Potential of Verbenone for Reducing Lodgepole and Ponderosa Pine Mortality Caused by Mountain Pine Beetle in High-Value Situations[1]

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Abstract: Antiaggregative pheromones of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae) have been known for a number of years, but only recently have they been used in efforts to minimize infestation in stands of trees. Early tests in lodgepole pine (*Pinus contorta* Douglas) significantly reduced infestation in verbenone-treated stands. However, subsequent tests gave nonsignificant results. In ponderosa pine (*Pinus ponderosa* Lawson), significant reductions in beetle infestation were never attained with verbenone. Some possible reasons for the variable results are offered, with some suggestions for future research in reducing tree losses with antiaggregative pheromones.

Environmentally acceptable strategies are needed to protect high-value trees and stands (such as those along roads, campgrounds, riparian areas, and lakeshores) from infestation by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), of the family Scolytidae (Schmitz 1989). Chemical insecticides are currently available to prevent attacks on high-value trees. Insecticides sprayed on the bole from ground level to the lower crown just before beetle emergence will prevent attacks for up to 2 years (Gibson and Bennett 1985; McCambridge 1982; Page and others 1985; Shea and McGregor 1987; Smith and others 1977). However, these preventive sprays also may affect nontarget insects, other invertebrates, and humans. Recent developments in the commercial production of mountain pine beetle (MPB) pheromones have led pest managers to consider antiaggregating pheromones as a substitute for preventive sprays for high-value trees.

Verbenone (4,6,6-trimethylbicyclo[3.1.1]-hept-3-en-2-one) was first isolated and identified from the mountain pine beetle pheromone complex by Pitman and others (1969), using the hindguts of newly emerged and feeding female mountain pine beetle. It was also identified from air passed over emergent male/female pairs (Rudinsky and others 1974). The first evidence of the antiaggregative properties of verbenone against the mountain pine beetle resulted when laboratory and field bioassays of (-)-verbenone inhibited mountain pine beetle response to selected host- and beetle-produced volatiles (Ryker and Yandell 1983). Verbenone previously exhibited antiaggregative properties against southern pine beetle (*Dendroctonus frontalis* Zimmerman) when used in traps (Renwick and Vite 1970), and also reduced landing on trees (Richerson and Payne 1979). The addition of verbenone to attractive lures also reduced the catch of western pine beetle (*D. brevicomis* LeConte) (Bedard and others 1980) response of *D. adjunctus* (Blandford) to attractive baits (Livingston and others 1983) and inhibits the response of *Ips paraconfusus* (Lanier) (Byers and Wood 1981) and *I. typographus* (L.) (Bakke 1981; Schlyter and others 1988).

Role of Verbenone in Host Colonization

The principal antiaggregative semiochemical regulating mountain pine beetle response to its host is (-)-verbenone (Borden and others 1987; Libbey and others 1985; Ryker and Yandell 1983). Verbenone originates from three sources: (1) female beetles (Pitman and others 1969); (2) auto-oxidation of alpha pinene to *cis*- and *trans*-verbenol, then to verbenone (Hunt and Borden 1989; Lindgren and Borden 1989); and (3) oxidation of *cis*- and *trans*-verbenol by microorganisms (primarily yeasts) associated with the beetle (Hunt and Borden 1989; Lindgren and Borden 1989). The following conceptual model proposed by Borden and others (1987) summarizes what is known about the sources of verbenone, the onset of production in relation to the sequence of attack, and its probable role in regulating the duration and density of attack.

At the onset of attack by female mountain pine beetle, volatiles (including the host monoterpenes alpha-pinene and myrcene, together with female-produced *trans*-verbenol) attract additional beetles to the tree. As males reach the tree, they release *exo*-brevicomin, which initially attracts primarily females, thereby enhancing the level of attraction. As additional males colonize the tree, concentrations of *exo*-brevicomin increase and are augmented by the male-produced antiaggregant, frontalin. Simultaneously, concentrations of the aggregative components, *trans*-verbenol, and the host monoterpenes begin to decline. At this stage in colonization, the concentration of verbenone produced (1) by auto-oxidation of the host monoterpene, alpha-pinene, to *cis*- and *trans*-verbenol and then to verbenone and (2) by conversion of *cis*- and *trans*-verbenol to verbenone by microorganisms deter additional beetles from attacking the focus tree. The effect of these antiaggregants limits attacks to a density that ensures survival of the ensuing brood.

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Verbenone Field Tests

Reducing Response to Attractive Traps

During summer 1986, Schmitz and McGregor (1990) conducted tests in the Wasatch National Forest in Utah to compare the number of mountain pine beetle attracted to the standard mountain pine beetle lure consisting of *trans*-verbenol, *exo*-brevicomin, and myrcene, with and without verbenone. The test was conducted in a mature lodgepole pine stand surrounded by stands in which mountain pine beetle populations were building to outbreak levels. The eight test blocks were 30 meters square and were separated from one another by 30-meter intervals. Funnel traps were hung at each of the four corners of a block. The four treatments–MPB lure, MPB lure with verbenone, verbenone alone, and empty trap–were randomly assigned to each of four positions. Effectiveness of verbenone as an antiaggregant was assessed by the number of mountain pine beetle caught, by treatment.

They caught a total of 1,130 mountain pine beetle, distributed among the four treatments as follows:

	Number	Percent
MPB lure alone	1,082	95.8
MPB lure with verbenone	19	1.7
Verbenone alone	7	0.6
Unbaited trap	22	.9
Total	1,130	100.0

Overall, the addition of verbenone to the synthetic MPB lure reduced the catch by 98 percent.

A similar test in British Columbia by Borden and others (1987) showed that when verbenone was released in funnel traps in the presence of the attractive synthetic mountain pine beetle lure, the response of males was reduced approximately 75 percent. Female response was reduced, but not significantly.

The encouraging results from these studies to suppress catch of mountain pine beetle in traps prompted tests to determine the efficacy of verbenone for reducing mountain pine beetle infestation in Rocky Mountain lodgepole and ponderosa pine stands.

Tests in Lodgepole Pine Stands

Field studies[3] to test the efficacy of verbenone in reducing mountain pine beetle infestation were conducted in Idaho, Montana, and British Columbia, starting in 1987. In Idaho, a 2 × 2 factorial design, replicated four times, was used to test verbenone in the presence of the mountain pine beetle tree bait (Amman and others 1989). Treatments consisted of (1) MPB tree bait, (2) verbenone, (3) MPB tree bait and verbenone, and (4) check. Verbenone was eluted from the standard plastic bubble cap at 5 mg/24 h/capsule at 25°C. Each treatment was applied individually to 1-ha plots. Five mountain pine beetle tree baits were used in each baited plot.

The three-part tree bait was stapled 2 m above ground level on the north side of a lodgepole pine 20 cm or larger d.b.h. Mountain pine beetle tree baits were placed at the center of the plot and at each cardinal direction from the center, approximately 20 m from the outside boundary of the plot.

Verbenone-treated plots had 100 verbenone bubble capsules per hectare, spaced in a grid pattern approximately 10 m apart. Each capsule contained 0.5 g of verbenone having a chemical purity of 98.6 percent and optical purity ee = (-)72 percent. In the plots treated with mountain pine beetle tree bait plus verbenone, baits and verbenone bubble capsules were distributed as described for each alone. Check plots were untreated.

Treatment effects were assessed by comparing the percentage of 1987 mountain pine beetle-infested lodgepole pine 15.2 cm d.b.h. and larger in each plot. Highly significant differences were found in percentages of infested trees among treatments. Plots having only mountain pine beetle tree baits had significantly more mass-attacked trees than other treatments. There was no significant difference among the other three treatments. Average numbers of lodgepole pine infested by mountain pine beetle were:

	Trees infested	
	MPB tree bait present	MPB tree bait absent
	pct	
Verbenone present	7.425	0.875
Verbenone absent	24.425	3.275

Verbenone in the presence of mountain pine beetle tree bait resulted in a 2.3-fold reduction in infested trees and a 2.7-fold reduction where tree baits were not used.

An examination of the percentage change in numbers of MPB-infested trees for the four treatments between 1986 and 1987 shows that only in verbenone-treated plots did an average reduction occur (-48.6 percent). In contrast, check plots showed an average increase of 64.7 percent. Changes in infestation in verbenone-treated and check plots were small when compared to baited plots, which showed an average 25-fold increase in infestation. Plots containing mountain pine beetle baits and verbenone had an average 4-fold increase in infestation. A test conducted in British Columbia also in 1987 gave similar results (Lindgren and others 1989). However, in a second test that used verbenone but no attractive baits, mountain pine beetle infestation was reduced but not significantly (Lindgren and others 1989). Shore and others (1992) showed that verbenone reduced the response of mountain pine beetle to trees baited with *exo*-brevicomin, one component of the mountain pine beetle tree bait.

Two questions arose from these tests: (1) Would a different dosage of verbenone be more effective than 100 capsules

[3]Pheromone products were obtained from Phero Tech Inc., Delta, BC, Canada. The use of trade or company names in this paper is for information only and does not imply endorsement by the USDA Forest Service.

per hectare, and (2) would mountain pine beetle be attracted into areas adjacent to verbenone-treated stands, resulting in increased numbers of infested trees in adjacent stands. These questions formed the basis for additional tests in Idaho and Montana in 1988 and 1989.

In 1988, a randomized complete block design, replicated seven times, was used to test densities of verbenone capsules of 0, 25, 49, 100, and 169 per hectare, spaced in a grid pattern within the treated plots. Plots were 1 ha in size and were located 100 m apart. Treatments within a block were randomly assigned. In 1988, the verbenone capsules were of the same design as those used in 1987.

To assess the possible attractiveness of mountain pine beetle to verbenone in stands adjacent to 1988 treatments, two 20-m-wide strips were established around each plot, and all trees infested in 1987 and 1988 were counted and tallied separately for each strip.

The 1989 test differed from the 1988 test as follows:

1. Only the dosage-response portion of the study was repeated.
2. Treatments were replicated eight times instead of seven.
3. A newly designed capsule was used, consisting of an opaque bubble with clear plastic membrane. Each capsule contained 0.8 g of verbenone.

The percentage of newly infested trees varied significantly among treatments in 1988. The four verbenone capsule treatments–25 ($\bar{x}$ = 1.80 percent), 49 ($\bar{x}$ = 0.21 percent), 100 ($\bar{x}$ = 0.51 percent), and 169 ($\bar{x}$ = 1.71 percent)–all had lower percentages of infested trees than the check ($\bar{x}$ = 5.39 percent) (Amman and others 1991).

In 1989, treatments also exhibited significant differences. The percentages of newly infested trees by treatment were: 25 ($\bar{x}$ = 3.89 percent), 49 ($\bar{x}$ = 2.52 percent), 100 ($\bar{x}$ = 0.72 percent), 169 ($\bar{x}$ = 1.58 percent), check ($\bar{x}$ = 4.93 percent). Although 49 capsules per hectare appeared to do as well as 100 capsules per hectare in 1988, mountain pine beetle infestation increased in the 49 capsules per hectare treatment in 1989 (Amman and others 1991).

Greater infestation rates in the 169 capsules per hectare treatment than in the 100 capsules per hectare treatment were observed in both 1988 and 1989 and in a similar test in Montana (Gibson and others 1991). Borden and Lindgren (1988) also noted more trees were attacked and at higher attack densities when high dosages of verbenone were used. A high concentration of verbenone may cause beetle confusion.

Studies similar to those in Idaho were conducted in Montana lodgepole pine stands in 1988 and 1989. In 1988, treatments were not significantly different. In 1989, however, treatments were significantly different and were very similar to Idaho results (Gibson and others 1991). As in the Idaho test, the 100 capsules per hectare treatment showed the greatest reduction in percent of infested trees ($\bar{x}$ = 0.3 percent), when compared to the check plots ($\bar{x}$ = 5.2 percent). The lack of significance in 1988 was attributed to the low number and poor distribution of infested trees because the average percentage of infested trees ranged between 0.2 and 2.5 when the study was installed.

Although significant results were shown in Idaho and Montana, no differences in numbers of infested trees were shown among application rates of verbenone in British Columbia (Borden and Lindgren 1988). Shore and others (1992) concluded from their study that verbenone is not repellent, because it neither significantly reduced the number of trees infested by mountain pine beetle nor lowered beetle attack densities. They stated that treating trees with verbenone does not appear to make them less attractive to mountain pine beetle than unbaited trees. However, differences in infestation among treated stands in the Idaho and Montana tests suggest a repellent action on an area basis.

In the two 20-meter-wide strips surrounding verbenone-treated blocks, the number of infested trees per hectare did not differ significantly among treatments. Beetles were expected to disperse from the plots to infest trees somewhere outside the plots, but most likely within 2 chains of the treated plot. Although none of the capsule treatments differed significantly, the trend was for fewer beetle-infested trees in strips surrounding blocks treated with verbenone than in check blocks. These data, although not significant, suggest the suppressing effect of verbenone could be extending beyond the treated plots, particularly in the 169 capsules per hectare treatment.

Tests were continued in Idaho in 1990 and 1991 to resolve the question of whether 49 capsules per hectare (the best treatment in 1988) or 100 capsules per hectare (the best treatment in 1989) would give consistent results (Rasmussen, unpublished data, Intermountain Research Station, Ogden, Utah). Surprisingly, treatments were not significantly different from check plots in either year. These results were totally unexpected, especially after previous tests demonstrated statistically significant reductions in mountain pine beetle infestation for three consecutive years.

Tests in Ponderosa Pine Stands

Although the use of verbenone to minimize infestation in the early lodgepole pine tests appeared quite promising, tests in ponderosa pine were judged not successful from the beginning. Bentz and others (1989), Gibson and others (1991), and Lister and others (1990) used methods similar to those I described for lodgepole studies in 1988 to test the effect of verbenone in ponderosa pine stands in southwestern Colorado, in western South Dakota, and in western Montana.

Mountain pine beetle infestations in these areas were in outbreak status, but the intensity of the infestations was much higher in southwestern Colorado, where over 150 trees per hectare were killed in 1988 (Bentz and others 1989). In the outbreak cycle, the Colorado area was considered at its peak. In contrast, the South Dakota area was in the early stages of an outbreak, with tree mortality averaging about 22 trees per hectare. The Montana area was intermediate, with an average of 32 infested trees per hectare.

In each area, as in the lodgepole pine tests, four replicates were used to test the five treatments: 0, 25, 49, 100, and 169 verbenone capsules per hectare. In 1988, no significant differences occurred among treatments in any of the areas. The number of mass-attacked trees in the strips surrounding each plot also were not significantly different among treatments.

In 1989, eight replicates were used to again test different densities of verbenone capsules in South Dakota and Montana. Mountain pine beetle populations had reached outbreak status, but the population trend was static in South Dakota (11.6 infested trees per hectare) and in Montana (11.0 infested trees per hectare).

In the 1988 South Dakota test, the mean numbers of infested trees were 35 per hectare for check, and 10, 14, 8, and 4, respectively, for the 25 to 169 capsule treatments (Bentz and others 1989), compared to 1989 means of 29.1 for the check and 14.4, 11.8, 7.5, and 5.6, respectively, for the verbenone treatments (Lister and others 1990). In the Montana test, mean numbers of infested trees in 1988 were 30.5 per hectare for the checks, compared to 6.0, 20.8, 11.3, and 2.3, respectively, and the 1989 results were 11.0 per hectare for the checks, and 9.5, 6.3, 7.5, and 2.5, respectively, for the 25 to 169 verbenone capsule treatments (Gibson and others 1991).

The South Dakota and Montana tests showed a downward trend in infestation rate with increased number of verbenone capsules, but the variance within treatments was so great that significant treatment effects could not be demonstrated.

Conclusions

The inconsistent results from year to year and between tree hosts of mountain pine beetle point to the need for much additional research before antiaggregative pheromones can be used effectively to reduce mountain pine beetle infestation of high-value trees. There are several possible explanations for the inconsistent results, ranging from a faulty verbenone product to genetic changes in the beetle population:

1. In the Idaho tests, the bubble capsule was judged adequate. The enantiomeric ratio of capsule contents was analyzed and found to be -80 percent.[4] Therefore, the ratio should not be a problem. Also, verbenone eluted at a rate consistent with previous tests (Rasmussen, unpublished data). However, observations in ponderosa pine suggest that some capsules do not elute at specified rates (Bentz and others 1989).

2. Stand microclimate may have changed from earlier tests because of trees killed by mountain pine beetle, particularly those of larger diameter. Dead trees may become warmer because of solar insolation and serve as chimneys that cause vertical movement of verbenone out of the stand.

3. Weather factors (particularly temperature) were considered a problem in the ponderosa pine tests (Bentz and others 1989). High temperatures may have caused above-average elution of verbenone.

4. Genetic change of mountain pine beetle (Stock and Amman 1985) related to smaller trees (in which phloem is usually thin) being infested after larger trees (in which phloem is usually thick) have been killed in prior years may have contributed to the selection of beetles that tend to ignore the verbenone signal.

Whether these or other unidentified factors are responsible, the promise of verbenone to protect high-value trees does not look as bright as we thought after the earlier tests. At best, verbenone was not completely effective in preventing mountain pine beetle infestation. Strategies that may improve verbenone effectiveness are (1) use mountain pine beetle baits in conjunction with verbenone treatments to attract beetles from stands where verbenone is deployed to stands scheduled for harvest (Borden and Lindgren 1988; Schmitz and McGregor 1990); (2) use verbenone in conjunction with other pheromones that have an aggregative effect on mountain pine beetle (Hunt and Borden 1988); and (3) use pheromones at low mountain pine beetle population levels rather than high population levels. These are the subject of current research.

[4]Chemical analysis was done by Dr. Lonne L. Sower, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR.

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