Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in British Columbia: baited-tree studies

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Lodgepole pines, *Pinus contorta* var. *latifolia* Engelm., in three interior British Columbia locations were baited with six monoterpenes alone or combined, and various combinations of the beetle-produced volatiles *trans*-verbenol, *exo*-brevicomin, and 3-caren-10-ol. Trees baited with *trans*-verbenol, *exo*-brevicomin, and the monoterpene 3-carene sustained higher attack densities by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and were surrounded by more attacked trees than trees baited with *trans*-verbenol and 3-carene or unbaited controls. Myrcene was apparently the best of six monoterpenes as a synergist for *trans*-verbenol. 3-Caren-10-ol appeared to have some activity in an early test but did not prove to be an attractive pheromone in extensive studies. In a 17-ha portion of an infestation, treatment of 99 trees with 3-carene and *trans*-verbenol apparently caused a higher attack rate, resulting in 56.4% of the available green trees being attacked, as opposed to 22.3% of the available trees in the 14-ha unbaited area. These data as well as the high attack rates associated with trees which also had an *exo*-brevicomin bait suggest that semiochemicals could be used to contain *D. ponderosae* infestations and to attract beetles to lethal trap trees.

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Six monoterpènes seuls ou combinés et diverses combinaisons de *trans*-verbenol, d'*exo*-brevicomin et de 3-caren-10-ol, substances volatiles dérivées d'insectes, ont servi de leurres sur des pins tordus, *Pinus contorta* var. *latifolia* Engelm., dans trois stations à l'intérieur de la Colombie-Britannique. Les arbres portant le *trans*-verbenol, l'*exo*-brevicomin et le monoterpène 3-carène ont subi des attaques de plus forte densité par le dendroctone du pin ponderosa, *Dendroctonus ponderosae* Hopkins, et furent entourés d'un plus grand nombre d'arbres attaqués que lorsque les arbres furent traités au *trans*-verbenol et 3-carène ou que chez les témoins. Myrcène fut apparemment le meilleur des six monoterpènes en synergisme avec *trans*-verbenol. Dans une expérience initiale, 3-caren-10-ol a semblé montrer une certaine activité; mais au cours d'études approfondies elle ne s'est pas révélée une phéromone attractive. Dans une portion de 17 ha d'une infestation, le traitement de 99 arbres avec 3-carène et *trans*-verbenol a semblé causer une proportion plus élevée d'arbres attaqués, soit jusqu'à 56,4% des arbres verts disponibles, alors que dans une superficie témoin (sans leurre) de 14 ha, seulement 22,3% des arbres disponibles étaient attaqués. Ces informations et le pourcentage élevé d'attaques chez les arbres garnis d'*exo*-brevicomin suggèrent que ces substances sémiochimiques pourraient être utilisées pour contenir des infestations de *D. ponderosae* et pour attirer les insectes dans des arbres servant de piège mortel.

[Traduit par le journal]

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is currently the number one forest insect pest in western Canada (Sterner and Davidson 1981). In British Columbia, it is in outbreak conditions in large areas of the Kootenays, the south Okanagan, and the Chilcotin, and threatens to explode in the Bulkley Valley. Effective control in the early phases of an infestation may be achieved by falling and burning newly attacked trees before the beetles emerge (Whitney *et al.* 1978), by partial cutting of large-diameter trees (Cahill 1978), or by sanitation salvage logging when roads and nearby markets are available (Safranyik *et al.* 1974). When an infestation has reached outbreak status, the only feasible option is to salvage dead trees to recover their value, and to extend the logging operation into currently attacked and threatened timber. This type of operation is now common in British Columbia (Alexander *et al.* 1976; Ruault 1981).

Semiochemicals (message-bearing chemicals) have been used to manipulate populations of several species of North American bark beetles. For example, a blend

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of the pheromones, *exo*-brevicomin and frontalin, with a host-produced monoterpene, myrcene, has been used successfully to mass trap the western pine beetle, *Dendroctonus brevicomis* LeConte (Bedard and Wood 1974). For the southern pine beetle, *D. frontalis* Zimmerman, trees within small infestations, "hot spots," were baited with frontalin and the monoterpene, α-pinene. This treatment apparently kept the beetles from dispersing and arrested attack on trees at the advancing front of the infestation (Richerson *et al.* 1980).

There is definite potential for the use of semiochemicals in manipulating *D. ponderosae*. Pondelure, a mixture of the aggregation pheromone *trans*-verbenol with the host monoterpene, α-pinene, has been used to attract large numbers of beetles to traps in white pine, *Pinus monticola* Dougl., forests and to induce attack on selected trees (Pitman 1971). In British Columbia it has been used to induce attack on lodgepole pines, *Pinus contorta* var. *latifolia* Engelm., within a treatment block at a higher rate than in an adjacent control block (E. D. A. Dyer and P. M. Hall, personal communication). The possibility of incorporating additional beetle-produced volatiles, such as *exo*-brevicomin and 3-caren-10-ol (Conn *et al.* 1983), and host tree monoterpenes (Billings *et al.* 1976; Conn *et al.* 1983) into a superior bait suggested that the art of manipulating populations of the beetle could be further refined.

This paper presents the results of field tests of three beetle-produced volatiles and six host-produced monoterpenes as baits for inducing attack on lodgepole pines in British Columbia. *Trans*-verbenol, 3-caren-10-ol, and 3-carene were chosen as candidate semiochemicals on the basis of their superior activity in laboratory bioassays (Conn 1981), *exo*-brevicomin for its intriguing and contradictory attractive or antiaggregative activity in other field tests (Rudinsky *et al.* 1974; Pitman *et al.* 1978; McKnight 1979; Ryker and Rudinsky 1982), α-pinene because of its synergistic properties with *trans*-verbenol (Pitman 1971), and four other monoterpenes, β-pinene, β-phellandrene, terpinolene, and myrcene, because they (along with 3-carene and α-pinene) represent the principal monoterpenes produced by lodgepole pine (Shrimpton 1973).

Methods and materials

Monoterpenes were released from glass vials and beetle-produced volatiles from capillary tubes or Conrel fibres (Albany International Co., Needham, Massachusetts) as described by Conn *et al.* (1983). In addition to the 0.2-mm internal diameter Conrel fibre used to release *exo*-brevicomin at 0.05 mg/day (Conn *et al.* 1983), three other release devices and rates were used: a Conrel fibre, 0.4 mm internal diameter, one end open, 0.14 mg day, and capillary tubes of 1.0 and 1.7 mm internal diameter releasing *exo*-brevicomin at 0.37 and 1.26 mg/day, respectively. The source and purity of all volatile stimuli were as given by Conn *et al.* (1983).

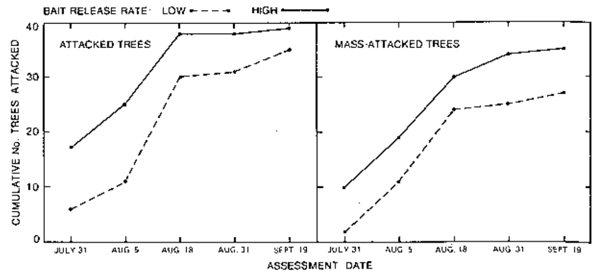

FIG. 1. Cumulative numbers of attacked trees (<62.5 attacks/m^2) and mass-attacked trees (≥62.5 attacks/m^2 in at least one of two counts), 49 trees baited on July 16, 1981, with volatiles at low release rates (3C = 7 mg/day; tV and 3C-ol = 0.2 mg/day each) and 50 at high release rates (3C = 28 mg/day; tV and 3C-ol = 0.8 mg/day each), Manning Park, B.C.

Candidate semiochemicals were affixed to living lodgepole pines in one of two receptacles. In 1980 a wooden block with holes drilled in it to hold release devices was wired to baited trees. A plastic lid to provide shade and shed rain was stapled to the block. In 1981 an aluminum holder was used. The holder was cut from sheet aluminum in the form of a cross. It was nailed to the tree through the body of the cross, the bottom and sides folded in to form a box to hold the release devices, and the top folded down to form a lid. The holders were light and could be carried easily through the forest in a tight stack. However, in northern British Columbia they apparently excited the curiosity of bears and numerous holders were clawed and bitten and lost their baits.

Five experiments were conducted, one in 1980 and four in 1981. All but one, as noted below, were of the randomized block design, with a minimum distance of 50 m between trees. Dates, locations, release rates for volatile baits as determined in the laboratory at 20°C (Conn *et al.* 1983), numbers of trees baited and statistical tests used are given in Tables 1–7 and Fig. 1. All baited trees were well over 20 cm diameter at breast height (dbh). The experiments were set up before beetles emerged. Some were assessed periodically during the attack phase by counting the attacks represented by pitch tubes and frass piles within two 20- by 40-cm frames held at eye level on opposite sides of a tree at 90° from the bait receptacle. All were assessed by checking for attack and recording attack density after the summer flight had ended. Mass attacked trees were arbitrarily designated as those with ≥62.5 attacks/m^2 in at least one of two counts.

In the 1980 experiment near Princeton, a stimulus of α-pinene + *trans*-verbenol was tested against *trans*-verbenol and 3-caren-10-ol alone, together, and in combination with 3-carene.

Two 1981 experiments were done from June to October in the Harold Price Creek drainage near Smithers, B.C. One assessed 3-carene + *trans*-verbenol with and without 3-caren-10-ol on trees 100 m apart around the boundaries of four clear-cut blocks. The order of each pair of baited trees was determined by the flip of a coin. Control trees were identified later as the first lodgepole pine greater than 20 cm dbh beyond

TABLE 1. Attack by *Dendroctonus ponderosae* on baited and control trees around Cut Blocks CP7-1 to CP7-4, Harold Price Creek near Smithers, B.C., June 23 – October 17, 1981

Treatment[a]	No. trees[b]	Trees attacked		Trees mass attacked		$\bar{\chi}$ attack density/m[2d]
		No.	%[c]	No.	%[c]	
Unbaited controls	124	5	4.0A	2	1.6A	19.4
3C, tV	59	18	30.5B	15	25.4B	86.3
3C, tV, 3C-ol	64	16	25.0B	11	17.2B	65.6

[a]3C = 3-carene, tV = *trans*-verbenol, 3C-ol = 3-caren-10-ol. Approximate release rates as follows: 3C = 14 mg/day; tV + 3C-ol = 0.4 mg/day each.

[b]Numbers of trees baited were 3C, tV, 69 trees; and 3C, tV, 3C-ol, 68 trees. Trees with baits destroyed, e.g., by bears, discounted.

[c]Percentages within a column followed by same letter not significantly different, Newman–Keuls test modified for testing frequencies, $P < 0.05$.

[d]Attack density on both treatments of baited trees significantly different from that on unbaited controls, *t*-test, $P < 0.05$.

25 m from the baited tree and not closer than 25 m to the next baited tree. The other experiment tested *trans*-verbenol or *trans*-verbenol + 3-caren-10-ol in combination with one of the six major monoterpenes in lodgepole pine or with the monoterpenes mixed in an equal part mixture. The experiment was laid out in 40 randomized blocks with 15 treatments per block.

At Manning Park, 99 trees within a 17-ha portion of an expanding infestation were baited in July 1981 with 3-carene, *trans*-verbenol, and 3-caren-10-ol, 49 at the low release rates used in 1980 (7 mg/day for 3-carene and 0.2 mg/day for *trans*-verbenol and 3-caren-10-ol), and 50 at four times these rates.

Exo-brevicomin was tested from June to September 1981 at four different release rates (Table 6) in combination with 3-carene, *trans*-verbenol, and 3-caren-10-ol in a 15-replicate, 105-tree experiment at the Diamond S Ranch near Pavillion, B.C. The trees were baited and checked once near the end of the flight period and once after.

Attack on unbaited trees was assessed in late September – early October for the experiments at Harold Price Creek and at the Diamond S Ranch. The diameters of all trees within 5- and 10-m radii of the treatment trees were taken and the attacks counted as on the baited trees.

Proportional data were subjected to an arc sine transformation and analyzed by a Newman–Keuls test modified for testing frequencies. All other data were converted by $\log_{10}(\chi + 1)$ and analyzed by ANOVA and the Newman–Keuls test.

Results and discussion

Effect of bait treatments

The most effective bait in inducing attack in 1980 was the ternary combination of 3-carene, *trans*-verbenol, and 3-caren-10-ol; seven of eight trees baited with this stimulus were attacked. These were followed by three trees baited with 3-carene and *trans*-verbenol, two trees baited with *trans*-verbenol, and one each baited with *trans*-verbenol and 3-caren-10-ol, 3-carene and 3-caren-10-ol, or 3-caren-10-ol alone. None of the eight trees baited with α-pinene and *trans*-verbenol was attacked, nor were any of the eight unbaited controls. The release rates for all three stimuli were very low compared with those used by other researchers, e.g., 120 mg/day · tree^{-1} for *trans*-verbenol in white pine forests (Pitman 1971), compared with 0.2 mg/day · tree^{-1} in our experiment. Therefore, considerable significance was placed on this result, and the apparently very active role of 3-caren-10-ol, which was further assessed in all of the 1981 experiments.

In none of the 1981 experiments did 3-caren-10-ol enhance attack on baited trees when added to a monoterpene + *trans*-verbenol stimulus (Tables 1, 2, 5). Therefore, it is probably not essential in an attractive pheromone bait used to manage the beetle.

The inferiority of α-pinene as a synergist for *trans*-verbenol in traps (Conn *et al.* 1983), and in the 1980 trap-tree experiment was corroborated by the 1981 trap-tree experiments (Table 2). While none of the other monoterpene treatments were significantly more effective than the unbaited controls, myrcene was the only one significantly better than α-pinene (Table 2). The numerical superiority of myrcene (Table 2), its superiority in traps (Conn *et al.* 1983) and its effectiveness in ponderosa pine forests (Billings *et al.* 1976) make it the monoterpene of choice for further use in *D. ponderosae* infestations in hard pines.

The data from Manning Park indicate that by July 31 release rates of 28 and 0.8 mg/day for 3-carene and *trans*-verbenol, respectively, were significantly better (χ^2 test, $P < 0.05$) in inducing attacks and mass attacks than release rates four times lower (Fig. 1). This trend continued throughout the infestation period and indicates that the higher release rates are more realistic for operational use. Attack densities on the baited trees increased with time (Table 3); the apparent decline on

TABLE 2. Attack by *Dendroctonus ponderosae* on lodgepole pines baited with selected monoterpenes plus candidate pheromones, Harold Price Creek near Smithers, B.C., June 23 − October 17, 1981

Treatment[a]	No. trees[b]	Trees attacked		Trees mass attacked		$\bar{\chi}$ attack density/m^2	Attack summary by terpene		
							Trees attacked		$\bar{\chi}$ attack density/m^2
		No.	%	No.	%		No.	%[c]	
Unbaited controls	32	2	6.3	1	3.1	37.5	2	6.3AB	37.5
αP, tV	30	1	3.3	1	3.3	87.5			
αP, tV, 3C-ol	30	2	6.7	2	6.7	118.8	3	5.0A	108.1
βPh, tV	28	5	17.9	3	10.7	47.5			
βPh, tV, 3C-ol	25	1	4.0	1	4.0	106.3	6	11.3AB	56.9
3C, tV	29	5	17.2	5	17.2	103.8			
3C, tV, 3C-ol	28	5	17.8	4	14.3	105.0	10	17.5AB	104.4
βP, tV	24	6	25.0	6	25.0	139.4			
βP, tV, 3C-ol	29	4	13.8	3	10.3	103.1	10	18.9AB	125.0
T, tV	27	4	14.8	3	11.1	115.6			
T, tV, 3C-ol	29	7	24.1	6	20.7	102.5	11	19.6AB	107.5
Tm, tV	22	2	9.0	1	4.5	90.6			
Tm, tV, 3C-ol	27	8	29.6	7	25.9	137.5	10	20.0AB	128.1
M, tV	28	7	25.0	6	21.4	125.6			
M, tV, 3C-ol	28	8	28.6	8	28.6	101.9	15	26.8B	113.1

[a]αP = α-pinene, βPh = βphellandrene, 3C = 3-carene, βP = β-pinene, T = terpinolene, Tm = terpene mix (equal parts, all six), M = myrcene, tV = *trans*-verbenol, 3C-ol = 3-carene-10-ol. Approximate release rates as follows: all terpenes and terpene mix = 7 mg/day; tV + 3C-ol = 0.2 mg/day each.
[b]Forty trees for each treatment (600 total) originally baited. Trees removed by construction or with baits destroyed, e.g., by bears, discounted.
[c]Percentages followed by same letter not significantly different, Newman−Keuls test modified for testing frequencies, $P < 0.05$.

TABLE 3. Attack density on lodgepole pines baited on July 16, 1981, with volatiles at low release rates (3C = 7 mg/day; tV and 3C-ol = 0.2 mg/day each) and high release rates (3C = 28 mg/day; tV and 3C-ol = 0.8 mg/day each), Manning Park, B.C.

Treatment	Date first attack recorded	No. trees	$\bar{\chi}$ attack density/m^2 by date				
			July 31	August 5	August 18	August 31	September 19
3C, tV, 3C-ol,	July 31	6	71.9	113.5	148.9	176.0	148.9
Low release	August 5	5	—	67.5	83.8	120.0	100.0
Rates	August 18	20	—	—	58.4	84.3	60.3
3C, tV, 3C-ol	July 31	17	103.7	100.7	102.6	134.2	116.9
High release	August 5	8	—	85.9	77.3	100.8	76.1
Rates	August 18	13	—	—	75.0	106.4	86.5
Unbaited trees	September 19[a]	39	—	—	—	—	107.8

[a]Trees not assessed until September 19. Attacks probably occurred throughout the period that baited trees were observed.

TABLE 4. Distribution of trees attacked by *Dendroctonus ponderosae* in treated and control areas before and after baiting 99 trees with 3-carene, *trans*-verbenol, and 3-caren-10-ol in 1981, Manning Park, B.C.

Attack status of trees	% total trees in area	
	Control (unbaited) area, 1194 trees on approximately 14 ha	Treated (baited) area, 2442 trees on approximately 17 ha
Grey: attacked before 1979	18.7	2.8
Red: attacked in 1980	17.9	11.0
Green: attacked in 1981	13.6	49.2
Green: unattacked	47.5	38.1

September 19 is probably due to loss of frass piles and pitch tubes in severe weather following the August 31 assessment. Attack densities were lower in trees attacked later in the flight season (Table 3). As the early attacked trees absorbed larger numbers of beetles, the importance of baiting trees prior to the first emergence and flight of the beetles is evident.

The high attack rate on the baited trees within the infestation suggested that the treatment may have helped at least partially to contain the infestation. This hypothesis is supported by data from a post-attack cruise of the infestation done by students at the British Columbia Institute of Technology (Table 4). The 13.6% of the trees attacked in 1981 in the unbaited area represent 22.3% of the available green trees before the attack occurred. In the adjacent baited area the 49.2% of the trees attacked in 1981 represent 56.4% of the available trees. Thus, the intensity of attack in the baited area (on 74 baited trees and 1127 unbaited trees) was approximately 2.5 times greater than in the unbaited area.

Exo-brevicomin at the three highest release rates was highly effective with 3-carene, *trans*-verbenol, and 3-caren-10-ol in inducing attack and mass attack on baited trees (Table 5). These *exo*-brevicomin baited trees became mass attacked and sustained higher attack densities earlier in the attack period than trees with other baits. By the time the attack was over, the differences in attack densities were not so striking, but densities on the trees releasing *exo*-brevicomin at the two highest rates were the only ones significantly higher than that of the unbaited control trees (Table 5). The data from Manning Park (Table 3) and the Diamond S Ranch (Table 5) suggest that attractive aggregation pheromones, particularly *exo*-brevicomin, can override the effect of the antiaggregation pheromone frontalin (Ryker and Libbey 1983), resulting in an unnaturally high attack density. This possibility could be exploited by concentrating a relatively large number of beetles into a relatively small number of trees. The superior attraction achieved with *exo*-brevicomin indicates that lethal trap trees pretreated with an arsenical arboricide or a surface insecticide on the bark may now be feasible for *D. ponderosae*.

All of the bait treatments induced significantly greater attacks and mass attacks, but not attack density, on trees surrounding them than on trees surrounding unbaited control trees (Table 6). The trees surrounding those baited with *exo*-brevicomin at the two highest release rates were particularly vulnerable to attack.

There is a strong possibility that a bait with *exo*-brevicomin incorporated in it could be used to induce heavy attack throughout a particular forest area. The potential for such an effect is exemplified by the Manning Park experiment, in which the extremely

TABLE 5. Attack by *Dendroctonus ponderosae* on lodgepole pines baited on June 17–19, 1981, with candidate semiochemicals, Diamond S Ranch, Pavillion, B.C.

Treatment	Respective release rates (mg/day)[a]	No. trees baited	No. trees attacked[b]		No. trees mass attacked[b]		$\bar{X}$ attack density/m^2 [c]	
			August 21	September 18	August 21	September 18	August 21	September 18
Blank control	—	15	5A	6A	0A	4A	27.5A	46.9A
3C, tV	14, 0.4	15	13B	14B	8BCD	12BCD	59.4A	89.4AB
3C, tV, 3C-ol	14, 0.4, 0.4	14	9AB	9A	6BC	7B	75.6AB	102.5AB
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.05	15	14B	14B	6B	11BC	50.0A	110.0AB
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.14	14	14B	14B	12DE	13CD	107.5B	121.9AB
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.37	15	15B	15B	13DE	13CD	139.4C	181.9B
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 1.26	15	15B	15B	14E	15D	135.6C	161.9B

[a]Release devices and rates as in Conn *et al.* (1983).
[b]Numbers within a column followed by same letter not significantly different, Newman–Keuls test modified for testing frequencies, $P < 0.05$.
[c]Means within a column followed by same letter not significantly different, Newman–Keuls test, $P < 0.05$.

TABLE 6. Comparison of attack by *Dendroctonus ponderosae* on lodgepole pines >20 cm dbh within 5- and 10-m radii of trees baited with semiochemicals, Diamond S Ranch, Pavillion, B.C., June 17 − September 18, 1981

Treatment on baited trees	Respective release rates (mg/day)[a]	No. of trees assessed		% of trees attacked[b]		% of trees mass attacked[b]		$\bar{x}$ attack density/m[2c]	
		Within 5 m	Within 5−10 m	Within 5 m	Within 5−10 m	Within 5 m	Within 5−10 m	Within 5 m	Within 5−10 m
Blank control	—	40	62	50.0A	54.8AB	40.0A	43.5A	89.9	106.6
3C, tV	14, 0.4	36	71	72.2AB	53.5A	58.3AB	45.1A	101.8	112.6
3C, tV, 3C-ol	14, 0.4, 0.4	33	77	72.7AB	68.8AB	69.7AB	48.1AB	121.9	89.4
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.05	48	95	60.9AB	57.8AB	43.5AB	48.4AB	80.8	81.6
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.14	38	86	68.4AB	72.1AB	57.9AB	57.0AB	101.9	96.0
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 0.37	32	75	87.5B	69.3AB	78.1B	58.7AB	124.7	105.8
3C, tV, 3C-ol, eB	14, 0.4, 0.4, 1.26	51	81	78.4B	79.0B	62.1AB	69.7B	105.2	108.7

[a]Release devices and rates as in Conn *et al.* (1983).
[b]Percentages within a column followed by same letter not significantly different, Newman−Keuls test modified for testing frequencies, $P < 0.05$.
[c]No significant differences between attack densities for either position, ANOVA, $P > 0.05$.

high *D. ponderosae* population appeared to compensate in part for the lack of *exo*-brevicomin in the bait (Table 4). Similar potential has been demonstrated for the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, which was induced to attack an estimated 8000 trees, 89% of which were within 40.2 m (two chains) of Douglure-baited trees (Ringold *et al.* 1975). This technique might be used to contain an infestation within a predesignated cutblock or to draw beetles into an area to be logged. In either case the beetles would be removed by logging and presumably killed at the mill site.

Attack dynamics

The diameter distribution of unbaited trees within 10 m of the treatment trees was very different in two experimental areas. At the Diamond S Ranch (Fig. 2), there was a diameter distribution typical of a stand in which an outbreak was likely to occur (Cole *et al.* 1976; Cole and Amman 1980). Susceptibility is indicated by the relatively large proportion of trees which were >10 cm dbh. The curve is slightly skewed to the right, because the few trees that were <10 cm dbh were not measured. At Harold Price Creek, the hazard is extreme (Fig. 2). The majority of the trees are over 20 cm dbh and over 11% are over 40 cm dbh.

The diameter distributions of attacked trees in both locations roughly follow the diameter distributions of all trees except that they reflect the preference of the beetles for larger diameter trees (Fig. 2).

The two locations apparently sustain very different population levels. At the Diamond S. Ranch, over 60% of the trees in each diameter class >20 cm dbh were attacked, with a high 84.6% of the trees attacked in the 32.1−34 cm dbh class (Fig. 2). This attack rate indicates that in 1981 the outbreak was at its peak. At Harold Price Creek, only about 10% of the trees in any diameter class were attacked, except for a 23.2% attack rate in trees over 40 cm dbh (a slightly inflated rate because of the grouping of over 11% of all trees into that class). This situation suggests a suboutbreak population that is ready to explode. Production of brood beetles can vary from 300 in trees 20.3−22.9 cm dbh (fewer beetles than necessary to mass attack and kill a tree of the same size) to over 18 000 in trees >45.7 cm (Cole and Amman 1969, 1980; Klein *et al.* 1978). The trees >40 cm dbh at Harold Price Creek should produce well over three times the number of beetles necessary to mass attack and kill trees of the same size (Cole and Amman 1980). Thus, if unchecked, the infestation could increase several fold each year.

At both locations, there was a positive linear relationship between dbh and attack density (Fig. 3). These relationships are similar to those observed previously (Parker and Stevens 1979). The increases in diameter and attack density undoubtedly correspond to increases in phloem thickness (Cole and Amman 1980) and brood production (Cole and Amman 1969; Amman 1972; Amman and Pace 1976; Cole 1978).

There are two possible hypotheses which account for the increased attack density with increasing diameter. One is that beetles simply respond preferentially to silhouettes of larger diameter. The other is that even if beetles attack larger diameter trees at the same initial density as smaller diameter trees, greater amounts of attractive pheromone will be produced per tree, attracting correspondingly more beetles. If the latter hypothesis is valid, a trap tree of a fairly small diameter might be made more effective by baiting it with semiochemicals released at a rate expected from a much larger diameter tree. However, if there is a true preference for larger diameter trees as Rasmussen's (1972) data suggest, only trees within the preferred diameter

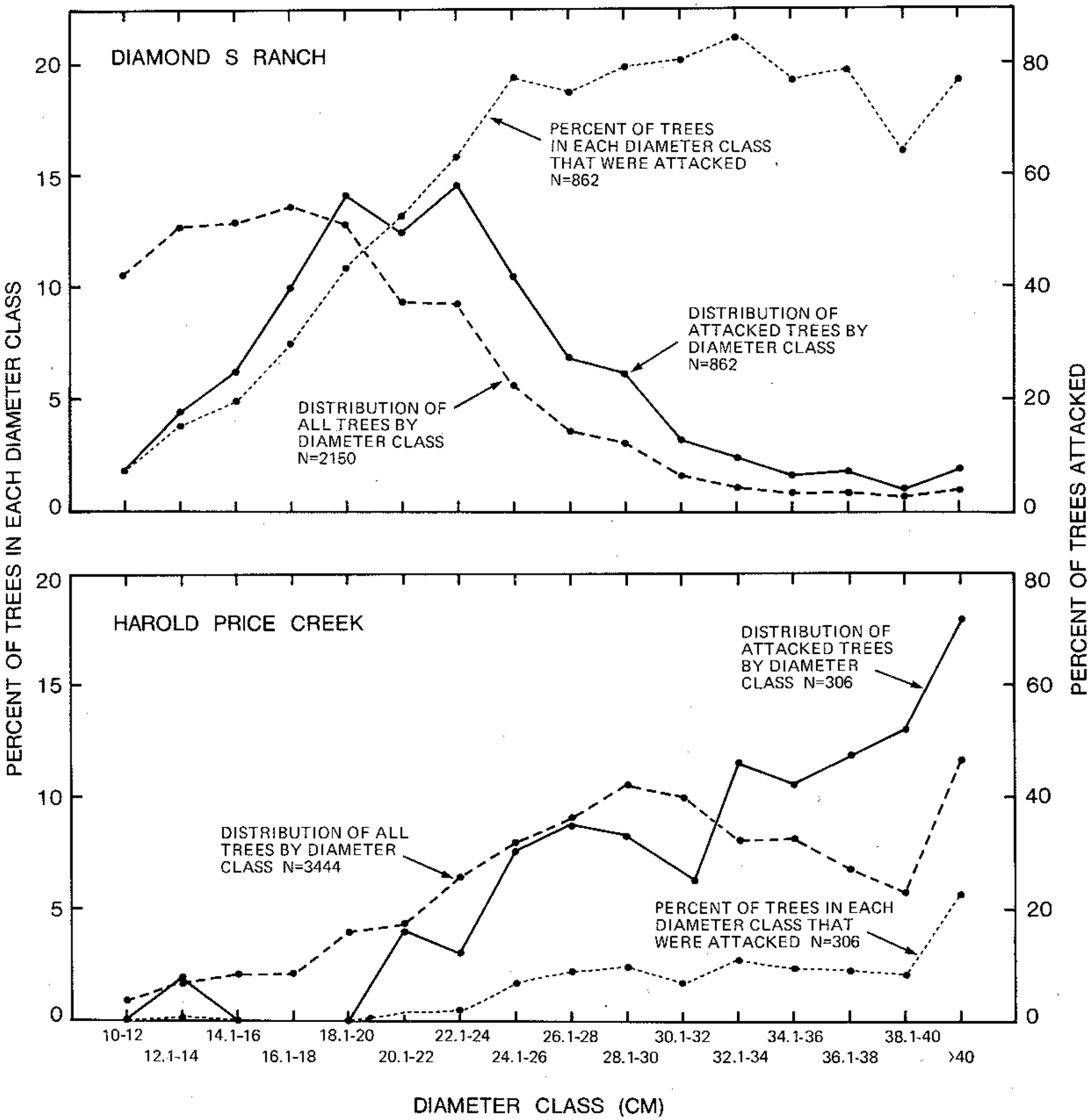

FIG. 2. Distribution by diameter class of unbaited, unattacked trees and trees attacked by *Dendroctonus ponderosae* (left margin) compared with the percent of trees in each diameter class that were attacked (right margin). Diamond S Ranch, Pavillion, B.C., June–September 1981, and Harold Price Creek, near Smithers, B.C., June–October 1981.

range should be baited.

The results of this study corroborate those of Conn *et al.* (1983) obtained in trapping experiments. Both *trans*-verbenol and *exo*-brevicomin are verified as aggregation pheromones for *D. ponderosae* in British Columbia. The monoterpene α-pinene was inferior and myrcene superior as a synergist for the pheromones. However, the baited-tree studies in 1981 failed to confirm the apparent early promise that 3-caren-10-ol was a highly active aggregation pheromone. The data definitely suggest that applied research on the use of semiochemicals to contain *D. ponderosae* infestations and to attract beetles to lethal trap trees should be vigorously pursued.

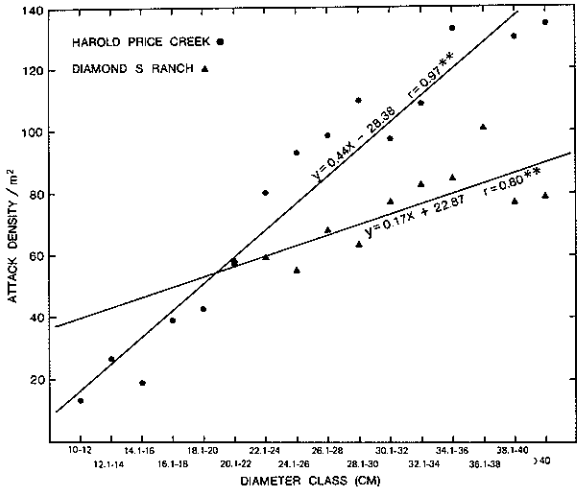

FIG. 3. Relationship between diameter of unbaited, lodgepole pines attacked by *Dendroctonus ponderosae* and attack density. Diamond S. Ranch, Pavillion, B.C., June–September 1981, 862 trees, and Harold Price Creek, near Smithers, B.C., June–October 1981, 306 trees.

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ALEXANDER, N. E., J. H. BORDEN, and J. M. VAKENTI. 1976. A pest management study of a mountain pine beetle outbreak in Tree Farm License Number 9. Simon Fraser Univ. Pest Manage. Pap. No. 8.

AMMAN, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. **65**: 138–140.

AMMAN, G. D., and V. E. PACE. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. U.S. Dep. Agric. For. Serv. Res. Note INT-209.

BEDARD, W. D., and D. L. WOOD. 1974. Programs utilizing pheromones in survey or control. Bark beetles—the western pine beetle. *In* Pheromones. *Edited by* M. C. Birch. North Holland Publ. Co., Amsterdam. pp. 441–449.

BILLINGS, R. F., R. I. CARA, 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.

CAHILL, D. B. 1978. Cutting strategies as control measures of the mountain pine beetle in lodgepole pine in Colorado. *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. Univ. Idaho, Moscow, ID, and U.S. Dep. Agric. For. Serv., Ogden, UT, and Washington, DC. pp. 188–191.

COLE, W. E. 1978. Management strategies for preventing mountain pine beetle epidemics in lodgepole pine stands: based on empirical models. *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. Univ. Idaho, Moscow, ID, and U.S. Dep. Agric. For. Serv., Ogden, UT, and Washington, DC. pp. 87–97.

COLE, W. E., and G. D. AMMAN. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. U.S. Dep. Agric. For. Serv. Res. Note INT-95.

——— 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part I: course of an infestation. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-89.

COLE, W. E., G. D. AMMAN, and C. E. JENSEN. 1976. Mathematical models for the mountain pine beetle – lodgepole pine interaction. Environ. Entomol. **5**: 11–19.

CONN, J. E. 1981. Pheromone production and control mechanisms in *Dendroctonus ponderosae* Hopkins. M.Sc. thesis, Simon Fraser University, Burnaby, B.C.

CONN, J. E., J. H. BORDEN, B. E. SCOTT, L. M. FRISKIE, H. D. PIERCE, JR., AND A. C. OEHLSCHLAGER. 1983. Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae*, in British Columbia: field trapping studies. Can. J. For. Res. **13**: 320–324.

KLEIN, W. H., D. L. PARKER, and C. E. JENSEN. 1978. Attack, emergence, and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. Environ. Entomol. **7**: 732–737.

MCKNIGHT, R. C. 1979. Differences in response among populations of *Dendroctonus ponderosae* Hopkins to its pheromone complex. M.Sc. thesis, University of Washington, Seattle, WA.

PARKER, D. L., and R. E. STEVENS. 1979. Mountain pine beetle infestation characteristics in ponderosa pine, Kaibab Plateau, Arizona, 1975–1977. U.S. Dep. Agric. For. Serv. Res. Note RM-367.

PITMAN, G. B. 1971. *trans*-Verbenol and alpha pinene: their utility in manipulation of the mountain pine beetle. J. Econ. Entomol. **64**: 426–430.

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. Univ. Idaho, Moscow, ID, and U.S. Dep.

Agric. For. Serv., Ogden, UT, and Washington, DC. pp. 165–181.

RASMUSSEN, L. A. 1972. Attraction of mountain pine beetles to small-diameter pines baited with *trans*-verbenol and alpha-pinene. J. Econ. Entomol. **63**: 1396–1399.

RICHERSON, J. V., F. A. MCCARTY, and T. L. PAYNE. 1980. Disruption of southern pine beetle infestations with frontalure. Environ. Entomol. **9**: 90–93.

RINGOLD, G. B., P. J. GRAVELLE, D. MILLER, M. M. FURNISS, and M. D. MCGREGOR. 1975. Characteristics of Douglas-fir beetle infestation in northern Idaho resulting from treatment with Douglure. U.S. Dep. Agric. For. Serv. Res. Note INT-189.

RUAULT, R. E. 1981. Mountain pine beetle (East Kootenays). Paper presented at public meeting of B.C. Forest Pest Review Committee, Feb. 17, 1981, Vancouver, B.C.

RUDINSKY, J. A., M. E. MORGAN, L. M. LIBBEY, and T. B. PUTMAN. 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. 1983. 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.

SAFRANYIK, L., D. M. SHRIMPTON, and H. S. WHITNEY. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Environ. Can. For. Serv. For. Tech. Rep. No. 1.

SHRIMPTON, D. M. 1973. Extractives associated with wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. Can. J. Bot. **51**: 527–534.

STERNER, T. E., and A. G. DAVIDSON (*Editors*). 1981. Forest insect and disease conditions in Canada 1980. Environ. Can. Can. For. Serv. For. Inst. Dis. Surv., Ottawa.

WHITNEY, H. S., L. SAFRANYIK, S. J. MURARO, and E. D. A. DYER. 1978. In defense of the concept of direct control of mountain pine beetle populations in lodgepole pine: some modern approaches. *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. Univ. Idaho, Moscow, ID, and U.S. Dep. Agric. For. Serv., Ogden, UT, and Washington, DC. pp. 159–164.