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Semiochemicals for Management of Mountain Pine Beetle: Status of Research and Application

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Abstract—Semiochemical research has led to the operational use of aggregation pheromones for management of the mountain pine beetle, *Dendroctonus ponderosae*, particularly in British Columbia. Extensive research has been conducted to investigate the use of the antiaggregation pheromone, verbenone, as a potential management tool. Initial research provided encouraging results, but more recent experiments yielded ambiguous data. Many potential problems with verbenone have been identified. Current research is investigating the use of other repellant compounds as synergists to verbenone.

The main pheromones of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, (Coleoptera: Scolytidae), have been known for many years (Borden 1982; Lindgren and Borden 1989). Advances in their synthesis and formulation in slow release devices during the past 10 years have led to considerable experimentation in operational scale applications for beetle population management and protection of stands and individual trees from infestation.

The mountain pine beetle is indigenous to the Western United States and Canada. It infests 13 species of pine native to North America (Wood 1982) as well as exotic pine species. Lodgepole pine, *Pinus contorta* Douglas, is the principal host of mountain pine beetle. Populations of the beetle periodically build up and kill most of the large dominant lodgepole pines over vast areas. The large trees usually have thick inner bark (phloem), which is the food of developing larvae, enabling good survival and high brood production. Frequency of infestations in a given area of forest appears to range from about 20 to 40 years (Roe and Amman 1970), depending on how rapidly some trees in the stand grow to large diameter and produce thick phloem, conditions conducive to buildup of beetle populations. During outbreaks, beetles may kill 70 to over 90 percent of the lodgepole pines 13 cm and larger in diameter at breast height (dbh) (McGregor and others 1987).

The mountain pine beetle usually completes one generation per year in lodgepole pine. However, 2 years may be required at high elevations and in the cooler climates of northern latitudes. New adults, which are about 5 mm long, emerge from the bark and attack live trees between late June and early September, depending on elevation, latitude, longitude, and local weather conditions (Bentz and others 1991; Rasmussen 1974; Reid 1962; Safranyik and others 1974).

The mountain pine beetle has an elaborate pheromone communication system that governs its attack behavior (Borden and others 1987; Lindgren and Borden 1989). At the onset of attack by female beetles, the host monoterpenes α-pinene and myrcene, together with female-produced *trans*- and *cis*-verbenol (Miller and Lafontaine 1991), attract primarily male beetles to the tree. As males reach the tree they release *exo*-brevicomin, which attracts primarily females, thereby enhancing the level of attraction. As additional males colonize the tree, attractiveness is reduced as concentrations of *exo*-brevicomin and frontalin increase (Borden and others 1987). Simultaneously, concentrations of the aggregation pheromones, *trans*- and *cis*-verbenol, and host monoterpenes begin to decline. At this stage in colonization, increasing concentrations of verbenone produced (1) by autoxidation of the host monoterpene, α-pinene, to *trans*- and *cis*-verbenol and then to verbenone (Hunt and others 1989), and (2) by conversion of verbenols to verbenone by microorganisms (Hunt and Borden 1989), deter additional beetles from attacking the focus tree. The effect of these antiaggregation pheromones limits attacks to a density that ensures survival of the ensuing brood. Beetles switch to adjacent trees where the process is repeated (Geiszler and Gara 1978).

Following mating, females lay eggs in irregularly alternating groups on the two sides of the vertical gallery within the phloem near the xylem. Eggs hatch in about 2 weeks and larvae feed individually in the phloem. Larval galleries usually extend at right angles to the egg galleries, thereby girdling the tree. There are four larval instars. Larvae usually pass the winter most successfully in larger instars. When mature in late May and June, larvae excavate oval cells in the phloem, lightly scoring the sapwood, where they pupate and become adults. New adults feed within the bark prior to chewing exit holes through the outer bark and then emerge to attack live trees and repeat the cycle.

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Research and Application of Aggregation Pheromones

Trapping

Detection trapping is generally done for quarantine purposes. The objective is to detect species that are perceived as potential threats to particular resources.

During epidemics there is a real risk of long range spread of mountain pine beetles. For example, mountain pine beetle appeared in the Cypress Hills area on the border of Alberta and Saskatchewan in Canada, as well as in ornamental and shelter belt pine plantations throughout southern Alberta in the 1980's (Cerezke 1989). The closest source of beetles was the Glacier National Park area in Montana and the adjacent Waterton Lakes Park in southeastern Alberta, some 200 km to the west. Introductions of mountain pine beetle to Eurasian pine forests could have potentially devastating consequences. Mountain pine beetles have been intercepted in New Zealand (Marchant and Borden 1976), demonstrating the potential of accidental introductions.

There are no programs in North America using pheromone traps for detection of the mountain pine beetle in areas outside its natural range. A limited number of traps are employed by the Forestry Commission in Great Britain for detection of mountain pine beetles (40 traps), the Douglas-fir beetle, *Dendroctonus pseudotsugae* (40 traps), and the European spruce bark beetle, *Ips typographus* (100 traps). So far no interceptions of either *Dendroctonus* species have been made (Burgess 1994).

Monitoring involves trapping with the objective of determining specific characteristics in the population dynamics of an insect species. The use of semiochemicals for monitoring bark beetle flight has been a recognized operational procedure in British Columbia for many years (Hall 1989; Province of British Columbia 1985), and several Forest Districts use pheromone-baited traps on a routine basis to determine the timing of the major mountain pine beetle flight. In the basis of this information, hauling bans from infested areas are implemented (Hall 1989; Stock 1984). No rigorous attempts at correlating catches with population densities have been made.

Mass trapping is the use of traps for actual population suppression. It was attempted for mountain pine beetles in 1984 by the U.S. Department of Agriculture, Forest Service in Montana and Idaho (Steele 1988). Lindgren funnel traps were placed in grids or clumped in infested stands. While statistical analyses of tree mortality data apparently provided some weak evidence for an effect due to the trapping, populations in all stands were generally declining during this trial. No further mass trapping attempts were made.

As with many other bark beetle species, the use of pheromone-baited traps for mountain pine beetles frequently results in extensive spillover attacks on trees near the traps. Until a more powerful attractant is identified, allowing placement of traps away from susceptible host trees, as is done in Europe for *Ips typographus* (Weslien 1992), there is probably little or no potential for mass trapping as a management tool for the mountain pine beetle.

Tree Baiting

Tree baiting was developed and refined as a management technique in British Columbia in the early 1980's (Borden 1990 and references therein). It has been operationally employed in British Columbia since the mid-1980's, and is a recognized operational procedure by the British Columbia Ministry of Forests (Province of British Columbia 1987; Hall 1989). In a recent document, extensive use of tree baiting was recommended as operational tactics for three of six mountain pine beetle management strategies in the Okanagan Timber Supply Area (Safranyik and Hall 1990). In the United States the technique has been tested (McGregor and others 1989), but has been implemented only on a very limited scale. Tree baits have been exempted from registration by the Environmental Protection Agency in the U.S., and their use is monitored in Canada while registration guidelines for so-called biorational pesticides are developed.

Tree baiting is not a control treatment in itself, but rather a tool designed to enhance the use of other direct control tactics. In fact, in the absence of harvesting or other follow-up control treatment, tree baits may exacerbate the beetle problem since both attack densities and tree mortality are increased where baits are used. In concert with silvicultural or other treatments, tree baits offer an effective means of predetermining where treatment efforts should be located; this substantially reduces the costs associated with ground probes needed to determine infestation spread (Hall 1989).

Tree baiting is normally done by ground crews during May and June, and sometimes July, the months prior to the mountain pine beetle flight. Baits are attached on the north sides of susceptible trees as high as the applicator can reach. A trained crew can bait a stand in this fashion fairly quickly.

There are four operational applications for tree baits for mountain pine beetle management: (1) detection and monitoring, (2) containment and concentration, (3) post-logging mop-up, and (4) spot suppression.

Tree baits can be used for detection and monitoring of mountain pine beetle populations. The drawback is that attacked trees must be destroyed. Nevertheless, tree baits are used for monitoring purposes in British Columbia. The Fort St. John Forest District used between 450 and 750 baits per year for this purpose between 1991 and 1993 (Hodgkinson 1993). Baits were used extensively in Alberta and Saskatchewan from 1983 to aid in the detection and monitoring of mountain pine beetle populations in lodgepole pine and limber pine stands (Cerezke 1989).

The objective of the containment and concentration tactic is to prevent dispersal of mountain pine beetles from infested stands, while maximizing immigration into and arrestment within the baited stand by beetles dispersing from surrounding areas. Baits are generally applied in a 50- by 50-m grid throughout the stand, leaving a 25-m buffer at the edge. For exceedingly large blocks, perimeter baiting may be an option. This will reduce the cost per ha by preserving baits. The objective of perimeter baiting is to prevent dispersal out of the infested block.

The objective of the post-logging mop-up tactic is to concentrate beetles left behind after harvesting. Beetles emerging from stumps, logging slash, or isolated infested trees beyond the cut block boundaries, can be attracted to predetermined areas, where they can be disposed of through additional limited harvesting, or by single tree treatment. In this manner residual populations can be held in check or eradicated, reducing risks for future population buildup.

The use of the herbicide monosodium methyl arsenate (MSMA) as a treatment of infested trees for spot suppression has become routine in inaccessible areas and stands where silvicultural or harvesting treatments cannot be used (Hall 1989). Tree baits have made this technique efficient and cost effective. The objective is to prevent reproduction in attacked trees. Susceptible trees are baited prior to mountain pine beetle flight. Shortly after attack, MSMA is applied to axe frills at the base of attacked trees (hack-and-squirt application). The MSMA applied within the prescribed 3-week window, when the pesticide is translocated throughout the tree, leads to the phloem tissues rapidly drying out; this in turn effectively prevents beetle reproduction.

Competitive Displacement

Resource partitioning on the basis of interspecific competition is a common phenomenon among bark beetles. Recent studies have shown that synthetic pheromones of competing (secondary) bark beetle species may disrupt aggregation, enhance the effect of antiaggregation pheromones such as verbenone, or induce attacks by the secondary species causing reproductive failure of the target species. Several secondary bark beetle species share lodgepole pine with the mountain pine beetle as a breeding resource (Furniss and Carolin 1977). The main competitor is the pine engraver, *Ips pini*, which frequently occupies the upper bole of mountain pine beetle infested trees.

Hunt and Borden (1988) found that ipsdienol, the principal aggregation pheromone of *I. pini*, significantly reduced catches of mountain pine beetles in traps baited with *trans*-verbenol, *exo*-brevicomin and myrcene. Safranyik and others (1993) found that simultaneous baiting of lodgepole pine with the aggregation pheromones for mountain pine beetles, and ipsdienol and lanierone, the aggregation pheromones of *I. pini*, resulted in significant reductions in mountain pine beetle attack, egg gallery, and brood densities.

Using ipsdienol, Rankin and Borden (1991) induced attacks by *I. pini* on trees recently infested by the mountain pine beetle, resulting in a 72.5 percent reduction in mountain pine beetle progeny, compared to untreated control trees. Safranyik and others (1994) used ipsdienol and lanierone to induce *Ips* spp. attacks on lodgepole pines at different times following mountain pine beetle attack. In this experiment the effect on mountain pine beetle reproduction was marginal.

Applications of Antiaggregation Pheromones

The antiaggregation pheromones that have been identified for mountain pine beetles are verbenone, *exo*-brevicomin at high release rates, frontalin at high release rates, and ipsdienol. Of these, verbenone appears to be the most promising for practical applications.

Beetle Response to Attractive Traps

Ryker and Yandell (1983) tested the effect of a "high" release rate (0.08 mg/24 h) of racemic verbenone around sticky traps baited with *trans*-verbenol and monoterpenes. Mountain pine beetle catch was reduced by 87 percent, or to the level of blank control traps. Verbenone released at a "low" rate (0.001 mg/24 h) did not have a significant effect on trap catch.

Schmitz and McGregor (1990) conducted tests in Northern Utah in 1986 to assess the response of mountain pine beetles to funnel traps baited with *trans*-verbenol, *exo*-brevicomin, and myrcene with or without verbenone released at 5 mg/day at 25 °C. Overall, the addition of verbenone to the synthetic mountain pine beetle lure reduced the catch by 98 percent.

A similar test in British Columbia by Borden and others (1987) showed that when verbenone was released at 1 and 5 mg/24 h, respectively, in funnel traps baited with the attractive synthetic mountain pine beetle lure, the response of males was reduced by approximately 75 percent. Female response was reduced similarly, but not significantly.

The encouraging results from these studies prompted tests to determine the efficacy of verbenone for reducing mountain pine beetle infestation in lodgepole and ponderosa pine, *P. ponderosa* Lawson, stands, and on individual lodgepole pines.

Ground Tests in Lodgepole and Ponderosa Pine Stands

Field studies to test the efficacy of verbenone in reducing mountain pine beetle infestation in stands were conducted in Idaho, Montana, and British Columbia, starting in 1987. Two experiments were conducted in British Columbia (Lindgren and others 1989). The first experiment compared (1) mountain pine beetle tree bait, and (2) tree bait and verbenone; the second compared (1) untreated control and (2) verbenone alone. In Idaho, all four treatments were compared in one experiment (Amman and others 1989). Each treatment was applied individually to 1-ha plots, except in the second experiment in British Columbia, which used 4-ha plots. Five mountain pine beetle tree baits were used in each baited plot, and verbenone plots were treated with 100 verbenone bubble capsules per ha applied on a 10- by 10-m grid.

The results from these two independent studies were remarkably similar. There was no significant difference between control and verbenone plots in either study, but highly significant effects were achieved by verbenone compared to the baited plots.

Percent reduction in mountain pine beetle-caused mortality

	Bait vs. verbenone + bait	Control vs. verbenone
Idaho	74.1	74.3
British Columbia	74.3	75.2

These encouraging studies led to additional studies in 1988 and 1989 to determine the relationship between verbenone dose and mountain pine beetle response in lodgepole pine stands of Idaho (Amman and others 1991), Montana (Gibson and others 1991), and British Columbia (Safranyik and others 1992).

In Idaho and Montana, five treatments consisting of different numbers of verbenone bubble caps (0, 25, 49, 100, and 169 caps/ha) were applied in grid patterns within plots in 1988. In addition, each plot had two 20-m wide strips established around the perimeter to determine if beetle infestation increased in the area immediately adjacent to verbenone treated plots (Amman and others 1991). The 1989 test was similar to the 1988 test except strips were not used around the plots. In 1988, treatments were replicated seven times and in 1989 they were replicated eight times.

All verbenone doses reduced tree mortality within treated plots in both years when compared to untreated control plots. There was a trend of lower mortality with increasing verbenone dose in both years. However, the highest dose sustained higher mortality than the intermediate doses. In the strips surrounding verbenone treated plots in 1988, there were no significant differences in number of trees mass attacked. However, the trend was for fewer infested trees as quantity of verbenone increased in the plots (Amman and others 1991).

In the Montana studies (Gibson and others 1991), designs were similar to those used in Idaho. In 1988, treatments were not significantly different. However, in 1989, treatments were significantly different, and the results were very similar to those in Idaho. As in the Idaho test, the 100 capsules/ha treatment showed the greatest reduction in percent of infested trees, with a mean of 0.3 percent compared to check plots that had a mean of 5.2 percent. The lack of significant treatment effect in 1988 was attributed to the low number and poor distribution of infested trees among plots. The average percentage of infested trees ranged between 0.2 and 2.5 when the study was installed.

Bentz and others (1989), Gibson and others (1991), and Lister and others (1990) used methods similar to those described in the previous section for lodgepole in Idaho to test the effect of verbenone in ponderosa pine stands in southwestern Colorado, in western Montana, and in western South Dakota. Tests were not successful.

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; the South Dakota area was in the early stages of an outbreak (22 infested trees/ha), and the Montana area was intermediate (32 infested trees/ha).

In each area, as in the lodgepole pine test, four replicates were used to test the five treatments; 0, 25, 49, 100, and 169 verbenone bubble caps/ha (elution rate 5mg/day/capsule at 25 °C). In 1988, no significant differences occurred among treatments in any of the areas. The numbers of mass-attacked trees in the strips surrounding the plots also were not significantly different among treatments, nor different from those within the plot.

In 1989, eight replicates were used to again test different verbenone treatments 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).

Both the South Dakota and Montana tests showed a downward trend in infestation with increased number of verbenone capsules, but due to high variance within treatments and low number of replicates, significant treatment effects could not be demonstrated.

The results from the dose response experiments in lodgepole and ponderosa pine are similar (fig. 1), in spite of the fact that statistical significance was not obtained in several of these experiments. The general trend of reduced mortality as a function of verbenone dose is consistent with dose-dependent response by the mountain pine beetle in trapping experiments (Miller and others in press). Even in the experiment in ponderosa pine in Colorado, where extremely high beetle populations probably precluded any possibility of a significant verbenone effect (Bentz and others 1989), and in one experiment in lodgepole pine in Montana, where control mortality was only 0.3 percent (Gibson and others 1991), there were slight (non-significant) reductions in mean mortality in treated blocks compared to controls.

Safranyik and others (1992) tested two release rates of verbenone for effects on mountain pine beetle dispersal, landing, and attack behavior in lodgepole pine stands. The two release rates were either one or two bubble caps attached to trees on a 10- by 10-m grid. Unbaited landing traps were placed on lodgepole pines in a 10- by 10-m

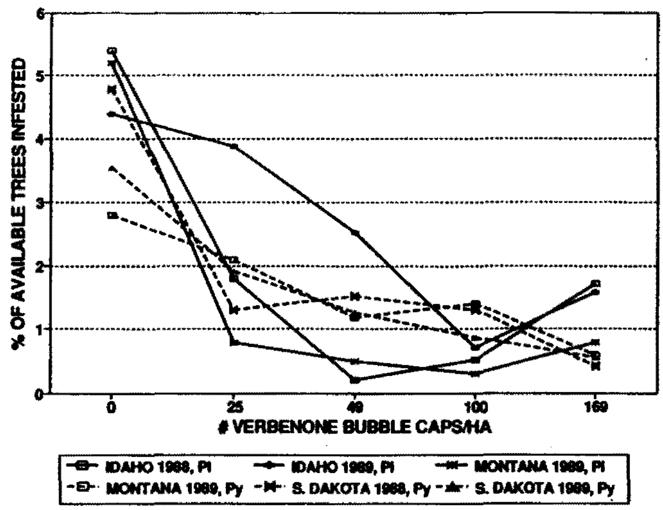

Figure 1—Comparison of results from verbenone dose experiments in lodgepole pine (solid lines) and ponderosa pine (dashed lines). Graph generated from data by Amman and others 1991 (Idaho 1988 and 1989), Gibson and others 1991 (Montana 1989), Bentz and others 1989 (South Dakota 1988), and Lister and others 1990 (South Dakota 1989). Pl = Lodgepole pine, Py = Ponderosa pine.

grid. Infested log sections dusted with different colored fluorescent dyes were positioned in the middle of each 100- by 100-m block to assess beetle movement in relation to verbenone applications.

There was no significant difference between the two verbenone treatments for number of attacked trees, or number of attacking beetles. However, the means of all experimental variables were lower in verbenone-treated plots than control plots. The difference in number of beetles trapped was statistically significant at $\alpha = 0.1$, with more marked beetles caught in the control than verbenone-treated plots.

L. Rasmussen (USDA Forest Service, Logan, UT, personal communication) established studies in 1990 and 1991 in Central Idaho to determine whether 49 or 100 bubble capsules of verbenone/ha were most effective in lodgepole pine, since each treatment had given the best results in previous tests (Amman and others 1991). A significant treatment effect was not shown either year when compared with controls, nor among verbenone rates, although significant effect of verbenone was shown for 1987, 1988, and 1989 (Amman and others 1989, 1991) for the same area in Idaho.

Rasmussen's results suggest that selection may be occurring for beetles that ignore or are attracted to the verbenone signal. In these studies most of the large diameter trees had been killed in previous years, leaving only smaller trees available for attack. In these trees, the larvae survival rate is usually lower than in large diameter lodgepole (Cole and others 1976) and beetles reared in thin phloem take longer to develop and are smaller in size (Amman and Cole 1983). Such beetles would be more typical of those found at low, non-outbreak population levels. Schmitz (1988) found that beetles in such populations tended to infest diseased trees and trees infested by secondary bark beetle species such as *Ips*, *Pityogenes*, and *Pityophthorus*. Low to moderate levels of verbenone produced by oxidation of pheromones and terpenes in such trees may attract the types of mountain pine beetles produced in poor host material, that is, trees of small diameter with thin phloem.

Aerial Application of Verbenone

Shea and others (1992) used verbenone formulated in controlled release, cylindrical, 5- by 5-mm plastic beads applied at the rate of 54 g verbenone per hectare from a helicopter in mountain pine beetle infested lodgepole pine stands of northwestern Montana. After treatment, the mean number of currently infested trees (1988) did not differ between treated and control plots. However, the control plots had four times as many infested trees as treated plots, and the mean ratio of 1988 to 1987 attacked trees per hectare was significantly higher in control plots than in treated plots. The mean number of unsuccessfully attacked trees per hectare was significantly higher in verbenone treated plots. Although these results were quite encouraging, a subsequent experiment failed to achieve the same response (P. Shea, USDA Forest Service, Davis, personal communication).

Shea and others (1992) discussed the possible influence of stand microclimate as a factor affecting results of verbenone tests. They found that verbenone eluted more rapidly from beads in open stands than from those in closed stands.

In a simulated aerial test of verbenone-impregnated beads, Kostyk and others (1993) observed that trap-catches of mountain pine beetle were 50 percent higher in traps hung above beads placed on the ground than in traps containing similar beads. They also found that 50 percent of verbenone vapors, when exposed to full sunlight, were converted to chrysanthenone in 75 and 100 minutes during two tests. Chrysanthenone had no influence on the response of mountain pine beetle to synthetic attractants.

The rate of photoisomerization of verbenone may vary according to geographic location, stand elevation, and density (Kostyk and others 1993). No chrysanthenone was found in bead samples from Idaho, but considerable amounts occurred in Montana samples (Lindgren 1991). In closed canopy samples, up to 36.7 percent of the sample was accounted for by chrysanthenone; in open canopy samples up to 51.5 percent.

Lindgren (1991) did a small aerial application test in conjunction with tests of verbenone bubble capsules in British Columbia. He used 4-ha plots replicated four times to compare 100 bubble capsules per hectare (80 g active ingredient/ha), aerial application of 2.8 kg of beads (84 g active ingredient/ha), and untreated control. He found that each verbenone application reduced infestation, but neither was statistically significant. Lack of significance was probably due to the small number of replicates and a treatment by replicate interaction. Nevertheless, treated plots had less than half the percentage of infested trees as the control plots, and almost twice the percentage of lightly infested trees (unsuccessfully attacked).

Push/Pull Strategy

The use of verbenone to repel beetles from one stand of trees, combined with aggregation pheromones to attract the beetles to an adjacent stand scheduled for logging was considered potentially the most operationally feasible tactic with pheromones (Borden and Lindgren 1989). Aggregation pheromones may shift infestations of mountain pine beetle (Borden and others 1983), as well as concentrate and contain them (Gray and Borden 1989). However, the maximum distance of attraction is considered to be 75 m (Borden and Lindgren 1988).

Lindgren and Borden (1993) designed an experiment to test displacement of beetles and their attraction to adjacent stands. Treatments were: (1) control, (2) verbenone in a central 50- by 150-m subplot, (3) mountain pine beetle tree baits in two flanking subplots, and (4) verbenone in the central subplot plus tree baits in flanking subplots, replicated seven times over 2 years. When verbenone was combined with tree baits, beetles were more consistently displaced from central subplots to the two flanking subplots than when verbenone was used alone.

L. Rasmussen (personal communication) tested the push-pull strategy in central Idaho using three treatments: (1) control, (2) verbenone only (100 bubble caps/ha), and (3) tree baits (5 baits/ha), randomly assigned to plots. He found that baits were highly effective in attracting beetles and inducing them to infest trees in the baited plots. However, verbenone and control plots had similar levels of infestation. He concluded that the attractive baits alone would be just as effective as using both baits in stands scheduled for logging and verbenone in adjacent stands.

Individual Tree Protection

The protection of individual trees of high value, such as those around homes and administrative sites, has been a long-term goal of research with antiaggregation pheromones. The protection of individual trees injured by prescribed fires is another goal, since such trees, particularly in plantations, are of high value.

Borden and Lindgren (1988) assessed the effect of different application rates of verbenone on lodgepole pine tree baited with the attractive mountain pine beetle bait. Treatments were (1) attractive tree bait alone, (2) bait and one verbenone bubble cap, (3) bait plus verbenone bubble cap and four additional verbenone bubble caps attached on adjacent trees, and (4) bait plus a verbenone bubble cap and nine additional verbenone capsules on adjacent trees. They reported no differences among the application rates of verbenone, all of which reduced the attack density on baited trees, the percent of available trees within 10 m of the baited tree that were attacked (spill-over attacks), and the numbers of spillover trees. Notably, the verbenone reduced the average attack density on baited trees well below the 40 attacks/m^2 believed necessary to kill the tree. More spillover trees occurred with the highest verbenone rate than with the two lower rates. In addition, only two of the 10 baited trees treated with one verbenone bubble cap were attacked. Five of the 10 trees receiving the higher rates of verbenone, and all 10 baited trees receiving no verbenone were attacked.

Amman and Ryan (1994) established a study to protect individual fire-injured trees in Central Idaho. Lodgepole pines were heat treated by burning peat moss around 70 percent of the basal circumference to kill the cambium. Treatments applied were: (1) fire-injured control, (2) uninjured control, (3) two verbenone capsules on fire-injured tree and, (4) two verbenone capsules and two ipsdienol capsules on fire-injured tree replicated 20 times. Mountain pine beetle were attracted into the plots by placing tree baits on metal posts 3 to 5 m from treated trees. Control treatments contained more unattacked and mass attacked trees; pheromone treatments contained more unsuccessfully attacked trees. Ipsdienol did not increase the efficacy of verbenone alone in protecting trees.

Shore and others (1992) tested the multifunctional role of *exo*-brevicomin and the response of mountain pine beetle to combinations of *exo*-brevicomin and verbenone. Their treatments consisted of: (1) verbenone bubble cap, (2) *exo*-brevicomin released from Eppendorf tubes at a "low" rate of 0.5mg/day, (3) *exo*-brevicomin released at a "high" rate of 2.5mg/day, (4) verbenone plus *exo*-brevicomin low rate, (5) verbenone plus *exo*-brevicomin high rate, and (6) unbaited control. Treatments were replicated 28 times.

They found that *exo*-brevicomin at both release rates induced mountain pine beetle attacks. Verbenone significantly reduced mountain pine beetle response to *exo*-brevicomin to the level of the response to unbaited controls. Verbenone treated trees were attacked less often than control trees, but not significantly so. None of the verbenone treated trees were mass attacked.

Discussion

Aggregation Pheromones

Aggregation pheromones are in operational use in British Columbia. Additional research on the semiochemical complex of the mountain pine beetle is under way (G. Gries, Simon Fraser University, Burnaby, BC, Canada, personal communication). In particular, there is a need for more efficient synthetic pheromones for use in artificial traps for mass trapping and detection purposes.

Antiaggregation Pheromones

At this time, the use of antiaggregation pheromones on an operational basis cannot be recommended. The inconsistent results from year to year within and between areas, and between tree hosts of mountain pine beetle, point to the need for much additional research before antiaggregation pheromones can be used effectively. There are several possible explanations for the inconsistent results, ranging from inappropriate verbenone release devices to genetic selection of beetles.

1. Stand microclimate may change as infestations progress within a given stand. As trees are killed holes are created in the canopy, thus allowing pheromone to dissipate out of the stem zone and into the area above the canopy (Fares and others 1980; Schmitz and others 1989). Shea and others (1992) have an excellent discussion of this topic and how it may have affected their aerial tests. The same may apply to ground applications of bubble caps.
2. Weather factors, particularly temperature, may have contributed to failure of tests, particularly in ponderosa pine stands. High temperatures result in above-average elution rates, causing some bubble caps to expire before the end of beetle flight period; cool temperatures result in low elution.
3. In the failed Idaho tests, the release of verbenone from bubble caps was consistent with previous tests. The enantiomeric blend of verbenone in the bubble caps was found to be (–)-80 percent. This blend should not be a problem (Rasmussen 1974). Genetic change of mountain pine beetle related to infestation of small diameter trees (in which phloem is thin) after larger trees (in which phloem is thick) have been killed may contribute to selection of beetles that tend to ignore the verbenone signal. K. Hobson (USDA Forest Service, Logan, UT, personal communication) found a significant difference in response of mountain pine beetle to traps baited with aggregation pheromones and verbenone in old compared to new mountain pine beetle infestations in Central Idaho. Verbenone reduced

attraction of mountain pine beetle by 99 percent in new infestations and 89 percent in old infestations.

4. Large beetle populations may lead to the treatment being overwhelmed, since attacks are initiated on many trees simultaneously. The likelihood of additional beetles landing on previously attacked trees increases, leading to a higher probability of successful attacks (tree mortality).
5. Sparse beetle populations may lead to non-significant results, since untreated blocks must sustain some level of attack to provide adequate controls. In several experiments, control blocks sustained little or no mortality.
6. Photoisomerization of verbenone to chrysanthenone, a compound that the mountain pine beetle does not respond to, increases with exposure to light (Kostyk and others 1993). Photoisomerization occurs much faster in stands of open canopy than those having a closed canopy because of the greater light penetration, and was a particular problem in some aerial applications.

Current research is aimed at discovering compounds that send a stronger message to beetles as to the unsuitability of the host resource. Semiochemicals currently being tested include pheromones of competing species (interspecific competition), compounds from non-host trees (Dickens and others 1992), and repellant host compounds (Hayes and others in press). Research using verbenone alone has provided some encouraging evidence that the use of antiaggregation pheromones may have operational utility. The addition of other repellant semiochemicals [illegible] provide consistent results, allowing antiaggregation semiochemicals to be included in operational tools for mountain pine beetle management.

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