USDA

United States
Department
of Agriculture

Forest Service

**Rocky Mountain
Research Station**

Research Note
RMRS-RN-31

September 2006

Testing Verbenone for Reducing Mountain Pine Beetle Attacks in Ponderosa Pine in the Black Hills, South Dakota

Jose F. Negron, Kurt Allen, Joel McMillin, and Henry Burkwhat

Abstract—In 2000 and 2002, Verbenone, a compound with anti-aggregation properties for mountain pine beetle, *Dendroctonus ponderosae*, was tested for reducing attacks by the insect in Ponderosa pine, *Pinus ponderosae* forests. The verbenone was released to the environment with the use of permeable membranes; the first year with plastic capsules (containing 0.8 g of verbenone) and the second year with an envelope-like pouch (containing 5.0 g of verbenone). The plastic capsules were deployed at a rate of 25 and 64 capsules per acre and a no capsule treatment served as control. The pouches were deployed at 30 and 50 pouches per acre and a no pouch treatment was the control. Mountain pine beetle attractants were placed on three trees at plot center to ensure insect population pressure. In neither experiment were there any observed differences in (1) number of mountain pine beetle-killed trees, (2) number of partial attacks (strip attacks), (3) number of unsuccessful attacks (pitch-outs), (4) diameter at breast height of infested trees, (5) attack height of infested trees, (6) mean distances of infested trees to verbenone releasers, (7) attractants located at plot center. The possible influence of stand environment is discussed as reason for lack of effectiveness. At this point, based on this and prior studies the operational use of verbenone for reducing mountain pine beetle-attacked trees in ponderosa pine forests is not advisable. Further studies on this topic should be conducted in the future as treatment technology is developed further or the appropriate release amount and timing is better understood.

Key words: mountain pine beetle, verbenone, ponderosa pine, *Dendroctonus ponderosae*, *Pinus ponderosae*

Introduction

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a primary mortality agent in ponderosa pine, *Pinus ponderosae* Dougl. Ex Laws, forests and has been at epidemic levels in the Black Hills of South Dakota since 2000. Abundant mountain pine beetle-caused tree mortality presents many forest management challenges to land managers. Some include, but are not limited to, the occurrence of mortality in high-value areas such as recreation areas, visual corridors, community watersheds, and vegetative sites designated as timber production areas. Under certain circumstances, mitigating the effects of mountain pine beetle-caused mortality is desirable, but methods to accomplish this are limited.

Jose Negron is a research entomologist with the USDA Forest Service, Rocky Mountain Research Station; **Kurt Allen** and **Joel McMillin** are entomologists with USDA Forest Service Forest Health in Rapid City, SD and Flagstaff, AZ, respectively; **Henry Burkwhat** is with the USDA Natural Resources Conservation Service, Hamilton, MT.

Bark beetles regulate the attack process on its host to avoid overcrowding the host through a very complex chemical communication system that includes the use of pheromones. Verbenone (4,6,6-trimethylbicyclo [3.1.1]-hept-3-en-2-one), has been identified as a chemical with anti-aggregation or repellent properties that arrests additional mountain pine beetle attacks on a tree. This anti-aggregation compound is insect-produced and is most likely released when the resource is fully utilized by the insects already present. The use of synthetically-produced verbenone has been experimentally tested for reducing the number of mountain pine beetle-attacked trees in various studies, primarily in lodgepole pine, *Pinus contorta* Dougl. Ex. Loud., forests. In the past, results have been mixed, but some studies have had encouraging results.

Various studies indicate that reduced mountain pine beetle catches result when verbenone is added to pheromone traps that contain a mountain pine beetle attractant (*trans*-Verbenol, exo-Brevicomin, and myrcene) (Borden and others 1987; Schmitz and McGregor 1990; Amman and Lindgren 1995; Miller and others 1995). Studies that also examined the use of verbenone to reduce mountain pine beetle attacks on lodgepole pine produced mixed results (Lindgren and others 1989; Amman and others 1989; Amman and others 1991; Gibson and others 1991). There are a variety of explanations associated with the mixed results that are discussed by Amman and Lindgren (1995) and Progar (2005).

Three verbenone studies in the Black Hills, South Dakota, Uncompahgre National Forest, Colorado (Lister and others 1990; Bentz and others 1989), Kootenai National Forest and other State and private lands south of Darby, Montana (Gibson and others 1991) did not demonstrate reduced attacks in ponderosa pine. These studies used bubble caps, plastic capsules that elute the verbenone to the environment through a permeable membrane.

In lodgepole pine stands in central Idaho, Progar (2005) examined verbenone efficacy over a 5-year period in the same stands. Reduced mortality was observed the first 2 years of treatment with no significant differences detected the following 3 years. The author concluded that verbenone may be effective in the early stages of an outbreak, but is no longer efficacious as insect populations increase. Bentz and others (2005) demonstrated efficacy of verbenone in lodgepole and whitebark pine sites in Idaho and Montana. These two studies (Progar 2005; Bentz and others 2005) used a pouch containing 5 g of verbenone as a release device instead of the bubble caps used in previous studies. The passive-release pouch is plastic and also elutes the verbenone through a permeable membrane but can hold larger amounts of the material. The amount and rapidity of verbenone release is based on ambient air temperatures.

In this research note we present results from a verbenone test conducted to examine potential reduction of mountain pine beetle attacks in ponderosa pine stands in 2000 and 2002 at the Black Hills, SD. In the 2000 test, we used bubble caps and in the 2002 test, we used the verbenone pouch.

Methods

The 2000 test was conducted near the town of Nemo in the Black Hills. Thirty 1-acre plots were delineated for the experiment in June, 2000. Plots were at least 2/10 of a mile apart. The diameter at breast height (dbh) was measured for every tree in each plot to calculate average tree diameter and stand stocking. Verbenone was deployed using passive release bubble caps (Phero Tech, Inc., Delta, British Columbia, Canada). Each cap contained 0.8 g of verbenone. The release rate provided by the manufacturer is 2 mg/day at 68° F and 15/per day at 86° F. Treatments included 25 or 60 bubble caps/acre and an untreated control. Treatments were randomly assigned to the experimental plots. In the treated plots, bubble caps were evenly distributed across the stand and stapled on the north side of trees about 6 to 7 ft above the ground. At the center of each plot, three mountain pine beetle attractants composed of *trans*-Verbenol, exo-Brevicomin, and myrcene were placed on host trees to assure beetle pressure in the plot. Each treatment was replicated 10 times. Bubble caps were deployed the first week in July. In the fall, after beetle flight was completed, every tree in each plot was examined for mountain pine beetle attack. We recorded whether the tree was alive (not attacked), mountain-pine beetle mass-attacked (successful attack), strip-attacked (partial beetle attack), a pitch-out (unsuccessful beetle attack), or mortality caused by other agents. We also recorded the distance from each mountain pine beetle-attacked tree to the closest verbenone bubble cap, distance to the plot attractant, and maximum attack height on each tree bole.

The 2002 test was also conducted near Nemo, SD. Fifteen 1-acre plots were used in this test, also at least 2/10 of a mile apart. Verbenone was deployed using a the permeable plastic pouch. Each pouch contained 5 g of 98 percent pure verbenone. Elution rate was 25 mg/day at 86° C. Treatments included 30 and 50 pouches/acre and an untreated control, all of which were assigned randomly to the study plots. Five replicates of each treatment were conducted. Plot layout and treatment evaluation was the same as described above for the 2000 test. In both years, insect populations could be characterized as endemic. A survey of the area in 1999 reported 2.5 infested trees/acre (McMillin and Allen 1999)

For both years, response variables were compared using the Multi-response permutation procedure[1], which is based on Euclidean distance (Mielke and Barry 2001). When significance differences were detected, multiple comparisons among treatments were based on the Peritz

[1] An Excel macro written by Rudy M. King, Station Biometrician, Rocky Mountain Research Station, Fort Collins, CO, was used.

Table 1. Ponderosa pine stand characteristics prior to treatment in experimental plots, summer 2000, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Mean DBH (in)	Mean Trees/Acre	Mean Basal Area (ft^2/acre)	Mean Stand Density Index
25 Bubble caps/Acre	9.2 (0.3)	261.9 (27.8)	116.3 (9.6)	224.3 (17.8)
64 Bubble caps/Acre	9.2 (0.3)	279.5 (18.1)	126.5 (6.0)	248.1 (10.7)
Control	8.4 (0.1) *	325.4 (23.6)	122.9 (7.2)	252.9 (17.1)

* Denotes a significant difference between both treatments and the control ($P < 0.05$). No other statistical differences observed ($p < 0.05$).

closure method (Petrondas and Gabriel 1983). This test maintains Type I error at or below 0.05.

Results

2000 Test. There were no significant differences in pre-treatment stocking levels among the plots that received the different treatments. Untreated control plots had a significantly smaller dbh compared to the plots treated with 25 or 64 bubble caps ($P < 0.01$) (table 1). There were no significant differences in the number of mountain pine beetle-killed trees, strip attacks, or pitch outs among treatments (table 2). Regarding mountain pine beetle-killed trees, there were no significant differences observed in dbh, attack height, or distance to attractant. Distance of attacked trees to the closest verbenone bubble cap was significantly higher in the 25 caps/acre treatment compared to the 64 caps/acre treatment. As there were no other treatment efficacy differences, this distance to verbenone difference is associated with the density of caps per acre and not any treatment effect (table 3).

2002 Test. No significant differences were observed in pre-treatment stocking or dbh among study plots with different treatments (table 4). No significant differences were detected in the number of mass attacked trees among the treatments. Only one pitch-out was

Table 2. Mountain pine beetle-killed Ponderosa pines, strip attacks, and pitch outs, 2000 verbenone test, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Mean Number of Mountain Pine Beetle-Killed Trees	Mean Number of Strip Attacks	Mean Number of Pitch-outs
25 Bubble caps/Acre	9.9 (2.7)	1.6 (0.5)	3.4 (0.9)
64 Bubble caps/Acre	5.8 (1.3)	1.7 (0.5)	1.5 (0.5)
Control	11.9 (3.7)	0.3 (0.2)	3.4 (0.9)

No statistical differences observed ($p < 0.05$).

Table 3. Mountain pine beetle-killed trees DBH, bark beetle attack height, and distances to attractant and closest verbenone bubble cap, 2000 verbenone test, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Mean DBH (in)	Mean Attack Height (ft)	Mean Distance to Attractant (ft)	Mean Distance to Verbenone (ft)
25 Bubble caps	9.7 (1.0)	10.9 (0.7)	27.4 (8.5)	18.5 (1.5) *
64 Bubble caps	10.0 (0.7)	11.4 (1.2)	13.9 (3.9)	12.4 (1.1)
Control	8.7 (0.9)	11.3 (1.1)	20.6 (4.8)	NA

* Denotes a significant difference between both treatments ($P < 0.01$). No other statistical differences observed ($p < 0.05$).

Table 4. Ponderosa pine stand characteristics prior to treatment in experimental plots, summer 2002, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Mean DBH (in)	Mean Trees per Acre	Mean Basal Area (ft^2/acre)	Mean Stand Density Index
30 Pouches/Acre	7.5 (0.4)	379.0 (17.8)	158.4 (27.3)	258.4 (12.6)
50 Pouches/Acre	8.1 (0.6)	409.6 (72.4)	152.0 (13.3)	289.4 (30.7)
Control	7.0 (0.8)	603.2 (214)	175.4 (33.9)	317.2 (46.3)

No statistical differences observed ($p < 0.05$).

Table 5. Mountain pine beetle-killed Ponderosa pines and pitch outs, 2002 verbenone test, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Number of Trees	Number of Mass-attacked Trees	Number of Pitch-outs
30 Pouches/Acre	6	1.2 (1.0)	Only 1 tree in one plot
50 Pouches/Acre	27	5.4 (1.6)	1.0 (0.4)
Control	26	5.2 (3.4)	2.8 (1.5)

No statistical differences observed ($p < 0.05$).

Table 6. Mountain pine beetle-killed trees DBH, bark beetle attack height, and distances to attractant and closest verbenone bubble cap, 2002 verbenone test, Black Hills National Forest, SD. Numbers in parenthesis denote standard error of the mean.

Treatment	Mean DBH (in)	Mean Attack Height (ft)	Mean Distance to Attractant (ft)	Mean Distance to Verbenone (ft)
30 Pouches per Acre	9.7 (0.7)	16 (2.7)	2.2 (1.3)	12.2 (3.2)
50 Pouches per Acre	8.6 (0.4)	12.7 (1.0)	25.9 (7.7)	10.7 (1.2)
Control	9.1 (0.5)	14.5 (1.6)	25.4 (7.2)	NA

No statistical comparisons made. See text for more details.

recorded in the 30 pouches/acre treatment; no differences occurred between the control and the 50 pouches/acre treatment (table 5). No strip attacks were observed in any of the plots. There were few plots with attacked trees in this test. In two of the control plots, three plots of the 30 pouches/acre treatment and one plot with 50 pouches/acre, no attacked trees were recorded. Therefore, comparing attacked tree characteristics among plots is not meaningful. For descriptive purposes, we present mean dbh, attack height, and distance to attractant and nearest verbenone pouch for all attacked trees in every plot (table 6). No trends of particular interest are noted.

Discussion

Mountain Pine Beetle-Caused Mortality Levels

In the 2000 test, a total of 119, 99, and 58 mountain pine beetle-killed trees were counted in the control, 25, and 64 bubble cap treatments, respectively. These numbers represent 3.7, 3.8, and 2.1 percent of the total trees in the control, 25, and 64 bubble cap plots, respectively. In the 2002 test there were 26, 6, and 27 mountain pine beetle-killed trees in the control, 30 pouches/acre, and 50 pouches/acre, respectively. These numbers represent 0.8, 0.3, and 1.3 percent of the total trees in the control, 30 pouches/acre, and 50 pouches/acre, respectively.

In their studies at the Black Hills and the Uncompahgre NF, Bentz and others (1989) examined the use of bubble caps in ponderosa pine using 10, 20, 40, or 80 caps/acre and a control and observed no differences among treatments. The percent of trees attacked in their study plots ranged from 1 to 7 percent in the Black Hills and from 15 to 41 percent in the Uncompahgre NF. The most promising results were presented by Lister and others (1990) in another experiment in the Black Hills, using the same rates of bubble caps as Bentz and others (1989). They did not observed significant differences among treatments yet reported a consistent decrease in the number of attacked trees per plot from 29.1 in the control to 5.6 in a 68 bubble caps per acre treatment. The authors did not report the percent of trees attacked by mountain pine beetle in the study. Gibson and others (1991) conducted another study in ponderosa pine in the Kootenai NF. They used the same bubble caps rates as above. They observed no differences among treatments. That study reported percent of attacked trees varied from 2.3 to 15.8 percent.

In lodgepole pine, Progar (2005), using the verbenone pouch releaser (eluting 25 mg/day at 86 °F) at a rate of 20 per ¼ acre, reported successful reduction in mountain pine beetle-caused mortality during the first 2 years of treatment, but no reduction was found in the following 3 years. In this study, median percent mortality levels after 2 years were 12 and 59 percent of the trees > 5.1 inches in the treated and untreated stands, respectively. After 5 years, the percentages were 67 and 87 in the treated and untreated stands, respectively. Bentz (2005) reported increased effectiveness using 40 pouches/acre (with a higher elution rate of 50 mg/day at 86 °F) compared to the control. In this study, the number of trees/plot ranged from 10 to 335 trees. Attacked tree percentages ranged from 0.1 to 20 percent in the control plots and from 4 to 60 percent in the verbenone-treated plots.

Although it is difficult to adequately compare differences in bark beetle population pressure, stand/site conditions, and treatments from the various studies, they do cover a wide range of attacked trees from as low as 1 percent to as high as 41 percent. This suggests that insect population densities, although certainly low in our study, may not be the single attribute affecting our results where no differences between treatments were observed.

Verbenone and Stand Microclimate

Amman and Lindgren (1995) discuss several potential reasons for inconsistencies in results of previous studies. They mention that weather factors, such as high temperatures, may cause verbenone to elute prior to beetle dispersal. Holsten and others (2002) measured release rates, under field conditions, from bubble caps filled with either verbenone or methylcyclohexenone (antiaggregant for Douglas-fir beetle, *Dendroctonus pseudotsugae*). They concluded that ambient air and litter layer temperatures were key determinants influencing release rates with higher temperatures resulting in faster release rates. Amman and Lindgren (1995) also indicate that when verbenone is exposed to light, isomarization takes place, which changes verbenone to chrysanthenone, a chemical that does not affect mountain pine beetle behavior.

Various studies using pheromone surrogates have demonstrated that turbulence and the meteorology within the forest canopy can influence pheromone dispersion (Aylor and others 1976; Murlis and Jones 1981; Elkinton and others 1984; Mafra-Neto and Carde 1994). Recently, Thistle and others (2005) started an examination in Mississippi of the influence of stand thinning on the dispersion of a chemical that acted as a pheromone surrogate. Preliminary results suggest that solar radiation increases in a loblolly pine, *Pinus elliotii* Engelm., stand thinned to 70 ft^2/acre basal area. This results in unstable air creating a turbulent environment compared to an unthinned stand. This may increase pheromone dispersion affecting pheromone cues used by insects to communicate.

Bartos and Amman (1989) examined stand microclimate in a thinned and an unthinned lodgepole pine stand. The unthinned stand had a basal area of 161 ft^2/acre, 441 trees/acre and a mean dbh of 7.3 in. The thinned stand had a basal area of 96 ft^2/acre, 287 trees/acre, and a mean dbh of 8.0 inches. All measurements were significantly different between the thinned and the unthinned stands. They observed increased light intensity, wind movement, and temperature in the thinned stand compared to the unthinned stand. In the Black Hills, Schmid and others (1992) indicated no significant differences in vertical wind speeds between a ponderosa pine stand thinned to 60 GSL, two stands cut to 80 GSL, and a unthinned stand of 150 GSL (GSL = Basal area when average stand diameter is 10 inches).

In another study, Schmid and others (1995) compared microclimate characteristics between a thinned and an unthinned ponderosa pine stand in the Black Hills. The unthinned stand had a basal area of 148 ft^2/acre and a mean dbh of 10.8 in, whereas the thinned stand had a basal area of 79.2 ft^2/acre and a mean dbh of 11.2 in. They observed no significant differences in air temperature or horizontal air speed, but reported increased solar radiation in the thinned stand. Comparing the lodgepole pine study with the ponderosa pine study is not feasible because overall environmental conditions and stand structures are most likely different. However, it is evident that a more open lodgepole pine stand had different environmental conditions than a dense, unthinned stand. Thistle and others (2005) suggest that pheromones may be more widely dispersed in open stands, making it less effective. Lodgepole pine forest canopy cover is denser than canopy structures found in ponderosa pine forests. Schmid and others (1995) only observed differences in solar radiation, yet it was not a replicated study and may have been conducted under abnormal weather conditions.

Conclusions

Because ponderosa pine stand structures are less dense, they probably experience higher temperatures, high solar radiation, and increased wind movement. These microclimate patterns may result in a more turbulent environment that disperses the pheromone affecting insect communication. This may explain the consistent observations where verbenone treatments applied in ponderosa pine stands are not efficacious. Further testing of verbenone applications in ponderosa pine stands should be conducted. These studies should include higher release rates and the use of timed release devices that target daily and seasonal bark beetle peak flight to enhance pheromone exposure to the insects and minimize loss to dispersion.

Management Implications

Studies to date on the use of verbenone to reduce mountain pine beetle-killed trees in ponderosa pine stands have not detected significant reductions in the number of trees attacked. Operational use of this strategy in ponderosa pine forests is not advisable at this point until further studies prove otherwise.

Literature Cited

Amman, G.D.; Lindgren, B.S. 1995. Semiochemicals for management of mountain pine beetle: status of research and application, pp. 14-22. In: Salom, S.M.; Hobson, K.R., eds. Application of semiochemicals for management of bark beetle infestations-Proceedings of an informal conference, GTR-INT-318, USDA Forest Service, Intermountain Research Station, Ogden, UT.

Amman, G.D.; Their, R.W.; McGregor, M.D.; Schmitz, R.F. 1989. Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetle in Idaho. Canadian Journal of Forest Research 19: 64-60.

Amman, G.D.; Their, R.W.; Weatherby, J.C.; Rasmussen, L.A.; Munson, S.A. 1991. Optimum dosage of verbenone to reduce infestation of mountain pine beetle in lodgepole pine stands of central Idaho. Research Paper INT-440, USDA Forest Service, Intermountain Research Station, Ogden, UT. 5 p.

Aylor, D.; Parlange, J.; Granett, J. 1976. Turbulent dispersion of disparlure in the forest and male gypsy moth response. Environmental Entomology 5: 1026-1032.

Bartos, D.L.; Amman, G.D. 1989. Microclimate: an alternative to tree vigor as a basis for mountain poine beetle infestations. Research Paper INT-400, USDA Forest Service, Intermountain Research Station, Ogden, UT. 10 p.

Bentz, B.; Lister, C.K.; Schmid, J.M.; Mata, S.A.; Rasmussen, L.A.; Haneman, D. 1989. Does verbenone reduce mountain pine beetle attacks in susceptible stands of ponderosa pine? Research Note RM-45, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 4 p.

Bentz, B.J.; Kegley, S.; Gibson, K.; Their, R. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) attacks. Journal of Economic Entomology 98: 1614-1621.

Borden, J.H.; Ryker, L.C.; Chong, L.J.; Pierce, H.D. Jr.; Johnston, B.D.; Oehlschlager, A.C. 1987. Response of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. Canadian Journal of Forest Research 17: 118-128.

Elkinton, J.; Carde, R.; Mason, C. 1984. Evaluation of time-average dispersion models for estimating pheromone concentration in a deciduous forest. Journal of Chemical Ecology 10: 1081-1108.

Gibson, K.E.; Schmitz, R.F.; Amman, G.D.; Oakes, R.D. 1991. Mountain pine beetles response to different verbenone dosages in pine stands of western Montana. Research Paper INT-444, USDA Forest Service, Intermountain Research Station, Ogden, UT. 11 p.

Holsten, E.H.; Webb, W.; Shea, P.J.; Werner, R.A. 2002. Release rates of methylcyclohexenone and verbenone from bubble caps and bead releasers under field conditions suitable for the management of bark beetles in California, Oregon, and Alaska. Research Paper PNW-RP-544, USDA Forest Service, Pacific Northwest Research Station 21 p.

Lindgren, B.S.; Borden, J.H.; Cushon, G.H.; Chong, L.J.; Higgins, C.J. 1989. Reductions of mountain pine beetle (Coleoptera: Scolytidae) attacks by verbenone in lodgepole pine stands in British Columbia. Canadian Journal of Forest Research 19: 65-68.

Lister, C.K.; Schmid, J.M.; Mata, S.A.; Haneman, D.; O'Neil, C.; Passek, J.; Sower, L. 1990. Verbenone bubble caps ineffective as a preventive strategy against mountain pine beetle attacks in ponderosa pine. Research Note RM-501, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 3 p.

Mafra-Neto, A.; Carde, R.T. 1994. Fine-scale structure of pheromone plume modulates upwind orientation of flying moths. Nature 369: 142-144.

McMillin, J.J.; Allen, K.E. 1999. Evaluation of mountain pine beetle activity in the Black Hills National Forest. Forest Health, USDA Forest Service, Renewable Resources, Rocky Mountain Region. Biological Evaluation R2-00-03. 18 p.

Miller, D.R.; Borden, J.H.; Lindgren, B.S. 1995. Verbenone: dose-dependent interruption of pheromone based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). Environmental Entomology 24: 692-696.

Mielke, P.W., Jr.; Kenneth, B.J. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York. 352 p.

Murlis, J.; Jones, C. 1981. Fine scale structure of odour plumes in relation to insect orientation to distance pheromone and other attractant sources. Physiological Entomology 6: 71-86.

Petrondas, D.A.; Gabriel, K.R. 1983. Multiple comparisons by rerandomization tests. Journal of the American Statistical Association 78: 949-957.

Progar, R.A. 2005. Five-year operational trial of verbenone to deter mountain pine beetle (*Dendroctonus ponderosae*; Coleoptera: Scolytidae) attack of lodgepole pine (*Pinus contorta*). Environmental Entomology 34: 1402-1407.

Schmid, J.M.; Mata, S.A.; Allen, D.C. 1992. Potential influences of horizontal and vertical air movement in ponderosa pine stands on mountain pine beetle dispersal. Research Note RM-516. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.

Schmid, J.M.; Mata, S.A.; Olsen, W.K. 1995. Microclimate and mountain pine beetles in two ponderosa pine stands in the Black Hills. Research Note RM-532, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 12 p.

Schmitz, R.F.; McGregor, M.D. 1990. Antiaggregative effect of verbenone on response of the mountain pine beetle to baited traps. Research Paper INT-423, USDA Forest Service, Intermountain Research Station, Ogden, UT. 7 p.

Thistle, H.W.; Peterson, H.; Alwine, G.; Lamb, B.; Edburg, S.; Strom, B. 2005. The influence of stand thinning on surrogate pheromone plumes. In: Proceedings 16th U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species, 2005. 18-21 January, Annapolis, MD. General Technical Report NE-337, USDA Forest Service, Northeastern Research Station, Newtown Square, PA.

You may order additional copies of this publication by sending your mailing information in label form through one of the following media. Please specify the publication title and series number.

Fort Collins Service Center

Telephone (970) 498-1392
FAX (970) 498-1122
E-mail rschneider@fs.fed.us
Web site http://www.fs.fed.us/rm
Mailing address Publications Distribution
Rocky Mountain Research Station
240 West Prospect Road
Fort Collins, CO 80526

Rocky Mountain Research Station
Natural Resources Research Center
2150 Centre Avenue, Building A
Fort Collins, CO 80526

RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of the National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

Research Locations

Flagstaff, Arizona	Reno, Nevada
Fort Collins, Colorado*	Albuquerque, New Mexico
Boise, Idaho	Rapid City, South Dakota
Moscow, Idaho	Logan, Utah
Bozeman, Montana	Ogden, Utah
Missoula, Montana	Provo, Utah

*Station Headquarters, Natural Resources Research Center, 2150 Centre Avenue, Building A, Fort Collins, CO 80526.

Federal Recycling Program Printed on Recycled Paper