

Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in response to their antiaggregation and aggregation pheromones

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Deployment of verbenone release devices at 10-m centres significantly reduced the percent of available lodgepole pines (*Pinus contorta* Dougl. var. *latifolia* Engelm.) that were mass attacked by mountain pine beetles (*Dendroctonus ponderosae* Hopkins) in 50 × 150 m subplots flanked on each side by identical subplots, regardless of whether the flanking plots were baited with tree baits or left untreated. Verbenone treatment also increased the percent of unsuccessful attacks (<31.25 attacks/m²) in the central subplot compared with when the central subplot was left untreated. Tree baits, composed of *trans*-verbenol, *exo*-brevicomin, and myrcene, applied in flanking subplots did not affect significantly the percent of trees mass attacked nor the attack density. However, assuming a 2:1 expected ratio of attacks in the two flanking subplots over the central subplot, χ^2 -tests indicated that the attack distribution was consistently altered only when both verbenone and aggregation pheromones were applied. This study suggests that a "push-pull" tactic using aggregation and antiaggregation pheromones may be feasible for managing this destructive pest.

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La mise en place de systèmes d'émission de verbénone distancés de 10 m diminue significativement la proportion de pins de Murray (*Pinus contorta* var. *latifolia* Engelm.) attaqués par le dendroctone du pin à bois lourd (*Dendroctonus ponderosae* Hopkins) dans des sous-parcelles de 50 × 150 m bordées de chaque côté par des sous-parcelles identiques, quelle que soit la présence ou l'absence d'appât dans les sous-parcelles adjacentes. Le traitement à la verbénone augmenta aussi la proportion d'attaques infructueuses (<31,25 attaques/m²) dans les sous-parcelles centrales comparativement aux sous-parcelles centrales non traitées. L'application de *trans*-verbénol, d'*exo*-brévicomine et de myrcène sur des arbres situés dans les sous-parcelles adjacentes n'influe pas de façon significative la proportion d'arbres attaqués et la densité des attaques. Néanmoins, en assumant un ratio anticipé d'attaque de 2 pour 1 dans les deux sous-parcelles adjacentes comparativement à la sous-parcelle centrale, les tests de χ^2 ont montré que la distribution des attaques était modifiée de façon appréciable seulement lorsqu'on appliquait à la fois les phéromones d'agrégation et la verbénone. Cette étude indique que l'utilisation de la tactique «attire-repousse» à l'aide de phéromones d'agrégation et d'anti-agrégation pourrait être praticable pour gérer ce ravageur d'importance.

[Traduit par la rédaction]

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the most destructive bark beetle in western North America (Furniss and Carolin 1977). In the western United States and British Columbia this insect annually kills millions of pine trees, particularly lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.).

Attractive tree baits, composed of *trans*-verbenol, *exo*-brevicomin, and myrcene, are now utilized operationally (Borden and Lindgren 1988; Borden 1990) primarily to contain and concentrate populations in stands scheduled for harvesting after the beetles emerge from infested trees and disperse. Borden *et al.* (1983) demonstrated that it is possible to shift infestations, i.e., draw beetles from one infested stand to an adjacent stand, using tree baits, but the effectiveness of this tactic has never been demonstrated consistently.

The antiaggregation pheromone verbenone has shown promise in reducing mortality caused by mountain pine beetle in lodgepole pine stands (Amman *et al.* 1989, 1991; Lindgren *et al.* 1989; Gibson *et al.* 1991; Shea *et al.* 1992). Even though mortality is not totally eliminated, the use of verbenone may be feasible in areas where some mortality can be tolerated,

but harvesting is not permissible, such as in riparian zones, parks, and wildlife corridors.

Borden and Lindgren (1988) suggested that the combined use of antiaggregation and aggregation pheromones may be the most operationally feasible tactic. Such an application would be desirable in situations such as where an unlogged buffer zone (leave strip) along a stream must be preserved adjacent to or within an area scheduled for harvesting. Payne and Billings (1989) tested the combined use of verbenone and an aggregation pheromone, frontalin, for disrupting the growth of spot infestations of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) with limited success.

Our objective was to evaluate the effect of verbenone and aggregation pheromones, alone and in combination, on mortality caused by mountain pine beetle of lodgepole pine trees in simulated leave strips.

Materials and methods

The experiment was conducted in south central British Columbia in predominantly lodgepole pine stands, with minor components of Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies*

TABLE 1. Percent of available trees attacked and mass attacked, and percent of attacked trees pitched out in central and flanking subplots

Subplot position	Treatment	Percent of available trees ($\bar{x} \pm 1$ SE)		Percent of attacked trees pitched out ($\bar{x} \pm$ SE)
		Lightly attacked	Mass attacked	
Central	Control	13.4 \pm 11.8		
	Baits only	8.5 \pm 7.5	18.1 \pm 14.6a	38.8 \pm 13.0bc
	Verbenone only	6.0 \pm 4.1	20.9 \pm 12.8a	30.2 \pm 14.6c
	Baits + verbenone	7.9 \pm 4.5	6.6 \pm 8.1b	64.6 \pm 29.6a
Flanking	Control	12.3 \pm 7.2	9.0 \pm 9.3b	58.6 \pm 21.7ab
	Baits only	12.3 \pm 6.6	18.8 \pm 11.4ab	37.4 \pm 9.0ab
	Verbenone only	7.5 \pm 4.5	30.3 \pm 20.7a	31.3 \pm 9.2b
	Baits + verbenone	11.9 \pm 4.7	12.4 \pm 12.1b	42.8 \pm 13.2a
			26.5 \pm 11.2a	30.1 \pm 9.0b

NOTE: Within columns and subplot position, means followed by the same letter are not significantly different; analysis of variance, followed by Student-Newman-Keuls test ($p < 0.05$). There were no significant differences among treatments in percent of available trees lightly attacked.

lasiocarpa (Hook.) Nutt.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and quaking aspen (*Populus tremuloides* Michx.).

Seven replicates, each consisting of four 150 \times 150 m plots subdivided into three 50 \times 150 m subplots (Fig. 1), were established. Mountain pine beetle infestation levels (previous year's attacks, $\bar{x} \pm 1$ SE) were 19.0 \pm 12.3% in central subplots and 18.1 \pm 14.9% in flanking subplots. Diameters ($\bar{x} \pm 1$ SE) at breast height (DBH, 1.3 m above ground) of lodgepole pines were 20.1 \pm 3.6 cm in central subplots and 20.6 \pm 2.8 cm in flanking subplots. Available susceptible pine densities (>15 cm DBH, $\bar{x} \pm$ SE) were 324.6 \pm 148.6 trees/ha in central subplots and 367.3 \pm 200.0 trees/ha in flanking subplots. Four replicates were laid out from 13 to 17 June 1988 at Spukunne Creek, about 20 km northeast of Princeton, British Columbia. The remaining three replicates were laid out from 20 to 23 June 1989, two east of Penticton, British Columbia (Chute Lake and Upper Carmi Road), and one west of Princeton (Dry Gulch). Each replicate was a randomized complete block with four treatments: (i) untreated central and flanking subplots (control), (ii) untreated central subplot and three tree baits in each flanking subplot (baits), (iii) 75 verbenone bubble caps in the central subplot and untreated flanking subplots (verbenone), and (iv) 75 verbenone bubble caps in the central subplot plus three tree baits in each flanking subplot (verbenone + baits) (Fig. 1). Replicates and plots within replicates were separated by a minimum of 100 m.

Treatments were applied 11–12 July 1988 and 11–13 July 1989. Three tree baits were applied at 50-m centres along the longitudinal centre line of each of the flanking subplots (Fig. 1). They were affixed at maximum reach from the ground on the north sides of susceptible (≥ 20 cm DBH) lodgepole pines. The baits released the aggregation pheromones 83% (–) and 17% (+) *trans*-verbenol (chemical purity 87%, 13% *cis*-verbenol) at 1 mg/24 h, and racemic *exo*-brevicomin (chemical purity 96.7%) at 0.2 mg/24 h, and the host monoterpene myrcene (chemical purity 92.5%) at 9 mg/24 h.¹ In the central subplots, bubble caps containing 84% (–) and 16% (+) verbenone (chemical purity 98.6%) were also affixed at maximum reach from the ground on the north sides of available trees or other objects on a 10 \times 10 m grid (75 bubble caps per subplot). Each bubble cap released verbenone at about 5 mg/24 h, giving a release rate of 0.5 g/ha per 24 h. Actual release rates in the field are temperature dependent.

Assessments were done by a 100% cruise on 20–22 September 1988, 20–21 and 26–28 September 1989, and 22 October 1989. The numbers of red (previous year's attack), newly attacked, and

unattacked trees were tallied, and attack densities of all newly attacked trees were recorded from the east and west sides of the trees in 20 \times 40 cm areas (0.16 m² in total). The data were expressed as percent of available trees lightly attacked (<31.25 attacks/m², assumed to survive), percent of available trees mass attacked (≥ 31.25 attacks/m², assumed to be killed), and percent of attacked trees pitched out, calculated as

$$\frac{N_l}{N_l + N_m} \times 100$$

where N_l and N_m are number of trees lightly attacked and mass attacked, respectively. The conservative assumption that trees with <31.25 attacks/m² would survive was based on a threshold of 40 attacks/m² needed to kill a lodgepole pine (Raffa and Berryman 1983).

The data were transformed as $x' = \arcsin \sqrt{x}$ before analysis of variance and the Student-Newman-Keuls test (Zar 1984). Central and flanking subplots were analyzed separately. To compare the levels of attack in central and flanking subplots, the ratios of number of attacked trees in the flanking subplots over the central subplots were analyzed by χ^2 -tests. Independence among the replicates was first tested by a row \times column contingency table. This analysis revealed interaction for both lightly attacked trees ($p < 0.05$) and mass-attacked trees ($p < 0.001$). Therefore, each treatment within a replicate was tested independently against the null hypothesis that the ratio of attacked trees in the flanking subplots over the central subplot would be 2:1.

Results

There was a significant treatment effect for both central and flanking subplots for percent of available trees mass attacked ($p = 0.01$ and 0.02 , respectively) and percent pitch out ($p = 0.02$ and 0.03 , respectively), but not for percent of trees lightly attacked ($p = 0.46$ and 0.19 , respectively) (Table 1).

Central subplots

There was a significantly lower percent of mass-attacked trees in subplots treated with verbenone than in control subplots (Table 1). The verbenone treatment had a significantly higher percent of pitch outs than control and baits treatments, but was not different from the verbenone + baits treatment. The verbenone + baits treatment had a significantly higher percent of pitch outs than the baits treatment, whereas the control was not different from either the baits or the verbenone + baits treatment.

¹All release rates were determined at 24°C. Release devices and chemicals were obtained from Phero Tech Inc., 7572 Progress Way, Delta, B.C., Canada V4G 1E9.

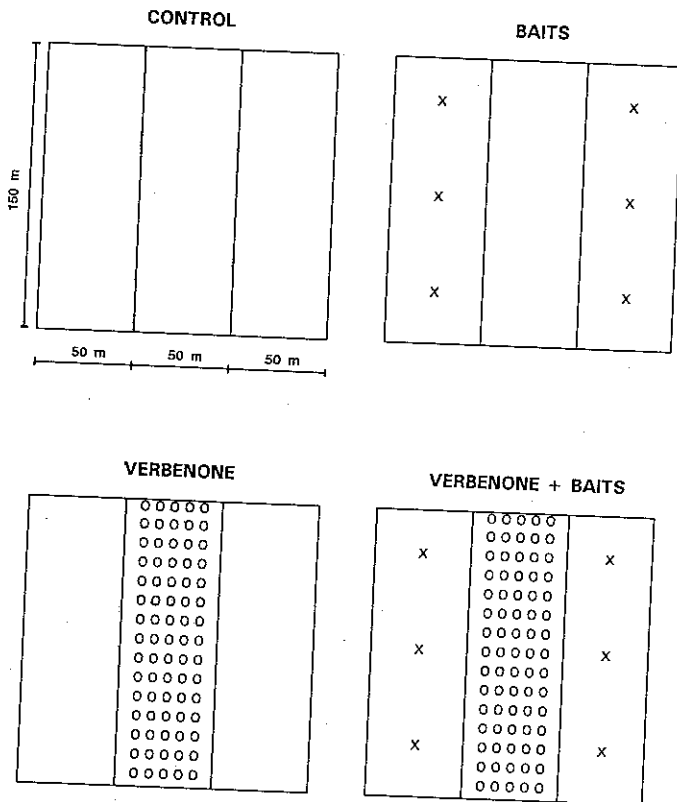


FIG. 1. Graphic representation of plot and subplot configuration, and deployment of antiaggregation and aggregation pheromones by treatment in the displacement and aggregation experiment for the mountain pine beetle. X, Tree bait; O, verbenone bubble cap.

Flanking subplots

There was a significantly lower percent of mass attacks and a higher percent of pitch outs in the verbenone treatment than in the baits treatments, whereas the control treatment was not different from any other treatment (Table 1).

Attack densities

Attack densities did not differ significantly among treatments, but approached significance in the central subplots (Table 2).

Attack distribution

The χ^2 -tests of all replicates showed that the ratio of the number of mass-attacked trees in the two flanking subplots over the the central subplot was consistently higher than 2:1 only for the verbenone + baits treatment (Table 3). The mass-attack ratio was consistently >2 for the verbenone treatment, but not significantly so (Table 3). There was no consistent pattern in the mass-attack ratio for either the control or the baits treatment. The ratio of lightly attacked trees in the two flanking subplots over the central subplot was not consistently affected by any treatment, although for the verbenone + baits treatment the ratio was always >2 (range 2.08–10.18).

Discussion

The results support the findings of earlier studies (Amman *et al.* 1989, 1991; Lindgren *et al.* 1989; Gibson *et al.* 1991; Shea *et al.* 1992), all of which showed that in most cases verbenone significantly reduces mortality caused by mountain pine beetle in lodgepole pine stands. The combination of

TABLE 2. Attack densities from flanking and central subplots

Treatment	Attack density, no./m ² ($\bar{x} \pm 1$ SE)	
	Central subplots	Flanking subplots
Control	48.1 \pm 17.4	42.5 \pm 5.9
Baits	45.6 \pm 7.3	45.6 \pm 7.3
Verbenone	27.5 \pm 20.4	40.0 \pm 16.0
Verbenone + baits	31.9 \pm 15.9	51.3 \pm 10.7

NOTE: Analysis of variance, $p = 0.07$ for central subplots and $p = 0.16$ for flanking subplots.

attractive tree baits and verbenone improved the consistency of the verbenone effect in the central subplot relative to flanking subplots (Table 3), but placing baits in flanking subplots did not cause lower mortality (mass-attacked trees) in the central subplots than did verbenone alone (Table 1). Similarly, mortality in the baited flanking subplots was increased by treating the central subplot with verbenone. It appears from these results that there was no interaction between verbenone and baits when deployed in adjacent subplots, but that each treatment acted independently within an area of deployment. This lack of interaction may have been due partially to the small plots used in this experiment, since the bait treatment in flanking subplots did not cause a significant increase in mortality (Table 1). The efficacy of tree baits when deployed as a grid over a large area has been well documented previously (Gray and Borden 1989).

The lack of a major effect by verbenone on attack density (Table 2) is consistent with earlier observations. Since beetles produced pheromones largely regulate attack density on trees, aggregation has been initiated on a tree, this lack of effect of verbenone is to be expected. However, the increased percentage of lightly attacked trees in verbenone-treated subplots indicates that the antiaggregation pheromone interferes with the ability of "pioneer" beetles to attract conspecifics to initiate the mass aggregation necessary to overcome tree defence. Consequently, verbenone can be expected to work optimally at low population densities ($\leq 10\%$ of available trees infested). At high population densities the probability of multiple pioneer beetles attacking the same tree will increase, leading to sufficient aggregation pheromone being released to override the effect of verbenone.

A displacement–attraction tactic using verbenone and attractive tree baits may be a feasible management tactic. In our experiment, the deployment of three tree baits in a line in each of our flanking subplots may have been too low to affect beetle behavior efficiently throughout the subplot. To determine the feasibility of this tactic, it must be tested in an operational setting, where larger blocks are used, and tree baits would be applied on a grid, possibly only on one side of the verbenone-treated area.

Safranyik *et al.* (1989, 1992) showed that mountain pine beetles generally disperse upwind or downwind along the predominant wind angle. Flanking subplots in our experiment were largely oriented across the predominant wind angle from the central subplots. Thus, the orientation of subplots may have been suboptimal in our experiment, contributing to the lack of interaction between subplot treatments.

TABLE 3. Ratios of mass-attacked trees in flanking subplots over central subplots, total number (N) of mass-attacked trees (≥ 31.25 attacks/m²), and probabilities (p) from χ^2 -tests of independence for individual treatment ratios

	Replicate							$\bar{x} \pm 1$ SE
	1	2	3	4	5	6	7	
Control								
Ratio	3.5	1.7	3.5	7.0	2.1	1.7	2.7	3.2 \pm 1.9
N	189	46	95	184	162	61	92	118.4 \pm 59.1
p	<0.005	ns	<0.025	<0.005	ns	ns	ns	
Baits treatment								
Ratio	1.6	1.6	3.8	2.6	2.5	7.6	3.5	3.3 \pm 2.1
N	442	92	296	213	145	94	157	205.6 \pm 126.2
p	<0.025	ns	<0.005	ns	ns	<0.005	<0.005	
Verbenone treatment								
Ratio	4.0	∞^a	13.8	4.4	20.3	4.0	3.0	7.1 \pm 7.2
N	199	15	89	107	85	35	16	78.0 \pm 65.0
p	<0.005	<0.01	<0.005	<0.005	<0.005	ns	ns	
Verbenone + baits treatment								
Ratio	3.9	24.6	11.2	6.0	17.3	4.6	∞^a	9.7 \pm 8.7
N	229	128	171	204	55	189	117	156.1 \pm 59.8
p	<0.005	<0.005	<0.005	<0.005	<0.005	<0.005	<0.005	

NOTE: Assuming an expected ratio of 2:1, a ratio of <2 indicates more mass-attacked trees in the central subplot than in the flanking subplots, whereas a ratio of >2 indicates fewer mass-attacked trees in the central subplot than in the flanking subplots. ns, Not significant.

^aNot included in the calculation of the mean.

Recent studies on several species of bark beetles have indicated that the effect of verbenone may be greatly enhanced by the addition of a pheromone from a competing species, e.g., racemic ipsdienol for *Dendroctonus brevicomis* LeConte and *Ips paraconfusus* Lanier (Paine and Hanlon 1991), and ipsenol for *Ips pini* (Say) (Borden *et al.* 1992). It is possible that ipsdienol and lanierone, the major aggregation pheromones of *I. pini* (Stewart 1975; Birch *et al.* 1980; Teale *et al.* 1991), would enhance the effect of verbenone. Nevertheless, our experiment confirms that verbenone treatments can reduce mortality caused by mountain pine beetle in lodgepole pine stands. Operational-scale experiments are required to determine whether the application of aggregation pheromones in adjacent blocks improves the efficacy of verbenone.

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