*-verbenol (Hughes 1975) and (ii) conversion of ingested or inhaled α -pinene to *trans*-verbenol (Hughes 1973a, 1973b; Conn et al. 1984). It is not known which production mode is the most rapid. Moreover, only a few females in a population appear to be capable of producing very large quantities of *trans*-verbenol (Borden et al. 1986b). Therefore, a mass attack might be predicated on successful initial attack by one or a few "good" producers, a larger number of "poor" producers, or some combination thereof.

trans-Verbenol is not attractive alone (Conn et al. 1983). Therefore, initiation of the mass attack sequence must occur only when volatile monoterpenes, the most active of which is myrcene (Conn et al. 1983; Borden et al. 1983a), are released from resin ducts severed by the beetles. In addition, the released α -pinene begins to autoxidize to *cis*- and *trans*-verbenol and verbenone, with the verbenols predominating during the first 24 h (Borden et al. 1986b). This volatile blend of attractive semiochemicals, the host tree kairomone, myrcene, and *trans*-verbenol produced by the host tree as well as female *D. ponderosae* would attract mainly male beetles (Conn et al.

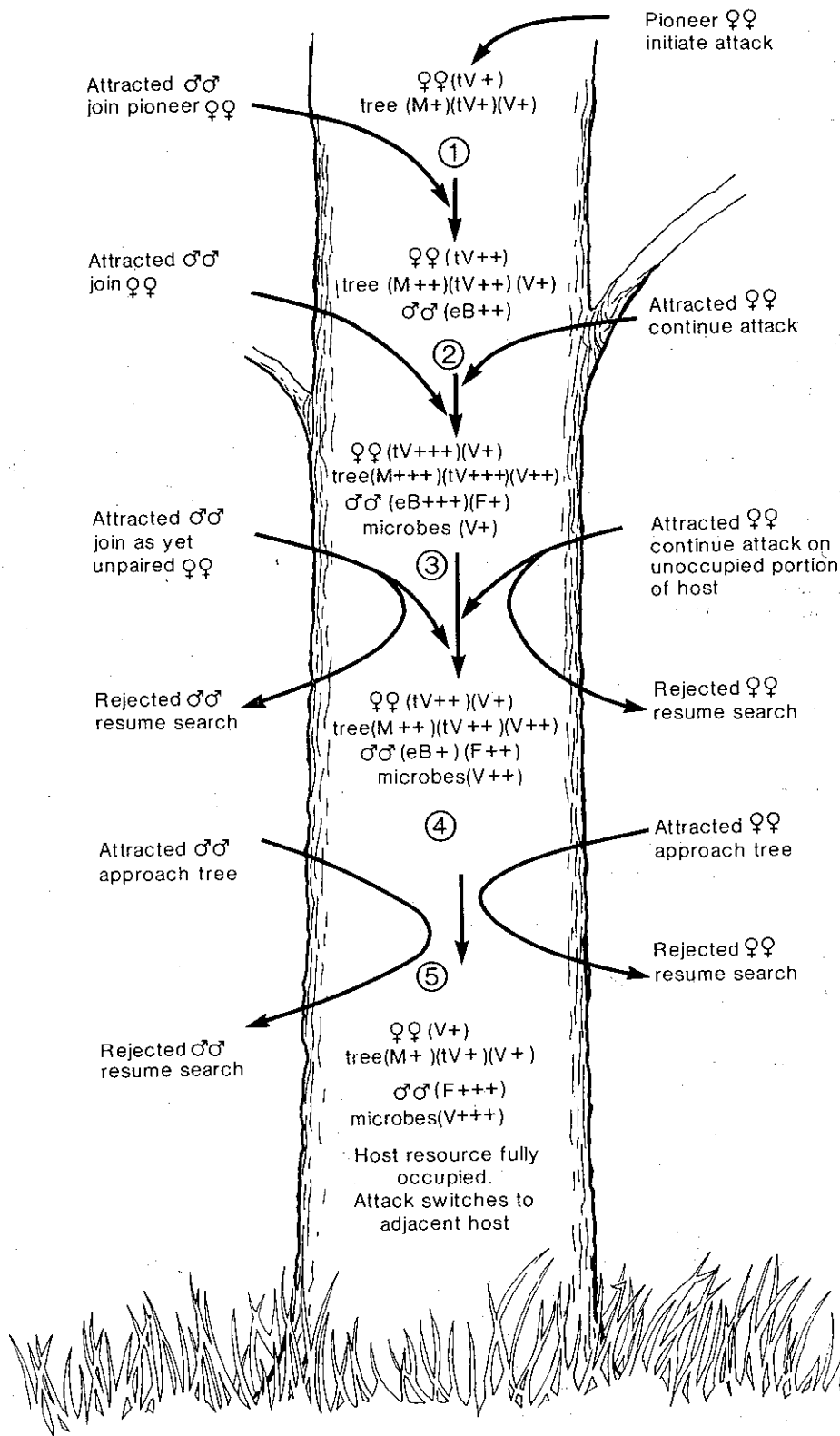


FIG. 8. Conceptual model proposing five phases of semiochemical-mediated mass attack by *D. ponderosae* on lodgepole pine in British Columbia. Responses by males and females are depicted on the left and right of the tree under attack. Production of semiochemicals (tV, M, V, eB, and F) by females, males; the host tree, and microorganisms shown on bole of the tree with light, moderate, and heavy production rates shown by +, ++, and +++, respectively.

1983) (Figs. 2, 3, and 8 (phase 1)). Further male specificity would be promoted by 3-carene-10-ol (Conn et al. 1983; Libbey et al. 1985). Although verbenone is an antiaggregation pheromone (Ryker and Yandell 1983) (Fig. 6), the small amount produced at this point by autoxidation of α -pinene would probably not deter orientation by the male beetles.

The attracted males bear *exo*-brevicomin in their guts (Libbey et al. 1985). Within 1–2 days after joining females and presumably mating with them, males still produced moderate amounts of *exo*-brevicomin (Libbey et al. 1985). However, after 6 days little *exo*-brevicomin remains (H. D. Pierce, Jr., unpublished results). In combination with the *trans*-verbenol

and myrcene already present, *exo*-brevicommin acts to increase the attraction of females (Fig. 2, 3), so that the sex ratio of attracted beetles approaches 1.0 (Conn et al. 1983). The increased levels of myrcene (and other attractive monoterpenes) produced as more resin flows from the freshly severed resin canals (Fig. 8 phase 2) will potentiate the response by both sexes.

If the attack rate is very rapid, the available host "real estate" may soon be fully occupied, possibly even within 48 h (Rasmussen 1974). Overpopulation might then be prevented by the large amounts of *exo*-brevicommin released as many males join females simultaneously. Its antiaggregative effect at high release rates (Rudinsky et al. 1974; Ryker and Rudinsky 1982; Libbey et al. 1985) (Fig. 2, Table 1) would deter close-range, positive orientation by host-seeking beetles even before other antiaggregation pheromones were produced. However, if the attack rate is slow, the physical flow of resin might impede or halt the progress of the attacking beetles. Within 24 h the production of verbenone from autoxidation of α -pinene (Borden et al. 1986b) might deter further attraction, allowing the tree to "forestall" mass attack. Examples of unsuccessfully attacked trees are often seen; the above explanation for this phenomenon is advanced as an alternative hypothesis to Raffa and Berryman's (1983) hypothesis that resistant trees somehow inhibit pheromone production by females in newly established galleries.

Frontalin is produced by male beetles within 24 h after they have joined a female (Ryker and Libbey 1982). If the mass attack were to proceed at a moderate rate over several days, the low concentrations of frontalin emanating from a tree with established galleries (Fig. 8, phase 3) would contribute to the attraction of other beetles, predominately females (Fig. 5), which would be induced to attack unexploited portions of the tree (Chatelain and Schenk 1984; J. H. Borden and L. J. Chong; unpublished results).

Early in phase 3 (Fig. 8), the tree would probably be in its most attractive state. *trans*-Verbenol produced by the attacking females, as well as through autoxidation of α -pinene from the tree, would be synergized by copious amounts of myrcene in fresh pitch tubes. Males would be releasing *exo*-brevicommin; the release rate from the tree would remain steady as the arriving males expelled their *exo*-brevicommin and produced moderate amounts after joining females. The frontalin released by those males in established galleries would complement the attractive bouquet.

Late in phase 3 (Fig. 8) the picture would begin to change, in part due to increased amounts of male-produced frontalin, which at high levels would deter positive orientation to the other semiochemicals (Fig. 4, Table 2). However, the predominant antiaggregative semiochemical would be verbenone, produced in three ways: by the female beetles, through autoxidation of α -pinene, and at increasing levels by microorganisms (primarily yeasts) growing in the established galleries. The importance of the microorganisms in termination of attack is doubtless increased by their ability to convert *trans*-verbenol to verbenone (Leufven et al. 1984; D. W. A. Hunt, personal communication), thus reducing the attractiveness of the tree while at the same time increasing its repellancy. To accentuate this change, the females after 36 h in established galleries produce very little *trans*-verbenol (Pitman and Vité 1969).

As the attractive semiochemicals become overwhelmed by antiaggregants, the mass attack would enter a transition phase 4 (Fig. 8), in which increasing numbers of beetles of both sexes would be repelled as the attack density increases. Finally, in

phase 5 (Fig. 8), the long-range attraction of the residual *trans*-verbenol and frontalin might draw beetles toward the tree, but the overwhelming odor of frontalin and verbenone at close range would cause the attracted beetles to resume their search. This attack could be redirected to suitable, nearby trees (Geiszler and Gara 1978; Geiszler et al. 1980), creating the characteristic spot infestations typical of the species (Safranyik et al. 1974).

Implications for the applied use of semiochemicals

Although (-)-*trans*-verbenol is attractive in British Columbia (Fig. 1) and elsewhere (McKnight 1979; Libbey et al. 1985), the presence of the antipode in British Columbia does not deter the response (Fig. 1). Similarly, neither enantiomer of *exo*-brevicommin or frontalin is more attractive or repellent than the racemic compound (Figs. 3, 5; Table 1), with the exception of a slight, unexplained inhibitory effect of frontalin enantiomers at low release rates (Fig. 5). Therefore, the results justify the current extensive use of racemic *trans*-verbenol and *exo*-brevicommin as tree baits in forest pest management programs (Borden and Lacey 1985). Moreover, if frontalin were to be incorporated into a tree bait, the racemic pheromone would suffice.

Although our experiments were performed with traps, it would appear from Fig. 7 that the currently used release rate for myrcene in tree baits is too low. The efficiency of such baits in inducing attack might be increased by a higher release rate of myrcene that would approach the presumed concentrations reached in phases 2 and 3 of attack (Fig. 8), when an attacked tree is exuding resin.

In no case did the use of chirally pure compounds or a varied concentration of a compound strikingly improve the efficiency of baited traps. Extensive studies of volatiles produced by *D. ponderosae* of both sexes (Libbey et al. 1985; Pierce et al. 1987) have revealed no promising new attractive semiochemicals other than frontalin. Therefore, while tree baits are a most effective pest management tool (Borden et al. 1983b, 1983c, 1986a) and semiochemical-baited traps can be well used in monitoring peak activity periods of the beetle (Stock 1984), the potential for using baited traps to suppress populations is not promising.

Acknowledgements

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- BILLINGS, R. F. 1985. Southern pine bark beetles and associated insects. Effects of rapidly-released host volatiles on response to aggregation pheromones. *Z. Angew. Entomol.* **99**: 483-491.
- BILLINGS, R. F., R. I. GARA, and B. F. HRUTFIORD. 1976. Influence of ponderosa pine resin volatiles on the response of *Dendroctonus ponderosae* to synthetic *trans*-verbenol. *Environ. Entomol.* **5**: 171-179.
- BORDEN, J. H. 1982. Aggregation pheromones. In *Bark beetles in North American conifers*. Edited by J. B. Mitton and K. B. Sturgeon. University of Texas Press, Austin. pp. 74-139.
- BORDEN, J. H., and T. E. LACEY. 1985. Semiochemical-based manipulation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins: a component of lodgepole pine silviculture in the Merritt Timber Supply Area of British Columbia. *Z. Angew. Entomol.* **99**: 139-145.
- BORDEN, J. H., J. E. CONN, L. M. FRISKIE, B. E. SCOTT, L. J. CHONG, H. D. PIERCE, JR., and A. C. OEHLISCHLAGER. 1983a.

- Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae* in British Columbia: baited tree studies. *Can. J. For. Res.* **13**: 325–333.
- BORDEN, J. H., L. J. CHONG, and M. C. FUCHS. 1983b. Application of semiochemicals in post-logging manipulation of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *J. Econ. Entomol.* **76**: 1428–1432.
- BORDEN, J. H., L. J. CHONG, K. E. G. PRATT, and D. R. GRAY. 1983c. The application of behaviour-modifying chemicals to contain infestations of the mountain pine beetle, *Dendroctonus ponderosae*. *For. Chron.* **59**: 235–239.
- BORDEN, J. H., L. J. CHONG, and T. E. LACEY. 1986a. Pre-logging baiting with semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae*, in high hazards stands of lodgepole pine. *For. Chron.* **62**: 20–23.
- BORDEN, J. H., D. W. A. HUNT, D. R. MILLER, and K. N. SLESSOR. 1986b. Orientation in forest coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. In *Mechanisms in insect olfaction*. Edited by T. L. Payne, M. C. Birch, and C. E. J. Kennedy. Oxford University Press, Oxford. pp. 97–109.
- CHATELAIN, M. P., and J. A. SCHENK. 1984. Evaluation of frontalin and *exo*-brevicomin as kairomones to control mountain pine beetle in lodgepole pine. *Environ. Entomol.* **13**: 1666–1674.
- CONN, J. E., J. H. BORDEN, B. E. SCOTT, L. M. FRISKIE, H. D. PIERCE, JR., and A. C. OEHLISCHLAGER. 1983. Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae*, in British Columbia: field trapping studies. *Can. J. For. Res.* **13**: 320–324.
- CONN, J. E., J. H. BORDEN, D. W. A. HUNT, J. HOLMAN, H. S. WHITNEY, O. J. SPANIER, H. D. PIERCE, JR., and A. C. OEHLISCHLAGER. 1984. Pheromone production by axenically reared *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae). *J. Chem. Ecol.* **10**: 281–290.
- DICKENS, J. C., T. L. PAYNE, L. C. RYKER, and J. A. RUDINSKY. 1985. Multiple acceptors for pheromonal enantiomers on single olfactory cells in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). *J. Chem. Ecol.* **11**: 1359–1370.
- GEISZLER, D. R., and R. I. GARA. 1978. Mountain pine beetle attack dynamics in lodgepole pine. In *Theory and practice of mountain pine beetle management in lodgepole pine forests*. Edited by A. A. Berryman, G. D. Amman, and R. W. Stark. University of Idaho, Moscow, and USDA Forest Service, Washington, DC. pp. 182–187.
- GEISZLER, D. R., V. F. GALLUCCI, and R. I. GARA. 1980. Modelling the dynamics of mountain pine beetle aggregation in a lodgepole pine stand. *Oecologia*, **46**: 244–253.
- HUGHES, P. R. 1973a. Effects of α -pinene exposure on *trans*-verbenol synthesis in *Dendroctonus ponderosae* Hopk. *Naturwissenschaften*, **60**: 261–262.
- . 1973b. *Dendroctonus*: production of pheromones and related compounds in response to host monoterpenes. *Z. Angew. Entomol.* **73**: 294–312.
- . 1975. Pheromones of *Dendroctonus*: origin of α -pinene oxidation products present in emergent adults. *J. Insect Physiol.* **21**: 687–691.
- HUNT, D. W. A., and J. H. BORDEN. 1987. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) to ipsdienol in the laboratory and the field. *J. Chem. Ecol.* In press.
- HUNT, D. W. A., J. H. BORDEN, H. D. PIERCE, JR., K. N. SLESSOR, G. G. S. KING, and F. K. CZYZESKA. 1986. Sex-specific production of ipsdienol and myrcenol by *Dendroctonus ponderosae* exposed to myrcene vapors. *J. Chem. Ecol.* **12**: 1579–1586.
- LEUFVEN, A., G. BERGSTROM, and E. FALSEN. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *J. Chem. Ecol.* **10**: 1349–1361.
- LIBBEY, L. M., L. C. RYKER, and K. L. YANDELL. 1985. Laboratory and field studies of volatiles released by *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Z. Angew. Entomol.* **100**: 381–392.
- LINDGREN, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *Can. Entomol.* **115**: 299–302.
- McKNIGHT, R. C. 1979. Differences in response among populations of *Dendroctonus ponderosae* Hopkins to its pheromone complex. M.Sc. thesis, University of Washington, Seattle.
- MIROV, N. T. 1961. Composition of gum turpentine of pines. USDA For. Serv. Tech. Bull. No. 1239.
- PIERCE, H. D., JR., J. E. CONN, J. H. BORDEN, and A. C. OEHLISCHLAGER. 1987. Monoterpene metabolism in female mountain pine beetles, *Dendroctonus ponderosae* Hopkins, attacking lodgepole and ponderosa pines. *J. Chem. Ecol.* In press.
- PITMAN, G. B. 1971. *Trans*-verbenol and α -pinene: their utility in manipulation of the mountain pine beetle. *J. Ecol. Entomol.* **64**: 426–430.
- PITMAN, G. B., and J. P. VITÉ. 1969. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. *Can. Entomol.* **101**: 143–149.
- PITMAN, G. B., J. P. VITÉ, G. W. KINZER, and A. F. FENTIMAN, JR. 1968. Bark beetle attractants: *trans*-verbenol isolated from *Dendroctonus*. *Nature (London)*, **218**: 168–169.
- PITMAN, G. B., M. W. STOCK, and R. C. McKNIGHT. 1978. Pheromone application in mountain pine beetle/lodgepole pine management: theory and practice. In *Theory and practice of mountain pine beetle management in lodgepole pine forests*. Edited by A. A. Berryman, G. D. Amman, and R. W. Stark. University of Idaho, Moscow, and USDA Forest Service, Washington, DC. pp. 165–181.
- RAFFA, K. F., and A. A. BERRYMAN. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecol. Mon.* **53**: 27–49.
- RASMUSSEN, L. A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and Southern Idaho. USDA For. Serv. Res. Note INT-180.
- RENWICK, J. A. A., and J. P. VITÉ. 1970. Systems of chemical communication in *Dendroctonus*. *Contrib. Boyce Thompson Inst.* **24**: 283–292.
- RUDINSKY, J. A., M. E. MORGAN, L. M. LIBBEY, and T. B. PUTNAM. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. *Environ. Entomol.* **3**: 90–98.
- RYKER, L. C., and L. M. LIBBEY. 1982. Frontalin in the male mountain pine beetle. *J. Chem. Ecol.* **8**: 1399–1409.
- RYKER, L. C., and J. A. RUDINSKY. 1982. Field bioassay of *exo*- and *endo*-brevicomin as antiaggregation pheromones for *Dendroctonus ponderosae* in lodgepole pine. *J. Chem. Ecol.* **8**: 701–707.
- RYKER, L. C., and K. L. YANDELL. 1983. Effect of verbenone on aggregation of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) to synthetic attractant. *Z. Angew. Entomol.* **96**: 452–459.
- SAFRANYIK, L., D. M. SHRIMPTON, and H. S. WHITNEY. 1974. Management of lodgepole pine reduces losses from the mountain pine beetle. *Environ. Can. For. Serv. For. Tech. Rep. No. 1*.
- SCHURIG, V., R. WEBER, G. J. NICHOLSON, A. C. OEHLISCHLAGER, H. PIERCE, JR., A. M. PIERCE, J. H. BORDEN, and L. C. RYKER. 1983. Enantiomer composition of natural *exo*- and *endo*-brevicomin by complexation gas chromatography/selected ion mass spectrometry. *Naturwissenschaften*, **70**: 92–93.
- SLESSOR, K. N., G. G. S. KING, D. R. MILLER, M. L. WINSTON, and T. L. CUTFORTH. 1985. Determination of chirality of alcohol or latent alcohol semiochemicals in individual insects. *J. Chem. Ecol.* **11**: 1659–1667.
- STOCK, A. J. 1984. Use of pheromone baited Lindgren funnel traps for monitoring mountain pine beetle flights. *B.C. For. Serv. Int. Rep. PM-PR-2*.
- TILDEN, P. E., and W. D. BEDARD. 1985. Field response of *Dendroctonus brevicomis* to *exo*-brevicomin, frontalin, and myrcene released at two proportions and three levels. *J. Chem. Ecol.* **11**: 757–766.