A Test of High-Dose Verbenone for Stand-Level Protection of Lodgepole and Whitebark Pine from Mountain Pine Beetle (Coleoptera: Curculionidae: Scolytinae) Attacks

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ABSTRACT The efficacy of verbenone as a stand-level protectant against mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attacks was tested in lodgepole and whitebark pine stands at five geographically separated sites, including three consecutive years at one site. Forty and 20 high-dose pouches, with a verbenone emission rate up to 50 mg/d per pouch, were spaced in a grid pattern throughout 0.40-ha plots, replicated up to six times at each site. Although the verbenone treatment did not prevent beetles from dispersing through treated stands, attacking large-diameter trees most frequently, the overall number of trees attacked was, on average, reduced significantly compared with nontreated stands. In a few blocks each year, verbenone-treated plots had more attacked trees than controls. These blocks tended to have a large emerging beetle population, exceeding 140 previously attacked trees within the hectare including and surrounding the treated area. Additional research is needed on the behavioral role of verbenone in mountain pine beetle population dynamics and quantification of the infestation level above which treatment efficacy tends to be reduced.

KEY WORDS bark beetle, pheromone, biological control, semiochemical, *Dendroctonus ponderosae*

BARK BEETLES IN THE GENUS *Dendroctonus* (Coleoptera: Curculionidae: Scolytinae) use kairomones and pheromones in the process of host selection and colonization (Wood 1973, Raffa 2001). For those species that attack living trees, it is particularly important to cooperate with conspecifics to overcome the resinous defensive mechanisms of host trees. A mass attack of individuals on a single tree over a short time (e.g., 3 to 4 d) is accomplished using species-specific pheromones that are biosynthesized either from de novo pathways or host tree precursors (Seybold et al. 2000). For example, after host selection and during the process of boring through the tree bark into the phloem, female mountain pine beetles, *Dendroctonus ponderosae* Hopkins, convert the host tree monoterpene α-pinene into *trans*-verbenol, a pheromone that attracts both sexes (Hughes 1973). *exo*-Brevicomin is produced de nova (Seybold and Tittiger 2003) by responding males and at low concentrations primarily attracts females (Conn et al. 1983), although it may inhibit beetles at higher concentrations (Rudinsky et al. 1974, Borden et al. 1987). This complex system of chemical communication concentrates an aggregation of individuals on a single focus tree, which is selectively advantageous for species such as the mountain pine beetle in overcoming tree host defensive mechanisms. As with most herbivores, however, there is an optimal density range of individuals on an exhaustible food resource (Pianka 1981).

One mechanism hypothesized to play a role in the termination of bark beetle attacks on a single tree is inhibitory pheromones and kairomones (Renwick and Vité 1970, Geiszler et al. 1980, Borden 1982, Berryman et al. 1985). Verbenone, 4,6,6-trimethylbicyclo[3.1.1]-hept-3-en-2-one, was first found associated with male *Dendroctonus frontalis* Zimmermann and *Dendroctonus brevicomis* LeConte (Renwick 1967) and subsequently has been found in association with several additional species of bark beetles (Pitman et al. 1969, Renwick and Vité 1970, Hughes et al. 1976). Verbenone is thought to have a general inhibitory effect (Borden et al. 2003), especially with phloeophagous insects using fresh phloem (Lindgren and Miller 2002). It is produced through a variety of pathways, including autoxidation of the oxygenated monoterpene α-pinene (found in pine phloem) in the absence of bark beetles (Hunt et al. 1989, Flechtmann et al. 1999), by bark beetles themselves (Rudinsky et al. 1974), and principally by metabolic conversion of *trans*-verbenol by yeasts and gut microorganisms associated with adult bark beetles (Leufvén et al. 1984, Hunt and Borden 1989). Although verbenone has been found to be associated with adult mountain pine beetle (Pureswaran et al. 2000), often only as a trace

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(Pitman et al. 1969), evidence suggests that microorganisms associated with beetles, including yeasts, are required for the production (Hunt and Borden 1989). The exact role of verbenone in bark beetle population dynamics is unclear, although behavioral inhibition is thought to have evolved as a response to host tissue degradation (Lindgren and Miller 2002) and intraspecific competition (Borden et al. 1987), perhaps when sensed as a threshold ratio of verbenone to attractive compounds (Raffa and Berryman 1983, Pureswaran et al. 2000, Pureswaran and Borden 2003).

When added to attractant-baited traps, verbenone reduced the catch of mountain pine beetles compared with traps with the attractants alone (Ryker and Yandell 1983, Borden et al. 1987, Schmitz and McGregor 1990, Miller et al. 1995, Lindgren and Miller 2002). In addition, verbenone reduced the mean attack density on trees baited with attractants (Borden and Lindgren 1988) and reduced the number of infested trees when applied in a grid manner throughout a stand (Amman et al. 1989, Lindgren et al. 1989). However, results from further stand level tests were inconsistent among years, stands, and host tree species (Bentz et al. 1989, Amman et al. 1991, Gibson et al. 1991, Shea et al. 1991, Shore et al. 1991, Amman and Lindgren 1995). More recently, Progar (2003) and Borden et al. (2003) observed that verbenone releasing at a higher dose improved stand level protection.

Throughout North America, bark beetle caused tree mortality is occurring at levels not recorded previously (Samman and Logan 2000). Although the causes are varied and complex, recent warming trends associated with climate change are having a significant influence on increased bark beetle activity (Logan and Powell 2001, Berg 2003), and the development, survival, and distribution of insect herbivores worldwide (Hill et al. 1999, Bale et al. 2002, Watt and McFarlane 2002). In recent years, the mountain pine beetle has expanded its range into lodgepole pine, *Pinus contorta* Dougl., forests in northern British Columbia that were previously thermally unsuitable for sustaining populations (Carroll et al. 2004). Ecologically important, high elevation species such as whitebark pine, *Pinus albicaulis* Engelm., in the western United States also are experiencing increased levels of mountain pine beetle activity (Keane and Arno 1993, Logan and Powell 2001, Meyer 2005), similar to the major outbreaks that occurred in these ecosystems during the warm periods of the 1930s and 1940s (Perkins and Swetnam 1996). Our objective was to test the efficacy and consistency of high doses of verbenone for protecting stands of high-value lodgepole pine and whitebark pine from mountain pine attack.

Materials and Methods

2001. Four study sites, two in whitebark pine and two in lodgepole pine, were chosen in June 2001 in areas of active mountain pine beetle populations in Idaho and Montana (Table 1). A randomized block design, replicated up to six times in each site, was used to test for differences among treatments. Each block consisted of two 63.6 by 63.6-m (0.40-ha) plots separated by at least 60 m. All blocks within a site were ≥100 m apart. An attempt was made to select blocks that had similar mountain pine beetle infestation rates in each plot. Also, to ensure mountain pine beetle pressure, plots were selected so that a minimum of three mountain pine beetle-infested trees were inside the plot or within 15 m of its boundary (Table 2).

Control (untreated) and verbenone pouch treatments were randomly assigned to each plot within a block. Forty verbenone pouches [84% (−)-enantiomer, 98% purity, 5.0-g releasing 50 mg/d at 30°C] (Phero Tech, Inc., Delta, British Columbia, Canada) were placed within each plot in a grid manner, attaching one pouch to the north face of the nearest tree, 2 m from the ground. At Snowbank-WB-01, which has a clumpy stem distribution of whitebark pine, verbenone pouches were placed on the north face of 1-m-tall stakes in areas with no trees to maintain a grid pattern. To ensure adequate beetle pressure, in all sites except Sawtooth-LP-01, a multiple-funnel trap (Lindgren 1983) baited with *trans*-verbenol and *exo*-brevicomin (Phero Tech, Inc.) was placed at the center of each plot. Verbenone and baited traps were placed in lodgepole pine plots during the week of 25 June and in the whitebark pine plots during the week of 31 May.

After beetle flight, all trees ≥12-cm-diameter at breast height (dbh) (1.3 m) within each plot were tallied. We recorded dbh, tree species, and mountain pine beetle attack status of each tree: 1) live tree,

Table 1. Study site information for verbenone treatment trials in 2001, 2002, and 2003

Site name	Host tree species	Yr	District, Forest	Elevation (m)	Latitude
Pyramid-WB-01	Whitebark pine	2001	Bonners Ferry Ranger District, Idaho Panhandle National Forest	1,768	48° 44′
Snowbank-WB-01	Whitebark pine	2001	Cascade Ranger District, Boise National Forest, ID	2,522	44° 30′
Lolo-LP-01	Lodgepole pine	2001	Superior Ranger District, Lolo National Forest, MT	1,585	46° 27′
Sawtooth-LP-01	Lodgepole pine	2001	Sawtooth National Recreation Area, Sawtooth National Forest, ID	1,920	44° 10′
Sawtooth-LP-02	Lodgepole pine	2002	Sawtooth National Recreation Area, Sawtooth National Forest, ID	1,920	44° 10′
Deerlodge-LP-02	Lodgepole pine	2002	Deerlodge National Forest, MT	1,878	45° 60′
Sawtooth-LP-03	Lodgepole pine	2003	Sawtooth National Recreation Area, Sawtooth National Forest, ID	1,920	44° 10′

Table 2. Stand conditions and mountain pine beetle attack levels in three treatment years averaged over replicated 0.40-ha plots within each treatment

Site-host-treatment yr	Live trees, all species, ≥12.0-cm dbh	Live host trees, ≥12.0-cm dbh	Mean no. trees attacked in previous yr	Mean no. trees attacked in treatment yr	
				Mass	Strip
Sawtooth-LP-01					
Control	338 ± 36	335 ± 37	16.8 ± 3.8	54 ± 20	17 ± 9
Verbenone-40	349 ± 29	345 ± 28	30 ± 16.4	10 ± 4	4 ± 3
Lolo-LP-01					
Control	217 ± 28	198 ± 30	6.5 ± 2.7	41 ± 3	4 ± 2
Verbenone-40	224 ± 25	200 ± 32	9.8 ± 3.9	3 ± 1	2 ± 1
Pyramid-WB-01					
Control	174 ± 13	10 ± 1	5.3 ± 2.4	6 ± 2	0
Verbenone-40	183 ± 17	15 ± 2	4.0 ± 1.6	3 ± 1	0
Snowbank-WB-01					
Control	114 ± 17	79 ± 26	0.5 ± 0.5	12 ± 11	1 ± 1
Verbenone-40	103 ± 10	69 ± 14	0.75 ± 0.5	0.75 ± 0.5	0.25 ± 0.5
Sawtooth-LP-02					
Control	257 ± 25.1	247 ± 25.1	18.3 ± 6.8	29 ± 10.7	33 ± 10.2
Verbenone-40	267 ± 28.4	258 ± 27.3	30 ± 10.6	9 ± 2.6	11 ± 5.9
Deerlodge-LP-02					
Control	282 ± 13.5	197 ± 22.4	1.5 ± 1.2	26 ± 7.0	6 ± 1.8
Verbenone-40	272 ± 32.5	248 ± 38	2.5 ± 0.5	10 ± 3.8	2 ± 0.5
Verbenone-20	323 ± 26.2	312 ± 26.3	5.7 ± 2.0	14 ± 6.1	3 ± 1.4
Sawtooth-LP-03					
Control	260 ± 30	242 ± 33	44.3 ± 13.4	45 ± 17.6	28 ± 6
Verbenone-40	260 ± 30	247 ± 31	19.7 ± 6.5	11 ± 5.1	12 ± 3.0

Data are mean ± SE. Six replicated blocks were used at all sites except Pyramid-WB-01 and Snowbank-WB-01 where four replicated blocks were used. Mass attacks encompass an entire tree bole and strip attacks are only on a portion of a treebole.

2) 2001 attack, 3) 2000 attack, 4) 2001 strip attack, 5) 2000 strip attack, 6) pitch out, and 7) other mortality. Additionally, 2000 and 2001 mass attacked host trees in a 20-m buffer strip around each plot were tallied.

2002. Two lodgepole pine sites near active mountain pine beetle populations in Idaho (Sawtooth-LP-02) and Montana (Deerlodge-LP-02) were chosen to evaluate the verbenone pouches in 2002 (Table 1). Although blocks were in the same general areas, treatments for Sawtooth-LP-02 were not replicated in the same blocks as used for Sawtooth-LP-01. A randomized block design, replicated six times in each site, was used to test untreated control plots against plots with 20 or 40 verbenone pouches per 0.40 ha at Deerlodge-LP-02, and 40 pouches per 0.40 ha at Sawtooth-LP-02. Twenty and 40 verbenone pouches per 0.40 ha correspond to 50 and 100 pouches per ha. Hereafter the two treatments are referred to as V20 and V40. All other aspects of the experimental setup were identical to those in 2001. At the Deerlodge-LP-02 site, but not the Sawtooth-LP-02 site, an attractant baited multiple-funnel trap was placed at the center of each plot. Verbenone pouches were installed on 1 July at Sawtooth-LP-02 and 25 June at Deerlodge-LP-02. After beetle flight, all trees ≥12-cm dbh within each 0.40-ha plot were tallied as in 2001.

2003. Verbenone was tested at one lodgepole pine site in 2003 (Sawtooth-LP-03), the same general area used in 2001 (Sawtooth-LP-01) and 2002 (Sawtooth-LP-03) (Table 1). Because we were interested in testing the potential for long-term protection of a single stand across multiple years, two of the same blocks used in 2002 were used again in 2003. All aspects of the experimental setup were the same as in 2002 except the verbenone pouch contained 0.35 g less verbenone and released 40 mg on day 25 at 20°C (Phero Tech, Inc.). Verbenone pouches were installed on 23 June. Evaluation after beetle flight was the same as in 2001 and 2002, including a count of previous-year and current-year attacked trees in a 20-m buffer strip around each plot.

Data Analysis. For each year, all trees were coded as 0 (live) or 1 (attacked), resulting in a binomial response variable. To analyze the effect of verbenone on attack success, trees coded as 1 were either mass-attacked or strip-attacked, depending on the objective of the particular analysis. GLIMMIX, a SAS procedure for fitting generalized linear mixed models (Littell et al. 1996), was used to accommodate the random effects of site within species (whitebark or lodgepole pine) in the 2001 data, and blocks within site in the analyses for all 3 yr. Species, dbh, and treatment were tested as fixed effects and the error distribution was specified as binomial. Tukey's honestly significant difference multiple comparison procedure was performed to test for differences among treatment and dbh means. Because a different number of treatments were tested at the Deerlodge and SNRA sites in 2002, each site was analyzed separately. Because only attacked trees were counted in the 20 m buffer (0.67 ha) surrounding each plot, Poisson regression using a split-plot design within GLIMMIX was used to test for differences in attacked tree counts per ha in the 20-m buffer and within the 0.40-ha treated and control plots in 2001 and 2003.

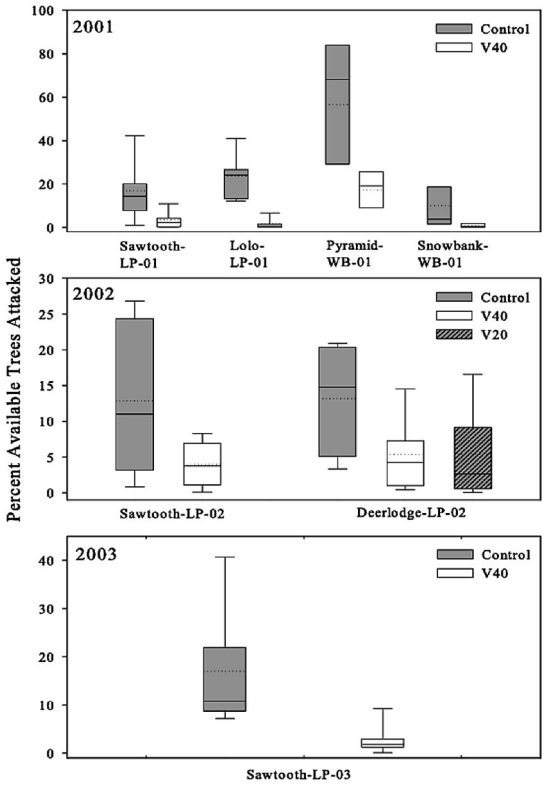

Fig. 1. Percentage of available trees mass attacked by the mountain pine beetle, averaged by site, in control, V40 (40 verbenone pouches per 0.40 ha), and V20 (20 pouches per 0.40 ha)-treated plots in 2001, 2002, and 2003. Shown are the median (dotted line), mean (solid line), and 5/95% confidence intervals (bars) for each site. See Table 1 for site information.

Results

2001. After the random effects of site and block were removed, both treatment ($F = 30.5$; df = 1, 19; $P < 0.001$) and dbh ($F = 291.6$; df = 1, 7063; $P < 0.001$) had a highly significant effect on the number of attacked trees in 2001. Significantly fewer available host trees were attacked in the V40 plots than control plots at all sites (Fig. 1). The interaction of species and dbh was also highly significant ($F = 99.2$; df = 1, 7063; $P < 0.001$), reflecting the larger size of whitebark compared with lodgepole pine ($F = 15.8$; df = 1, 7047; $P < 0.001$), and mass attacked whitebark compared with mass attacked lodgepole pine ($F = 578$; df = 1, 892; $P < 0.001$) (Table 3). Despite intersite differences in stand density and emerging mountain pine beetle population size (Table 2), species, the species × treatment interaction, and stand density were not significant in explaining the number of currently attacked trees. In V40 plots at all sites, the mean number of currently attacked trees was less than in the previous year, whereas in all control plots, except Pyramid-WB-01, the reverse trend occurred (Fig. 2).

At all sites, there were no significant differences between the treatments in the number of strip-attacked trees. At lodgepole pine sites, the number of attacked trees in the buffer strip surrounding verbenone-treated plots was not significantly greater than within the verbenone-treated plot, but it was significantly lower than the number of attacked trees within 0.40-ha control plots ($t = 4.31$, df = 4.98, $P < 0.001$) and in the buffer surrounding the control plots ($t = 2.91$, df = 4.99, $P = 0.028$). At whitebark pine sites, there was no difference in the number of attacked

Table 3. Mean dbh (centimeters) of trees mass attacked, strip attacked (including pitch-out trees), and remaining live trees (≥12.0 cm) by host type (WB, whitebark pine; LP, lodgepole pine) after treatment in 2001, 2002, and 2003

Attack type	2001[a,b]		2002[a]	2003[a]
	WB	LP	LP	LP
Live	35.02 ± 0.56a	20.88 ± 0.08d	20.62 ± 0.07a	18.24 ± 0.11a
Mass	45.06 ± 1.26b	26.54 ± 0.21e	28.71 ± 0.29b	24.33 ± 0.33b
Strip/pitch-out	27.74 ± 3.62c	22.87 ± 0.32c	24.4 ± 0.28c	21.98 ± 0.33c

Data are mean ± SE. No significant differences in dbh were found between verbenone-treated and control plots.

[a] Means within a column followed by the same letter are not significantly different ($P < 0.05$).

[b] In 2001, means within a row (between WB and LP) followed by the same letter are not significantly different ($P < 0.05$).

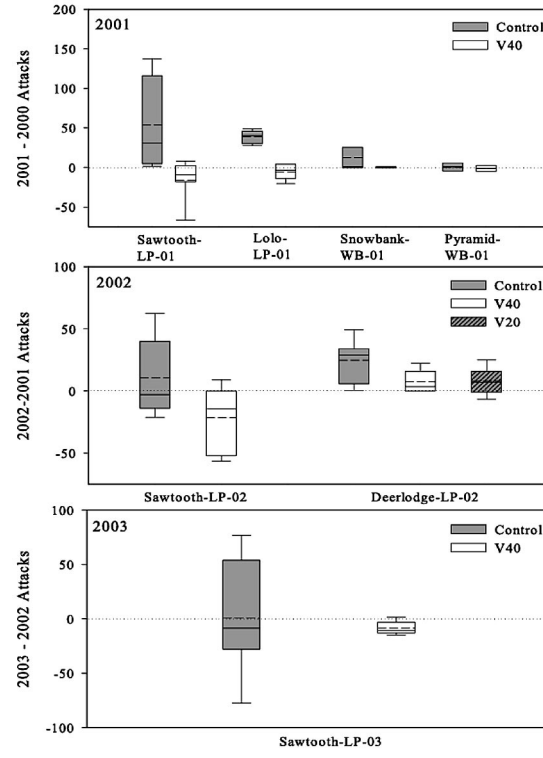

Fig. 2. Difference in the number of current and previous year mountain pine beetle-attacked trees within treatment plots in 2001, 2002, and 2003. Shown are the median (dotted line), mean (solid line), and 5/95% confidence intervals for each site. See Table 1 for site information.

trees among any of the buffers or between buffers and the 0.40-ha verbenone-treated or control plots.

2002. Within a site, no differences were found in 2002 among control and treatment plots in the number of live host trees (Table 2). At both sites, dbh was highly significant in explaining the number of mass attacked trees (Sawtooth-LP-02: $F = 272$; df = 1, 3006; $P < 0.001$) (Deerlodge-LP-02: $F = 415$; df = 1, 4518; $P < 0.001$). In both the treated and control plots, mass and strip attacked trees were, on average, significantly larger than unattacked trees (Table 3). There was a significant reduction in the number of mass attacked trees in the V40 treatment plots compared with control plots at Sawtooth-LP-02 ($F = 13$; df = 1, 6; $P = 0.011$). Overall, treatment was also significant at the Deerlodge-LP-02 site ($F = 4.5$; df = 2, 11; $P = 0.037$), and least square means differences between control and V40 plots were also significant ($t = 0.02$: df = 2, 11; $P = 0.051$), but the control and V20 plots were not ($t = 2.5$; df = 2, 11; $P = 0.074$). At Sawtooth-LP-02, but not Deerlodge-LP-02, there were significantly more strip-attacked trees in the control than V40 plots ($F = 13.5$; df = 1, 6; $P = 0.010$). Fewer available trees were attacked in both the V40 and V20 plots than control plots (Fig. 1). In the V40 plots at Sawtooth-LP-02, the mean number of currently attacked trees was less than the previous year, although this was not the case for either of the verbenone-treated plots or the control plots at the Deerlodge-LP-02 site (Fig. 2).

2003. No differences were found between control and treatment blocks in the number of live lodgepole pine trees before beetle flight in 2003 (Table 2). The emerging beetle population was greater within the 2003 treatment plots than either 2001 or 2002 (Table 2). As in 2001 and 2002, dbh was significant in explaining the number of mass attacked trees ($F = 153.8$; df = 1, 3411; $P < 0.001$) (Table 3). The number of attacked trees was lower in the V40 plots than control plots, and the difference approached significance ($F = 6.0$; df = 1, 5; $P = 0.057$) (Fig. 1). Reduction in treatment effect was due to one block (Redfish) in which 150 trees were mass or strip attacked in 2002 within the 0.40-ha plots (≈60% of available trees) and an additional 67 trees were attacked within the 20-m buffers surrounding them (217 total 2002 attacked trees) (Fig. 3). In 2003, the number of trees mass attacked in the V40-treated plot within the Redfish block was significantly greater than in the control plot. With the exception of Camp, where the 0.40-ha plots contained 148 trees attacked in 2002, the other blocks used in 2003 had significantly fewer 2002 infested trees nearby and subsequently fewer 2003 mass attacked trees in V40 than control plots (Fig. 3). Despite these trends, the number of previous year attacked trees was not significant in explaining treatment effects. The mean number of 2003 attacked trees within the V40 plots was less than the number of trees attacked in 2002, but many control plots also had fewer currently attacked trees than in the previous year (Fig. 2).

There was no difference between treatments in the number of strip-attacked trees, nor between the number of attacked trees in the buffers and within the V40 plots. However, the mean number of attacked trees in the 20-m buffer surrounding V40 plots was significantly less than within the 0.40-ha control plots ($t = 3.58$, df = 5.7, $P = 0.009$) or the buffer surrounding the control plots ($t = 3.05$, df = 5.51, $P = 0.029$).

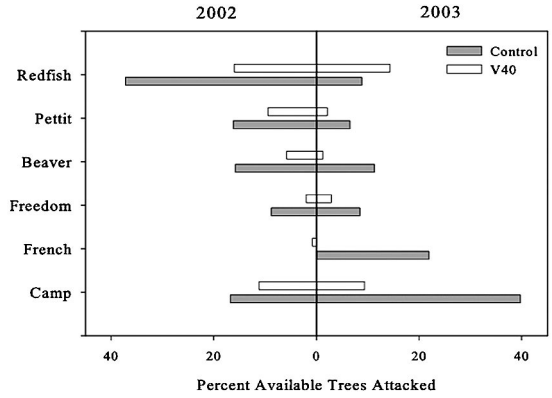

Fig. 3. Percentage of available trees attacked in 2002 and 2003 in the control and V40 (40 verbenone pouches per 0.40 ha)-treated plots in six blocks at the Sawtooth-LP-03 site.

Discussion

We found a dose of 40 verbenone pouches per 0.40 ha to significantly reduce the number of mountain pine beetle attacked trees. Although a dose of 20 verbenone pouches per 0.40 ha also reduced the number of attacked trees at the Deerlodge-LP-02 site where it was tested, the effect was not significant. The efficacy of verbenone for protection of small stands of lodgepole and whitebark pine was improved from earlier studies (Bentz et al. 1989, Amman et al. 1991, Gibson et al. 1991, Shore et al. 1991), at least in part by increasing the total emission of the compound from ≈5 mg/d from bubble capsules used previously to ≈50 mg/d from the pouches. Our results from five geographically separated sites, including three consecutive years at one site, support recent experiments that also tested the high-release verbenone pouch (Borden et al. 2003, Progar 2003).

Compared with control plots, the number of currently attacked trees within verbenone-treated plots was, on average, lower than in the previous year. This effect was most evident at the Sawtooth-LP-01, Sawtooth-LP-02, and Sawtooth-LP-03 sites where no baits were used in the plots (Fig. 2). All other sites contained traps with attractant baits at the center of each plot, which may have retained more emergent beetles within the plot. When no bait was used, the high release verbenone pouch seemed to disperse beetles emerging from within the treated plots to attack trees outside the treated area. The significantly lower number of attacked trees in the buffer surrounding the verbenone treated plots at lodgepole pine sites in 2001 and 2003 than in either the buffer surrounding control plots or within them suggests that the effect of the verbenone treatment extended at least partially

into the 20-m buffer. The trend at the whitebark pine sites was not as clear, possibly due to the low number of attacked trees at these sites, the low number of available live hosts at Pyramid-WB-01, and the open nature of the stands.

In the Redfish test block in 2003, the verbenone treatment was unsuccessful when ≈60% of the available trees in the control and verbenone-treated 0.40-ha plots had been infested the previous year (150 trees), and the emerging beetle population in the surrounding buffer was also large (an additional 67 infested trees) (Fig. 3). The Camp plots also contained a large number of 2002 infested trees (148 trees), and the verbenone-treated plot in this block had the highest number of 2003 mass attacked trees (31 trees) of all the verbenone-treated plots. However, apparently because the percentage of remaining available host trees was also high at Camp, especially in the control plot, the verbenone treatment had a significant effect. The other four blocks had 4, 45, 58, and 84 trees attacked within the 0.40-ha plots in 2002, and the V40 treatment in 2003 significantly reduced the number of mass attacked trees compared with the controls. These results, and those of Progar (2003), suggest a threshold infestation level above which verbenone is ineffective. Although more data are necessary to quantify a threshold, our results suggest that the verbenone treatment becomes ineffective when there are at least 140 attacked trees the previous year within the hectare including and surrounding the treated area.

In 2001, attacked whitebark pines were larger, on average, than attacked lodgepole pines, most likely a consequence of the larger mean dbh in whitebark pine plots. At all sites each year, the mean dbh of attacked trees was significantly larger than remaining live trees, regardless of the treatment. Increased mountain pine beetle activity on large-diameter lodgepole and whitebark pine trees has been attributed to random landing on large surfaces, a preference for large-diameter trees (Hopping and Beall 1948, Cole and Amman 1969, Preisler and Mitchell 1993, Kegley et al. 2004), and a high rate of pheromone release (Borden et al. 1983, Gray and Borden 1989). Although the immediate landscape contained an odor suggesting nonsuitable hosts, the verbenone treatment did not deter beetles from dispersing through the area, arresting, and initiating an attack focus on larger diameter hosts.

Mechanisms underlying the termination of mountain pine beetle attacks on a single tree, although unclear, are most likely based on a response to a threshold ratio of many compounds, including verbenone, emitting from a tree during the attack process (Raffa and Berryman 1983, Pureswaran et al. 2000, Pureswaran and Borden 2003). Although it is unclear whether verbenone is a kairomone or pheromone in the mountain pine beetle–host tree system (Lindgren and Miller 2002), our results suggest that high doses can be used to reduce the number of attacked trees in small stands of lodgepole and whitebark pine when beetle populations within and surrounding the stand are below a threshold level. Quantification of this threshold level is needed. Managers must understand, however, that when placed in a grid throughout a stand, verbenone does not protect all trees within the treated area, and large diameter trees are still attacked most frequently. Also, semiochemical treatments such a verbenone do not remove beetles from the system, and therefore are ideally one component of an overall management strategy that also includes removal of dispersed beetles. Additional research on the behavioral role of this compound in mountain pine beetle population dynamics will greatly enhance its use in protection of high-value pines in western forest ecosystems.

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