Five-Year Operational Trial of Verbenone to Deter Mountain Pine Beetle (*Dendroctonus ponderosae*; Coleoptera: Scolytidae) Attack of Lodgepole Pine (*Pinus contorta*)

R. A. PROGAR[1]

USDA Forest Service, PNW Research Station, Forest Science Laboratory, Corvallis, OR 97330

Environ. Entomol. 34(6): 1402–1407 (2005)

ABSTRACT The antiaggregation pheromone verbenone was operationally tested for 5 yr to deter mass attack by the mountain pine beetle on lodgepole pine in campgrounds and administrative areas surrounding Redfish and Little Redfish Lakes at the Sawtooth National Recreation Area in central Idaho. Each year, five-gram verbenone pouches were evenly distributed (≈10 m apart) within seven of 14 0.2-ha plots. During the first 2 yr of the study a median of 12% of the host trees >13 cm dbh were attacked and killed on the treated plots, whereas trees on the untreated plots incurred a median mortality of 59%. When ≈50% of the trees on the untreated plots were killed a detectable beetle response to verbenone on the treated plots dramatically declined. After 5 yr, mountain pine beetle had killed a median of 87% of the lodgepole pine trees >13 cm in untreated plots and 67% in plots containing verbenone pouches. Beetle pressure was higher on untreated plots in 2000 and 2001, nearly equal between treatments in 2002, higher on verbenone-treated plots in 2003, and similar between treatments in 2004. It is hypothesized that the lack of response to verbenone after 2 yr may be related to both population size and spatial scale, i.e., large numbers of vigorous beetles in a local area with a reduced number of preferred large-diameter trees become crowded and stressed, causing a decline in the response to verbenone. The 2-yr delay in widespread pine mortality caused by verbenone would have given land managers time to use other management tactics to deter catastrophic loss of trees caused by mountain pine beetle.

KEY WORDS pheromone, verbenone, mountain pine beetle, lodgepole pine

MOUNTAIN PINE BEETLE (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), is one of the most aggressive bark beetles in North America (Furniss and Carolin 1977) attacking healthy green host trees. Populations build up to outbreak levels every 20–40 yr and outbreaks may last for 20 yr or more (Parker and Stipe 1995). Most of the large dominant lodgepole pine, *Pinus contorta* variety *latifolia* Engelmann, are killed over vast areas (Cole and Amman 1969, Roe and Amman 1970, Safranyik et al. 1974, Amman 1977, Klein et al. 1978, Kegely et al. 2003, Jorgensen and Mocettini 2004). Large trees provide thick phloem that enables offspring a higher probability of survival (Amman 1969, 1975, Klein et al. 1978). As much as 70–90% of the lodgepole pine >13 cm (5 in) in diameter at breast height (dbh) may be killed (McGregor et al., 1987). The evolutionary relationship between MPB, lodgepole pine, and a host of predators, parasites, and microorganisms comprises a dynamic ecological relation that affects succession, diversity, and climate. (The effects of mountain pine beetle on forest structure, stand composition, and fire regimens [Safranyik et al. 1974, Amman 1977, Parker and Stipe 1993] may have severe impacts on economic and recreational resources.)

Current management practices to reduce tree mortality by MPB in a general forest setting rely primarily on stand manipulation to remove infested and susceptible trees (Amman and Baker 1972, Amman et al. 1977, Amman et al. 1991, Anhold et al. 1996). In recreation sites or administrative areas, insecticidal sprays are effective for protecting individual high value trees (Gibson 1982, Gibson and Bennett 1985, Shea and McGregor 1987, Hastings et al. 2001). These approaches, however, have limitations. High value areas are often in or near riparian zones where the use of pesticides is restricted due to potential effects on aquatic fauna. Baiting trees with aggregation pheromone can be used to contain and concentrate infestations prior to sanitation harvesting (Gray and Borden 1989). Beetle behavior has been influenced through the combined application of antiaggregation and aggregation pheromones used as a "push/pull" strategy (Ross and Daterman 1994). More recently, emphasis has been placed on deterring attack by mountain pine beetle using the antiaggregant verbenone alone (4,5,5-trimethylbicyclo [3.1.1] hept-3-en-2-one) (Lindgren et al. 1989, Amman et al. 1989,

[1] Corresponding author, e-mail: rprogar@fs.fed.us.

Amman et al. 1991, Gibson et al. 1991, Kegley et al. 2003, Bentz et al. 2004) and in combination with non-host volatiles (Wilson et al. 1996, Huber and Borden 2000, Borden et al. 2003).

The inconsistencies of verbenone for managing populations of mountain pine beetle are well documented. Early tests of verbenone showed significantly less mortality on treated plots than untreated plots with a trend of lower mortality with increasing verbenone dose, although plots treated with the highest dose incurred the highest mortality (Lindgren et al. 1989, Amman et al. 1991, Gibson et al. 1991, Safranyik et al. 1992, Amman and Lindgren 1995). Subsequent tests gave inconsistent or ambiguous results over time, geographical area (Gibson et al. 1991), or tree species (Bentz et al. 1989). However, reasons for the inconsistencies are uncertain. Amman and Lindgren (1995) list several potential explanations: (1) Beetle caused changes in stand structure alter the microclimate to permit the verbenone pheromone plume to dissipate above the tree canopy rather than disperse among the tree boles (Schmitz et al. 1989, Shea et al. 1992). (2) Weather-related factors such as higher temperatures may promote elution of the verbenone before beetle flight ends, causing the tests to fail. (3) Beetles may alter their response to verbenone with increasing age of an outbreak; late outbreak infestations of small diameter trees with thin phloem produce small, weak beetles that may be attracted to, or ignore, the verbenone signal. (4) Large populations of beetles at the peak of an outbreak may overwhelm the verbenone treatments. (5) Low beetle populations lead to nonsignificant results. (6) Exposure of verbenone to light causes photoisomerization to chrysanthenone, a compound to which beetles do not respond (Kostyk et al. 1993). (7) The release rate from the bubblecaps (PheroTech, Delta, British Columbia, Canada) used in early studies was too low to achieve consistent results (Borden et al. 2003). This led PheroTech to develop a high-dose verbenone pouch.

The objective of this study was to operationally test the ability of verbenone to deter mass attack of mountain pine beetle in susceptible lodge pole pine stands for the duration of an outbreak. All other studies using verbenone have been conducted for a single season or the investigator used different plots in different years, moving to different locations when beetle caused mortality became too high. Mountain pine beetle outbreaks occur over several years (Cole and Amman 1980), with populations increasing as long as trees of a suitable dbh are available (Cole and Amman 1980). With beetle populations changing with host availability (Cole and Amman 1980), stand structure changed with beetle caused mortality (Amman and Cole 1983), and a possible change in beetle response to verbenone with increasing levels of stress on the beetle population (Amman and Lindgren 1995), a prudent operational test of the ability of verbenone to deter beetle-caused mortality, should be conducted on the same study plots for the entire span of an outbreak. This study is unique from other studies testing the ability of verbenone to deter mountain pine beetle attack of lodgepole pine because it operationally evaluates the ability of verbenone to deter mass attack by mountain pine beetle among different dbh size class trees for the duration of a mountain pine beetle outbreak.

Materials and Methods

Fourteen 0.2-ha plots (30 by 67 m) were established along the shoreline of Little Redfish and Redfish lakes (115°0′00″ W, 44°7′30″ N) in the Sawtooth National Recreation Area (SNRA) in central Idaho in 2000. At the beginning of the study, the dbh of all trees on each plot was surveyed. The plots were randomized, and one-half were treated with pouches containing 5 g of 98% technical grade verbenone, 80% releasing the compound at ≈25 mg/24 h at 20°C (Phero Tech). Verbenone pouches were affixed 4 m above the ground on the north-facing side of the same 20 lodgepole pines, at a spacing of 10 m, providing a treatment of 20 pouches per plot. After beetle flight each year, all plot trees were examined for beetle attack. Trees were considered to be successfully mass attacked when the circumference of the tree bole was covered with pitch tubes or the ground at the base of the tree was covered with bark dust from beetle boring. The foliage of successfully attacked trees yellows within a few months after attack, turning red within a year, indicating tree death.

Tree mortality was measured on the same plots across 5 yr. The data covariance matrix did not have the required compound symmetry form for univariate analysis, therefore repeated-measures multivariate analysis of variance was used to analyze the data (Crowder and Hand 1996, Ramsey and Schafer 1997). An arcsine square-root transformation was used to stabilize the variance and satisfy the assumptions of ANOVA for the proportion data (Sokal and Rohlf 1981). The median proportions of mortality for untransformed data are reported in the figures. Beetle pressure was defined as the ratio of the number of current attacks (trees killed) divided by the number of suitable host trees remaining on the plots. One-way ANOVA (Sokal and Rohlf 1981) was used to test for differences in beetle pressure between treated and untreated plots each study year.

Results

Pretreatment analysis showed no significant difference in the number of host trees between plots receiving verbenone and those in the untreated check (Progar 2003). When the plots were established in 2000, there was an average of 0.08 currently infested trees on the untreated plots and 0.27 infested trees on plots containing verbenone. During the course of the mountain pine beetle outbreak, most of the suitable host trees (>13 cm) in the study were killed by beetles regardless of the presence of the antiaggregant verbenone. In plots without verbenone pouches, a median of 87% of the lodgepole pine trees >13 cm were killed, and 67% of the suitable host trees in plots containing verbenone pouches were killed (Fig. 1). At

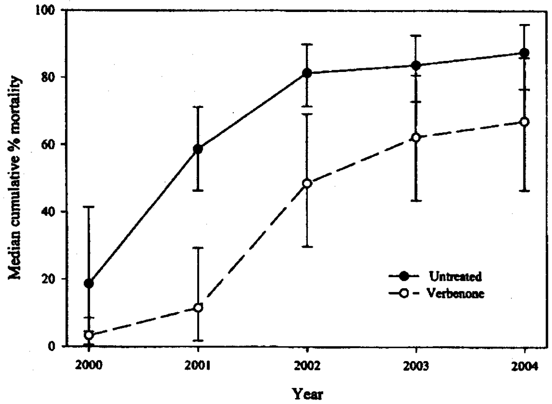

Fig. 1. Median percent mortality of lodgepole pine >13 cm dbh on plots treated with verbenone pouches and untreated plots during a mountain pine beetle outbreak. Analysis of data with repeated-measures MANOVA indicated there was no evidence that the cumulative proportion of trees killed by MPB was different between treatments ($F = 2.16$; df = 3,10; $P = 0.16$). Vertical bars are the 95% confidence interval of the median response.

the conclusion of the study there was no evidence that the proportion of dead trees on plots containing verbenone was different than the proportion of tree mortality on untreated plots ($F = 2.16$; df = 3,10; $P = 0.16$). When median cumulative percent mortality was partitioned by size class, it was evident that mortality was higher and occurred earlier in the outbreak in trees in size classes that were >28 cm (Fig. 2).

Beetle pressure was higher on untreated plots in 2000 ($F = 3.53$; df = 1,12; $P = 0.08$; Fig. 3) and in 2001 ($F = 6.55$; df = 1,12; $P = 0.02$). In 2002, the ratio of trees that were attacked and killed by mountain pine beetles to living trees >13 cm dbh was nearly equal ($F = 0.0025$; df = 1,12; $P = 0.96$). In 2003, beetle pressure was higher on plots containing verbenone pouches than on plots that were untreated ($F = 6.55$; df = 1,12; $P = 0.02$). In 2004, beetle pressure was similar between treated plots ($F = 0.06$; df = 1,12; $P = 0.80$).

The elution rate of verbenone was given as 25 mg/d at 20°C. Redfish and Little Redfish Lakes are at 1,500–1,800 m in elevation in the Idaho Batholith. The average summer temperature is 13°C and ranges from an average low of 2°C to an average high of 24°C (Western Regional Climate Center). July is the warmest month of the year with an average of 14°C and ranging between 2 and 26°C. In 2002 and 2003, the temperatures averaged 2.7°C higher at 16.6° and 16.1°C in July. The average maximum temperatures in both years were also higher at 28 and 25°C, respectively. At these temperatures, verbenone elutes at the rate defined by the manufacturer (RD-0372/000; PheroTech), and there was ample volume in the pouch to encompass the flight period of the beetle (late June to early September) (Progar 2003).

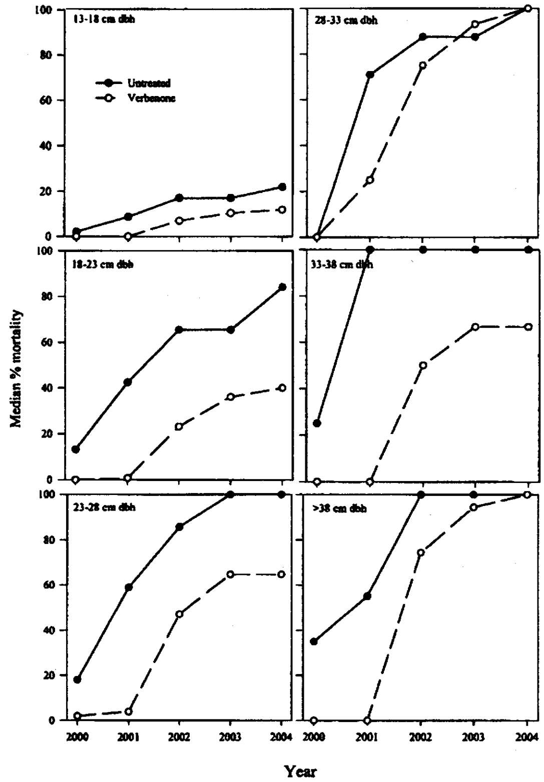

Fig. 2. Median cumulative percent mortality of trees in 5-cm size classes from 13 to >38 cm dbh on plots treated with verbenone and untreated plots during a mountain pine beetle outbreak around Redfish and Little Redfish Lakes at the Sawtooth National Recreation Area in central Idaho.

Discussion

These results show that verbenone treatment alone can partially protect high-hazard stands from attack by the mountain pine beetle at the beginning of an outbreak. However, in the absence of other management tactics to suppress the population (Amman et al. 1977, Gibson 1982, Gibson and Bennett 1985, Shea and McGregor 1987), verbenone alone will not save a stand from devastating mortality. These results are comparable to a previous study (Amman and Lindgren 1995) in which significant verbenone treatment effects were detected in 1988 and 1989, but not in 1990 and 1991, regardless of the application rate. In trials conducted in 1990 and 1991, most of the large diameter trees preferred by mountain pine beetles had been killed in previous years of the outbreak (Amman and Lindgren 1995). As the preferred host material was depleted, beetles were compelled to occupy smaller, less suitable diameter trees for brood development. In the Amman and Lindgren study (1995) and in this study, attack on the larger, most desirable host trees occurred in the early years of the outbreak and apparently enabled the population density to increase strikingly. As a result, the beetle population may have simply overwhelmed the verbenone

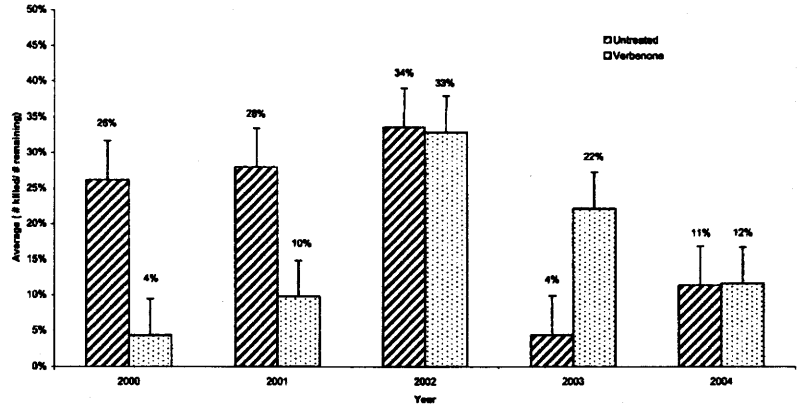

Fig. 3. Average number of beetle killed trees divided by the average number of available trees of suitable dbh for MPB attack indicates beetle pressure on untreated and plots treated with verbenone. Vertical bars are ±SE.

treatment signal (Amman and Lindgren 1995). Higher beetle populations over years would produce more verbenone, increasing the ambient level in the stand and potentially obscuring the verbenone signal from the treated plots. The increasing amounts of naturally produced verbenone most likely lessened the gradient between the treated plots and surrounding untreated areas. In addition, when verbenone levels are high and the number of available hosts are limited, beetles may remain in a treated area long enough to become habituated, after which they would be incapable of responding to the verbenone signal (J. H. Borden, 2004).

One of the most interesting observations from this study is the relatively quick change in the response of mountain pine beetles to verbenone. During the first 2 yr of the outbreak (2000–2001), only a slight increase in beetle caused mortality (median 12%) occurred in the verbenone-treated plots. During this period, nearly 60% of the suitable host trees had been killed by beetles on the untreated plots (Fig. 1). Assuming that the untreated plots were representative of beetle attack at the landscape level, the emergent population in the third year of this study (2002) would have been huge, and because they emerged from larger diameter trees, their vigor would have been high (Atkins 1975, Amman and Cole 1983). Therefore, MPB populations are increasing at the landscape scale, and the abundance of suitable hosts is decreasing simultaneously. The verbenone-treated plots had become islands of desirable hosts in the midst of a vast area made devoid of larger living trees by mountain pine beetles. Even though the ratio between the portion of available suitable host trees and trees under current attack was similar between treatments in the third year (2002) (Fig. 3), nearly twice as many trees were mass attacked and killed on the plots containing verbenone than on untreated plots because the treatment deterred beetle attack during 2000–2001. Thus, the lack of response to verbenone in the third year may be related to both population size and spatial scale, i.e., large numbers of vigorous beetles in a local area with a reduced number of available large-diameter trees. The preference for large-diameter trees may be of greater adaptive significance than the avoidance of potential intraspecific competition (signaled by verbenone). Hence, in the third year, the beetles would have oriented visually to, and attacked, the large diameter trees within the relatively small verbenone-treated plots (Fig. 2). Also, at high population levels, beetles may be unable to avoid intraspecific competition no matter which tree the beetles choose; therefore, the verbenone signal would have no meaning and the beetle would not respond.

Supporting the hypothesis of Amman and Cole (1983) and Atkins (1975), the beetles emerging during the later years of the outbreak would have developed in smaller trees with thin phloem. They would have been small, weak, and with low content of body fat. This could impair their ability to disperse long distances, so they remained close to the trees from which they emerged and attacked the largest trees they could find, regardless of the presence of verbenone. It is not know whether these physiologically weak beetles have a higher threshold response to verbenone than stronger beetles.

Verbenone did delay the onset of outbreak scale mortality on the treated plots for 2 yr. There was slight mortality (3%) during the first treatment year (2000); therefore, earlier application most likely would not have deterred mass attack. The delay in mass attack in the treated areas would provide forest managers the opportunity to implement a multiyear integrated pest management (IPM) program that incorporated additional management techniques. These could include thinning of high hazard trees (Amman et al. 1977) and sanitation harvesting, as well as felling and burning or insecticidal sprays applied to protect individual trees (Gibson 1982, Gibson and Bennett 1985, Shea and McGregor 1987). Structural changes in stand characteristics from such treatments will influence attack behavior of the insect, thereby reducing residual tree susceptibility (Bartos and Booth 1994, Anhold et al. 1996). To maximize the chance of success, these tactics would need to begin in the first year of an outbreak, when only 5–10% of the trees are infested. This would probably have been the year before the start of this study (Fig. 1).

Acknowledgments

Thanks to D. Bennett, J. Borden, K. Gibson, R. Kelsey, S. Munson, B. Strom, and R. Thier for helpful reviews of this manuscript. Also thanks to D. Bennett, B. Bentz, M. Hansen, C. Jorgensen, D. Halsey, P. Mocettini, R. Their, and J. Vandygriff for expertise and field assistance.

References Cited

Amman, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole bark. Research Note INT-96, Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 8 pp.

Amman, G.D. 1975. Insects affecting lodgepole pine productivity, pp. 310–341. *In* D. M. Baumgartner (ed.), Management of lodgepole pine ecosystems: symposium and proceedings 9–11 October 1973, Pullman, WA. Washington State University Cooperative Ext. Serv. pp. 310–341.

Amman, G.D. 1977. The role of mountain pine beetle in lodgepole pine ecosystems: impact on succession. *In* J. Mattson (ed.), Proceedings in life sciences: the role of arthropods in forest ecosystems. Springer: New York.

Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole stand and structure. J. For. 7: 204–205.

Amman, G.D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: population dynamics. USDA For. Serv. Gen. Tech. Rep. INT-145. 59 pp. Ogden, UT.

Amman, G.D., and B.S. Lindgren. 1995. Semiochemicals for management of mountain pine beetle: status of research and application. USDA For. Serv. Gen. Tech. Rep. INT-GTR-318. 22 pp. Ogden, UT.

Amman, G. D., M. D. McGregor, D. B. Cahill, and W. H. Klein. 1977. Guidelines for reducing the losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA For. Serv. Gen. Tech. Rep. INT-36. 19 pp. Ogden, UT.

Amman, G. D., R. W. Thier, M. D. McGregor, and R. F. Schmitz. 1989. Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetles in Idaho. Can. J. For. Res. 19: 60–64.

Amman, G. D., R. W. Thier, J. C. Weatherby, L. A. Rasmussen, and S. A. Munson. 1991. Optimum dosage of verbenone to reduce infestation of mountain pine beetle in lodgepole pine stands of central Idaho. USDA For. Serv. Rep. INT-440. 5 pp. Ogden, UT.

Anhold, J. A., M. J. Jenkins, and J. N. Long. 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. W. J. Appl. For. 11: 50–53.

Atkins, M. D. 1975. On factors affecting the size, fat content and behavior of a scolytid. Z. Ang. Entomol. 78: 209–218.

Bartos, D. L., and G. D. Booth. 1994. Effects of thinning on temperature dynamics and mountain pine beetle activity in an lodgepole pine stand. USDA For. Serv. Intermountain Res. Sta. INT-RD-479. 9 pp. Ogden, UT.

Bentz, B., C. K. Lister, J. M. Schmid, D. A. Mata, L. A. Rasmussen, and D. Haneman. 1989. Does verbenone reduce mountain pine beetle attacks in susceptible stands of ponderosa pine? USDA For. Serv. RMRS Rep. RM-495. 4 pp. Ogden, UT.

Bentz, B., S. Kegley, K. Gibson, and R. Thier. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae scolytinae) attacks. J. Econ. Entomol. (in press).

Borden, J. H., L. J. Chong, T. J. Earle, and D.P.W. Huber. 2003. Protection of lodgepole from attack by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using high doses of verbenone in combination with nonhost bark volatiles. For. Chron. 79: 685–691.

Cole, W. E., and G. D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA For. Exp. Sta. Res. Note INT-95. 7 pp. Ogden, UT.

Cole, W. E., and G. D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: course of an infestation. USDA For. Serv. Gen. Tech. Rep. INT-89. 56 pp. Ogden, UT.

Crowder, M. J., and D. J. Hand. 1996. Analysis of repeated measures. Chapman & Hall, London, UK. 257 pp.

Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. U.S. Dep. Agric. Forest Service, Pub. No. 1339. 654 pp. Washington, DC.

Gibson, K. E. 1982. Management alternatives for lodgepole pine recreational facilities threatened by the mountain pine beetle. U.S. Dep. Agric. Forest Service Pest Mgmt. Rep. 82-27. 3 pp. Missoula, MT.

Gibson, K. E., and D. D. Bennett. 1985. Carbaryl prevents attacks on lodgepole pine by mountain pine beetle. J. For. 83: 109–112.

Gibson, K. E., R. F. Schmitz, G. D. Amman, and R. D. Oakes. 1991. Mountain pine beetle response to different verbenone dosages in pine stands of western Montana. USDA For. Serv. Res. Pap. INT-444. 11 pp.

Gray, D. R., and J. H. Borden. 1989. Containment and concentration of mountain pine beetle (Coleoptera: Scolytidae) infestations with semiochemicals: validation by sampling of baited and surrounding zones. J. Econ. Entomol. 82: 1399–1405.

Hastings, F. L., E. H. Holsten, P. J. Shea, and R. A. Werner. 2001. Carbaryl: a review of its use against bark beetles in coniferous forests of North America. Environ. Entomol. 30: 803–810.

Huber, D.P.W., and J. H. Borden. 2000. Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. Entomol. Exp. Appl. 92: 131–141.

Jorgensen, C., and P. Mocettini. 2004. Monitoring mountain pine beetle-caused mortality of lodgepole pine in the sawtooth and bear valleys of south central Idaho. Rep. #BFO-PR-05-01. 9 pp.

Kegley, S., K. Gibson, J. Schwandt, and M. Marsden. 2003. A test of verbenone to protect individual whitebark pine from mountain pine beetle attack. USDA For. Serv. Rep. 03-9. 6 pp.

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

Kostyk, B. C., J. H. Borden, and G. Gries. 1993. Photoisomerization of antiaggregation pheromone verbenone: biological and practical implications with respect to the mountain pine beetle, *Dendroctonus ponderosae* I Hopkins (Coleoptera: Scolytidae). J. Chem. Ecol. 19: 1749–1759.

Lindgren, B. S., J. H. Borden, G. H. Cushon, L. J. Chong, and C. J. Higgins. 1989. Reductions of mountain pine beetle (Coleoptera: Scolytidae) attacks by verbenone in lodgepole pine stands in British Columbia. Can. J. For. Res. 19: 65–68.

McGregor, M. D., G. D. Amman, R. F. Schmitz, and R.D. Oakes. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Can. J. For. Res. 17: 1234–1239.

Parker, D. L., and L. E. Stipe. 1993. A sequence of destruction: mountain pine beetle and wildfire. USDA For. Serv. SW Region, Yellowstone Nat. Park.

Progar, RA. 2003. 2000–2002 Redfish Lake verbenone trial progress report. USDA For. Serv. Rep. BFO-TR-03-01. 16 pp.

Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, London, UK

Roe, A. L., and G. D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. U.S. Dep. Agric. Forest Service, Odgen, UT.

Ross, D. W., and G. E. Daterman. 1994. Reduction of Douglas-fir beetle infestation of high risk stands by antiaggregation and aggregation pheromones. Can. J. For. Res. 24: 2184–2190.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. For. Tech. Rep. 1 Environment Canada For. Serv., Victoria, BC. 24 pp.

Safranyik, L., T. L. Shore, D. A. Linton, and B.S. Lindgren. 1992. The effect of verbenone on dispersal and attack of the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Colepotera: Scolytidae) in a lodgepole pine stand. J. Appl. Entomol. 113: 391–397.

Schmitz, R. F., M. D. McGregor, G. D. Amman, and R. D. Oakes. 1989. Effects of partial cutting treatments of lodgepole pine stands on the abundance and behavior of flying mountain pine beetles. Can. J. For. Res. 19: 566–574.

Shea, P. J., and M. McGregor. 1987. A new formulation and reduced rates of carbaryl for protecting lodgepole pine from mountain pine beetle attack. W. J. Appl. For. 2: 114–116.

Shea, P. J., M. D. McGregor, and G. E. Daterman. 1992. Aerial application of verbenone reduces attack of lodgepole pine by mountain pine beetle. Can. J. For. Res. 22: 436–441.

Sokal, R. R., and F. J. Rolf. 1981. Biometry. W. H. Freeman and Company, New York.

Western Regional Climate Center. 2005. Website: http://www.wrcc.dri.edu/index.html.

Wilson, I. M., J. H. Borden, R. Gries, and G. Gries. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J. Chem. Ecol. 22: 1861–1874.

Received for publication 2 April 2005; accepted 26 July 2005.