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Evaluation of Semiochemical Strategies for the Protection of Whitebark Pine Stands Against Mountain Pine Beetle Attack Within the Greater Yellowstone Ecosystem

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EVALUATION OF SEMIOCHEMICAL STRATEGIES FOR THE PROTECTION OF WHITEBARK PINE STANDS AGAINST MOUNTAIN PINE BEETLE ATTACK WITHIN THE GREATER YELLOWSTONE ECOSYSTEM

by

Greta Schen-Langenheim

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Evaluation of Semiochemical Strategies for the Protection of Whitebark Pine Stands Against Mountain Pine Beetle Attack Within the Greater Yellowstone Ecosystem

by

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Utah State University, 2010

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High-dose verbenone, verbenone plus nonhost volatiles (NHVs), and both semiochemicals in combination with aggregant-baited funnel traps were tested for stand-level protection against mountain pine beetle attack for two consecutive years (2004-2005) at three seral high elevation whitebark pine sites in the Greater Yellowstone Ecosystem. In 2004, two 0.25-hectare treatments comprised of 25 high-dose verbenone pouches or verbenone pouches combined with single baited funnel traps were tested in a push-pull strategy. In 2005, 25 high-dose verbenone and 25 NHV pouches, or verbenone and NHV in combination with baited funnel trap clusters were tested. In both years, treatments were compared to 0.25-hectare control plots with no semiochemicals or funnel traps. The proportion of trees attacked by mountain pine beetle in treated plots was significantly reduced, when compared to control plots, at only one site treated with verbenone in 2004, and at only one site in 2005. High-dose verbenone alone, verbenone and NHVs, and both semiochemicals combined with baited funnel traps in a push-pull strategy did not consistently reduce the proportion of mountain pine beetle attacked trees relative to control plots. No covariates tested, including stand density, beetle population size, or tree size were consistently significant in explaining proportion of trees attacked.

(52 pages)

DEDICATION

I dedicate this thesis and all publications that follow to my good friend, Brian Layton Cardall (December 7, 1976 – June 9, 2009); his widow, Anna Schmidt Cardall (the strongest, kindest person I know, period); and their two daughters, Ava Skye and Bella Aspen. All who remain here will carry on your spirit and passion for discovery and join it with our own.

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Most importantly, I am extremely grateful for my friends and husband's continuing support in all of my endeavors as well as my daughter's powerful and inspiring zest for life.

Greta Schen-Langenheim

CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

INTRODUCTION

Whitebark pine (*Pinus albicaulis* (Engelmann) Rydberg) is a slow-growing, long-lived pioneering stone pine (subgenus *Strobus*, section *Strobus*, subsection *Cembrae*; Critchfield and Little 1966) often found on exposed, high elevation sites with soils that are shallow with limited profile development (Arno and Hoff 1989, Hansen-Bristow et al. 1990). Whitebark pine occurs in pure stands as a climax species or co-dominate with subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) (Steele et al. 1981, Arno 1986). It is intermediate or intolerant of shade and its large, wingless seeds enveloped in an indehiscent cone regenerate well in mineral soils which have resulted from either fire or silvicultural practices (Arno and Weaver 1990). Whitebark pine is considered to be a keystone species (Lanner 1996) because it is important in watershed protection and snow retention (Farnes 1990), and is also a critical component of wildlife habitat. Seeds are an integral source of nutrition for the Clark's nutcracker, red squirrel (*Tamiasciurus hudsonicus* Erxleben), black bear (*Ursus americanus* Pallus), endangered grizzly bear (*U. arctos horribilis* Ord), and others (Arno 1986, Mattson and Jonkel 1990, McCaughey 1994). Whitebark pine is considered by many to be a mutualist with Clark's nutcracker (*Nucifraga columbiana* Wilson) which is the primary disperser of whitebark pine seeds (Tomback et al. 1990, Lanner 1996).

Whitebark pine mortality has exceeded rates of establishment in recent years, leading to its status as a 'species of concern' for western Washington (http://www.fws.gov/westwafwo/pdf/species_list.pdf), and the Natural Resources Defense Council's 2008 petition to the Fish and Wildlife Service, seeking federal protection for the whitebark pine under the Endangered Species Act (http://docs.nrdc.org/legislation/files/leg_08120801a.pdf). Whitebark pine decline is due to a combination of factors including: 1) replacement by the shade tolerant subalpine fir due to effects of fire suppression (Morgan and Bunting 1990, Keane 2001); 2) the exotic white pine blister rust (*Cronartium ribicola* Fischer) which has caused considerable tree mortality, cone crop reduction, and diminished seedling establishment (Maloy 1997, Zeglen 2002, McKinney and Tomback 2007); and 3) tree mortality due to mountain pine beetle (*Dendroctonus ponderosae* (Hopkins) Coleoptera: Curculionidae: Scolytinae) (Logan and Powell 2001, Gibson 2006). Although multiple factors are contributing to whitebark pine mortality, mountain pine beetle is currently the leading cause of tree death in the Greater Yellowstone Ecosystem. Furthermore, given the above factors, the resulting reduction in basal area and consequent decrease in cone crop reduction have not only threatened the mutualism between whitebark pine and Clark's nutcracker, but the potential for local and regional whitebark pine regeneration (McKinney et al. 2009).

Mountain pine beetle is a phloeophagous insect that feeds on the cambial tissue of *Pinus* species and is widely considered the most destructive bark beetle in western North America (Furniss and Carolin 1977). Mountain pine beetle outbreaks have been extensive across western North America the past century, most notably in lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann ex S. Watson) (Alfaro et al. 2004), and these outbreaks are considered integral components of ecosystem function (Amman 1977, Romme et al. 1986). Although tree mortality associated with mountain pine beetle was observed in high elevation whitebark pine ecosystems during intermittent warm periods the past century (Perkins and Swetnam 1996, Furniss and Renkin 2003), mountain pine beetle populations were not sustained for successive years due to a lack of seasonal thermal input (Amman 1973). Increasing temperature associated with climate change is thought to be influencing recent widespread tree mortality in these critical high elevation ecosystems (Logan and Powell 2001, Logan et al. 2003, Bentz and Schen-Langenheim 2007). The role of mountain pine beetle driven disturbance, related survival mechanisms, and management strategies and are not well understood in climatically diverse whitebark pine ecosystems.

Management practices aimed at reducing bark beetle-caused mortality in low elevation pine stands include manipulation of stand structure and composition (Amman et al. 1977, Anhold et al. 1996, Fettig et al. 2007). Silvicultural manipulation of whitebark pine stands is not a common practice because this species is not valued for timber production, and the isolated location of high elevation stands makes access difficult. There have been efforts, however, to restore and maintain this species on a landscape using prescribed fire and selective logging (Keane and Arno 1996, Keane et al. 2007). A survey of mountain pine beetle activity following such treatments in stands of mixed whitebark and lodgepole pine were unclear due to low level mountain pine beetle activity in the area prior to treatment (Waring and Six 2005). However, the authors caution that prescribed burning treatments could result in increased beetle-caused mortality to fire injured whitebark pine when population size is large. Because of difficulties associated with implementing silvicultural treatments in isolated high elevation stands, in addition to lack of knowledge regarding efficacy in protection against mountain pine beetle attacks, semiochemical strategies may be a preferred alternative.

Semiochemicals have been used extensively in low elevation pine systems to control mountain pine beetle populations by manipulation of the insect's chemical communication system. Within a forest, a beetle must decipher the correct host out of a number of possibilities using an assortment of visual (Shepherd 1966, Moeck and Simmons 1991) and chemical cues such as host and nonhost volatiles (Huber et al. 2000, Zhang and Schlyter 2004). Once a host is located, beetles must overcome host defenses to successfully colonize the selected tree; it is thought that this is accomplished by mass attack. There are two hypotheses concerning cessation of mass attack. Renwick and Vite (1970) proposed that mass attack ceases once resin exudation declines. Rudinsky et al. (1974) argued that production of an anti-aggregative pheromone caused termination of mass attack. Indeed, a semiochemical known as verbenone was described by Renwick (1967) and was initially associated with *D. frontalis* Zimmermann and *D. brevicomis* LeConte. Pitman and others (1969) found verbenone in trace amounts in the hindguts of female mountain pine beetles, and Ryker and Yandell (1983) subsequently described verbenone as an anti-aggregation pheromone for mountain pine beetle. Verbenone can also be produced in the absence of bark beetles, through auto-oxidation of α-pinene and by microbes, primarily yeasts (Hunt and Borden 1990), and has been associated with host aging and deterioration (Fletchmann et al. 1999). Verbenone may be more than a simple beetle-produced anti-aggregant, also providing cues about tissue quality to attacking beetles (as a kairomone) (Lindgren and Miller 2002).

A variety of forms of synthesized verbenone have been extensively evaluated for protection of both stands and single trees from mountain pine beetle attack by deterring onset of host colonization. Results from field-based trials have been mixed, although interpretation is difficult due to differences among studies in quantity/quality of the compound and elution device, host tree species, stand conditions, and beetle population levels, or the ‘push-pull’ component.

Initial studies conducted in lodgepole pine stands in British Columbia, Canada and central Idaho, USA found that low-dose verbenone capsules significantly reduced the number of mountain pine beetle mass attacks relative to control areas (Lindgren et al. 1989, Amman et al. 1989). Subsequent tests at both the stand and tree levels showed continued promise in reducing mass attacked lodgepole pine (Amman et al. 1991, Shore et al. 1992, Lindgren and Borden 1993), although the same capsules did not significantly reduce mountain pine beetle attack in ponderosa pine (*Pinus ponderosa* Lawson) stands (Bentz et al. 1989, Lister et al. 1990, Gibson et al. 1991). Next, release devices with an increased emission rate were tested. Using pouches that emitted 10 times the amount of verbenone than capsules used in previous tests, Progar (2005) observed a significant reduction in mountain pine beetle attacked trees the first and second year, although by year five as beetle population size increased in the surrounding area, there were no differences between treated and control areas. Bentz et al. (2005) also observed a reduction in high-dose verbenone efficacy when beetle pressure was high. In addition to tests for stand-level protection, two high-dose verbenone pouches were found to protect individual whitebark pine in field trials wherein approximately 75% of treated trees showed no sign of mountain pine beetle attack (Kegley and Gibson 2004). Other forms of verbenone that have been tested for stand-level protection against mountain pine beetle attack, with varying success, include verbenone-impregnated plastic beads (Shea et al. 1992), and more recently verbenone-releasing laminated flakes that show promise in reducing the number of mountain pine beetle attacks in stands (Gillette et al. 2009) and individual trees (Gillette et al. 2006).

Given the variable nature of results from verbenone field experiments, the addition of nonhost volatiles (NHVs) was suggested as an option for improving the efficacy of verbenone in protecting pines from mountain pine beetle attack (Miller et al. 1995). The 'semiochemical diversity hypothesis' suggests that mixed species forests have greater semiochemical diversity, and thus lower potential for bark beetle outbreaks (Zhang and Schlyter 2004). Nonhost volatiles are six carbon alcohols, esters, and aldehydes found in plants. An array of NHVs have been tested and found to have 'repellent' properties in several species of bark beetles. In fact, many NHVs are antenally active in a variety of bark beetle species, suggesting that they aid in habitat-scale host selection, and could possibly be used for response inhibition (Huber et al. 2000). Dickens and others (1992) found several NHVs (e.g. hexanal) inhibited pheromone response in southern pine beetle (*D. frontalis* Zimmermann), although they were not as effective as verbenone. Schroader (1992) found that baits composed of nonhost wood in addition to ethanol significantly reduced sticky trap-catch of *Tomicus piniperda* L. and *Hylurgops palliatus* (Gyllenhal) compared to ethanol baits alone. In field trapping experiments in British Columbia two NHVs, (Z)-3-hexen-1-ol and (E)-2-hexen-1-ol, were as effective at reducing trap-catches of mountain pine beetle as verbenone, and attack density was significantly reduced on lodgepole pine baited with aggregation pheromones as well as NHVs (Wilson et al. 1996). Wilson and others (1996) concluded that NHVs used in addition to verbenone may effectively protect single stems and stands against attack when mountain pine beetle population levels are low. Subsequent field trails in lodgepole pine found that mountain pine beetle attack was significantly reduced by combining high doses of verbenone with a NHV blend (Borden et al. 1998, Borden et al. 2003). In later studies, however, efficacy was not increased when NHVs and verbenone were combined for protection of lodgepole pine stands (Borden et al. 2006), or individual ponderosa pine, lodgepole pine, or whitebark pine (Kegley and Gibson 2009).

An additional semiochemical strategy that has been repeatedly proposed although not fully explored is the push-pull strategy (Lindgren et al. 1989, Amman et al. 1989, Miller et al. 1995, Vandygriff et al. 2000, Cook et al. 2007). In this strategy, aggregation baits are used with funnel traps or on live trees as population sinks to relocate dispersing beetles out of areas treated with repellent semiochemicals. Two studies have investigated the push-pull strategy with mixed results. Vandygriff et al. (2000) successfully ‘pulled’ mountain pine beetles into areas targeted for harvest, although there were no significant differences in number of attacked lodgepole pine in areas treated with low-dose verbenone capsules relative to control areas, suggesting the ‘push’ was not successful. In a study conducted in British Columbia, areas treated with high-dose verbenone and NHVs had fewer attacks than untreated areas and also there were more trees attacked in surrounding areas where baits were used to ‘pull’ beetles into live lodgepole pine

(Borden et al. 2006). The push-pull strategy has not been evaluated in high elevation whitebark pine ecosystems.

Although results from previous field trials are variable, semiochemical-based strategies may be the best option for the protection of whitebark pine stands against mountain pine beetle attack when other options are constrained by location, aesthetics, and perceived ecosystem fragility. Our objective was to evaluate semiochemical strategies for the protection of whitebark pine stands against mountain pine beetle attack. Specifically, we tested high-dose verbenone and a combination of high-dose verbenone with NHVs in a push-pull strategy with aggregant-baited funnel traps as a population sink for dispersing mountain pine beetle.

METHODS

Site Selection and Description. The study was conducted for two consecutive years (2004 and 2005) at three sites within the Greater Yellowstone Ecosystem (GYE) (Table 1): 1) Sawtell Peak, Idaho; 2) Black Butte, Montana; and 3) Togwotee Pass, Wyoming. These areas were chosen because mountain pine beetle populations were at endemic to building levels just prior to the study, and therefore potentially more conducive to population suppression strategies. All sites were identical in that whitebark occurred in multiple-stems or ‘clumps’, and were best characterized by Steele et al. (1981) as seral, PIAL/ABLA. Conifer associates at all sites include Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall). Although the experimental design was slightly modified for 2005, the same three sites were used in 2004 and 2005.

Table 1. Location and description of sites used to test push-pull strategies for protection of whitebark pine stands from mountain pine beetle attack in 2004 and 2005.

Site	**Forest**	**Elevation (m)**	**Coordinates**
Black Butte	Beaverhead-Deerlodge, MT	2743	N 44.92036° W 111.82649°
Sawtell Peak	Targhee, ID	2743	N 44.55579° W 111.44157°
Togwotee Pass	Shoshone, WY	2926	N 43.74401° W 110.05324°

2004 Experimental Design. At each of the three sites, two 0.25-hectare treatment plots and a control plot were installed in a Completely Randomized Block Design with four replicated blocks. Control and treatment plots were randomly assigned to each plot within a block and were installed mid June through early July. Treatment I (VERB) or the 'push' only component, consisted of 25 high-dose verbenone pouches (7.5 g, Synergy Semiochemicals, B. C., Canada) that were attached to stems in a grid-like fashion throughout the plot (approximately spaced at 10 x 10 meters). Treatment II (T+VERB) or the 'push-pull' component, included 25 high-dose verbenone pouches (push) attached to stems in a grid-like fashion throughout the plot (approximately spaced at 10 x 10 meters) with the addition of four 12-unit funnel traps (Lindgren 1983) baited (pull) with a mountain pine beetle aggregation blend (145 mg *trans*-verbenol, 9 g *exo*-brevicomin, 12 g terpinolene; Synergy Semiochemicals, B.C. Canada). Funnel traps were placed 2 to 3 meters perpendicular from the perimeter of each plot, centered on each of the four sides. Plastic cubes impregnated with dichlorovinyl dimethyl phosphate were placed in funnel trap cups to ensure accurate counts by reducing beetle mortality to predators and preventing possible escape. The two treatments were tested against a control that contained no traps or verbenone pouches. All plots were square, with 50 meters on each side, and were placed 60 meters apart. Replicates were placed several hundred meters apart.

In an attempt to minimize beetle attacks on live trees near traps, baited funnel traps were placed as far away from whitebark pine as possible and hung using aluminum conduit (stabilized with rebar segments which were then pounded into the ground).

Additionally, two verbenone pouches were placed on all whitebark pine stems greater than 3 inches diameter at breast height (DBH) within 3 meters of funnel traps, and a single pouch was used on whitebark pines located three to 5 meters from traps. Attack status of trees within a 6-meter radius surrounding the trap was monitored weekly. Funnel traps were also checked weekly, and the number of beetles caught recorded.

After beetle flight concluded in late September, a 100% survey of each 0.25-hectare plot (12 plots per site; all tree species recorded) and a 20-meter buffer (only whitebark pine recorded) surrounding each plot was conducted. Tree species and mountain pine beetle attack status (e.g. 2004 mass, 2004 strip, 2004 pitch-out, 2003 mass, 2003 strip, 2003 pitch-out) and DBH (estimated using a Biltmore stick) were recorded for each tree. A tree was recorded as mass attack if greater than 90% of the bole circumference was attacked successfully, and trees with less than 90% of the bole attacked were considered a strip attack. Trees with only a few attacks and/or dead beetles in pitch tubes were recorded as a pitch-out. When infested trees were located within a clump of other host trees, the size of the clump was recorded, noting the year of attack of each tree.

2005 Experimental Design. At each of the three sites, two 0.25-hectare treatment plots and an untreated control plot were installed in a Completely Randomized Block Design with four blocks. Control and treatment plots were randomly assigned to each plot within a block and were installed late May through early July. Due to lack of living host type and spatial constraints, only three replicates were installed at the Black Butte site. In 2005, NHVs were added to the verbenone treatment to potentially enhance the repellant effect (Wilson et al. 1996). Additionally, a cluster of three funnel traps was used rather than a single funnel trap as in 2004. Laidlaw and Weiser (2002) found that funnel trap clusters absorbed more dispersing beetles than otherwise may have been caught by a single funnel trap, thereby removing more beetles from the immediate population and also potentially reducing spillover attacks on nearby trees. Treatment I (VNHV) or the 'push' only component, consisted of 25 high-dose verbenone pouches (7.5 g. Synergy Semiochemicals, B. C., Canada) and 25 NHV pouches (10.0 g Z-3-*Hexen*-1-ol, Synergy Semiochemicals, B. C., Canada) attached to alternating stems in a grid-like fashion throughout each plot (total spacing including both semiochemicals at approximately 5 x 5 meters). Treatment II (T+VNHV) or the 'push-pull' component, included 25 high-dose verbenone pouches and 25 NHV pouches that were attached to alternating stems in a grid-like fashion throughout each plot (total spacing including both semiochemicals at approximately 5 x 5 meters) with the addition of a cluster of three 12-unit funnel traps per plot side. Only one funnel trap per cluster was baited with a mountain pine beetle aggregant pheromone (145 mg *trans*-verbenol, 9 g *exo*-brevicomin, 12 g terpinolene; Synergy Semiochemicals, B.C. Canada). Funnel trap clusters were located approximately 25 meters outside and perpendicular to the perimeter of treatment plots. Plastic cubes impregnated with dichlorovinyl dimethyl phosphate were placed in funnel trap cups to reduce beetle mortality to predators and prevent possible escape. The two treatments were tested against a control that contained no traps, verbenone, or NHV pouches. Plots were 80-100 meters apart and replicates were several hundred meters apart.

Funnel traps were installed concurrently with treatment and control plots and monitored as described for the 2004 field trial. However, due to the number of spillover attacks observed in the 2004 field trials, a slight adjustment was made to the number and distance of verbenone pouches deployed on live whitebark pine around funnel trap clusters. Two verbenone pouches were placed on all whitebark pine stems greater than 3 inches DBH within 3 meters of funnel trap clusters, and a single pouch was used on whitebark pines located 3 to 6 meters from funnel trap clusters (whereas in 2004, the single pouch range was a distance of 3 to 5 meters. Attack status of trees within a 9-meter radius (instead of 6 meters as in 2004) surrounding the trap clusters was monitored weekly.

Passive traps, which were not baited with an aggregant pheromone and are designed to measure non-directed beetle flight, were used to evaluate the influence of semiochemical treatments on beetle dispersal within treated plots. We hypothesized that passive traps in treated plots would catch fewer mountain pine beetle than traps placed in control areas. The passive traps used were similar to those first developed by Schmitz (1984), but with some structural and size modifications. Two passive traps were erected near plot center of each semiochemical-treated and control plot, and were suspended between trees using parachute cord shot up into the canopy with a bow and arrow. The traps hung about 2 to three 3 meters above the ground. Plastic cubes impregnated with dichlorovinyl dimethyl phosphate were placed in the passive trap cups to reduce beetle mortality to predators and prevent possible escape. Both the funnel and passive traps were checked weekly and the number of beetles caught recorded.

Following conclusion of beetle flight in late September, a 100% survey of each 0.25-hectare plot (all tree species) and a 25-meter buffer (extended from 20-meter used in 2004; whitebark only) surrounding each plot was conducted and mountain pine beetle attack status including year of attack and type of attack (e.g. mass, strip, pitch-out) and DBH of each tree estimated with a Biltmore stick. When infested trees were located within a clump of other host trees, the size of the clump was recorded, noting year of attack for each stem.

Analytical Methods. The main objective was to test the efficacy of the two treatments (for each of the two years) compared to each other and a control. Efficacy was measured as the proportion of living trees attacked (mass and strip) by mountain pine beetle during the treatment year within the treated plots, compared to an untreated control. Proportion of attacked trees in the perimeters surrounding each plot was also compared. The data were analyzed using mixed model analysis in SAS 9.2 (Littell et al. 1996) with a binomial error distribution. Site and replicate were treated as random variables in data analyses including all sites. Replicate was a random variable when data were analyzed by site. Differences in treatment means were analyzed using Tukey's Honestly Significant Difference multiple comparison procedure.

A number of covariates were tested for significance in explaining treatment efficacy and the proportion of living trees attacked. Covariates included relative density (stand density index or SDI), absolute density (trees per 0.25-hectare), species diversity (number of non-host species), beetle pressure (number of trees attacked one and two years before treatment year), whether or not a tree was a member of a clump, and mean whitebark pine DBH. These covariates were also used to examine pretreatment differences by site. Due to differences in experimental design in 2004 and 2005, each year was analyzed separately.

Assessment of verbenone efficacy in reducing mountain pine beetle attacks on host trees around baited funnel traps was measured as the proportion of living trees attacked (mass and strip) by mountain pine beetle and by distance from baited trap (2004) or trap cluster (2005). The data were analyzed using mixed model analysis (SAS Institute Inc., ver 9.2) with a binomial error distribution. Site and replicate were treated as random variables in data analyses including all sites. Replicate was a random variable when data was analyzed by site. Differences in treatment means were analyzed using Tukey's Honestly Significant Difference multiple comparison procedure.

Differences in passive trap-catch were compared among treatments and controls using mixed model analysis (SAS Institute Inc., ver 9.2) with a Poisson error distribution. Covariates tested for significance in explaining differences in passive trap catch among plots included relative density, absolute density, species diversity, and beetle pressure.

Differences in total funnel trap-catch among treatments, and years were made using mixed model analysis (SAS Institute Inc., ver 9.2) with a Poisson error distribution. Pair-wise differences were analyzed using Tukey's Honestly Significant Difference multiple comparison procedure.

RESULTS

2004. Pretreatment conditions were similar at all three sites except for the number of living trees of all species (F = 20.41; df = 2, 8.881; p = 0.0005) (Table 2). Togwotee Pass site contained the greatest number of trees of all species per 0.25 hectare when compared to both Black Butte (t = -5.40 df = 2, 8.762; p = 0.0012) and Sawtell Peak (t = -5.62 df = 2, 8.787; p = 0.0009).

Table 2. Host and nonhost metrics within treated and control plots (0.25-ha each) at three whitebark pine (WBP) sites (four replicates at each site) in 2004. All trees with DBH > 7.6 cm included in metrics. Treatments were: verbenone pouches only (VERB), and verbenone pouches and baited funnel traps (T+VERB). Proportion trees attacked among treatments within a site with different letters are significantly different at p=0.05 based on Tukey's Honestly Significant Difference test.

Treatment	**Mean (±SE) number WBP**	**Mean (±SE) number trees (all species)**	**Mean (±SE) DBH WBP**	**Mean (±SE) number WPB previously attacked***	**Mean (±SE) proportion WPB attacked in 2004 within treated plots**
Black Butte					
T+ VERB	103 (±20.7)	153 (± 8.0)	28.0 (±2.5)	15.0 (±7.6)	4.6 (±4.6)^{a}
Control	103 (±22.5)	119 (±21.8)	24.6 (±3.9)	70.2 (±25.4)	14.8 (±9.1)^{b}
VERB	98 (±25.1)	108 (±2.8)	27.6 (± 3.3)	33.0 (± 30.1)	2.2 (±2.2)
Sawtell Peak					
T+ VERB	95 (±23.1)	133 (±20.3)	30.6 (±2.9)	4.7 (±2.6)	2.3 (±0.7)
Control	106 (±42.7)	136 (±38.7)	30.2 (±3.7)	11.5 (±4.1)	1.4 (±1.4)
VERB	63 (±12.9)	105 (±10.2)	33.0 (±1.2)	11.2 (±2.6)	0 (±0)
Togwotee Pass					
T+ VERB	167 (±34.2)	282 (±23.6)	28.8 (±2.8)	17.0 (±5.1)	0.8 (±0.4)
Control	108 (±29.5)	265 (±20.6)	28.9 (±1.2)	11.5 (±6.3)	0 (±0)
VERB	126 (± 16.6)	277 (±31.7)	30.2 (±1.2)	17.5 (±6.1)	1.0 (±0.6)

*Previously attacked trees were defined as the total number of trees strip and mass attacked one and two years prior to treatment year with in the confines of both inside and outside perimeters of treatment and control plots (2004, .81-ha total size).

When all sites were analyzed together, including covariates, the proportion of mountain pine beetle attacked trees was not significantly different among treated plots or plot perimeters. However the number of trees attacked one and two years prior to treatment in and surrounding the treated and control plots was significant in explaining the proportion of 2004 attacked trees within plots (F = 21.71; df = 1, 19.88; p = 0.0002) and the perimeter surrounding each plot (F = 7.42; df = 1, 16.85; p = 0.0145). No other covariate tested was significant in explaining differences in proportion of trees attacked within the treated plots or the 20-meter perimeter surrounding each plot.

When analyzed by site, no significant differences in proportion of trees attacked were observed among treatments (Table 2) or in perimeters (Table 3) at Sawtell Peak. At Togwotee Pass, treatment significantly influenced the proportion of trees attacked in the perimeters (F = 7.96; df = 2, 7; p = 0.0157) with T+VERB treatments incurring significantly higher proportions of attack in the perimeters than found in the VERB perimeters (t = 3.16; df = 2, 7; p = 0.0376) (Table 3). At the Black Butte site, treatment was significant (F = 8.93; df = 2, 7; p = 0.0118) with a greater proportion of attacks found in control plots compared to both VERB (t = 3.22; df = 2, 7; p = 0.0346) and T+VERB (not significant) plots (Table 2). Treatment was significant in explaining attack proportions in treatment perimeters compared to control perimeters (F = 12.67; df = 2, 7; p = 0.0047). Significantly higher proportions attacked trees were observed in VERB perimeters when compared to control perimeters (t = -4.26; df = 2, 7; p = 0.0091) (Table

3). While there was no observed preference for larger trees within the treated plots, DBH approached significance in explaining proportion of trees attacked in perimeters surrounding all plots (F = 10.37; df = 1, 3.002; p = 0.0485). Mountain pine beetle pressure did not affect treatment efficacy within the treated plots. However, plot perimeters containing a higher proportion trees attacked one and two years previous had greater proportions of 2004 attacks (F = 22.21; df = 1, 1.877; p = 0.0476). No other covariate tested explained differences in attacks within the treated plots or in the 20 meter perimeter surrounding each plot.

Table 3. Host and nonhost metrics within treated and control plot perimeters at three whitebark pine (WBP) sites (four replicates at each site) in 2004. All trees with DBH > 7.6 cm included in metrics. Treatments were: verbenone pouches only (VERB), and verbenone pouches and baited funnel traps (T+VERB). Proportion trees attacked among treatments within a site with different letters are significantly different at p=0.05 based on Tukey's Honestly Significant Difference test.

Treatment	**Mean (±SE) number WBP**	**Mean (±SE) DBH WBP**	**Mean (±SE) number WPB previously attacked**	**Mean (±SE) proportion WPB attacked in 2004 in plot perimeters**
Black Butte				
T+ VERB	175 (±45.1)	27.0 (±3.3)	15.0 (±7.6)	3.2 (±1.6)
Control	236 (±58.9)	23.9 (±3.1)	70.2 (±25.4)	3.2 (±1.8)[a]
VERB	166 (±43.5)	27.8 (±2.9)	33.0 (±30.1)	8.8 (±5.9)[b]
Sawtell Peak				
T+ VERB	164 (±40.5)	28.3 (±1.9)	4.7 (±2.6)	1.9 (±0.6)
Control	235 (±97.1)	28.3 (±3.0)	11.5 (±4.1)	1.7 (±1.2)
VERB	145 (±26.9)	31.9 (±2.4)	11.2 (±2.6)	1.3 (±0.8)
Togwotee Pass				
T+ VERB	224 (±43.9)	28.8 (±1.5)	17.0 (±5.1)	2.4 (±1.2)[a]
Control	190 (±13.6)	29.8 (±1.1)	11.5 (±6.3)	1.2 (±0.5)
VERB	221 (±28.4)	31.1 (±1.2)	17.5 (±6.1)	0.5 (±0.3)[b]

*Previously attacked trees were defined as the total number of trees strip and mass attacked one and two years prior to treatment year with in the confines of both inside and outside perimeters of treatment and control plots (2004, .81-ha total size).

At the three sites combined, there were a total of 212 live trees within 6 meters of funnel traps, 86 of those trees were treated with a verbenone pouch. Thirty trees (14%) were attacked, including 15 treated trees, and the proportion of trees attacked decreased as distance from the trap increased, although not significantly. The presence of verbenone pouches did not protect trees surrounding baited funnel traps from mountain pine beetle attack.

Mountain pine beetle were caught in pheromone-baited traps from early July to early October (Figure 1a), with peak trap-catch in mid-July. Overall, although not significant, pheromone traps at the Black Butte site absorbed a greater number of beetles than both Sawtell Peak and Togwotee Pass.

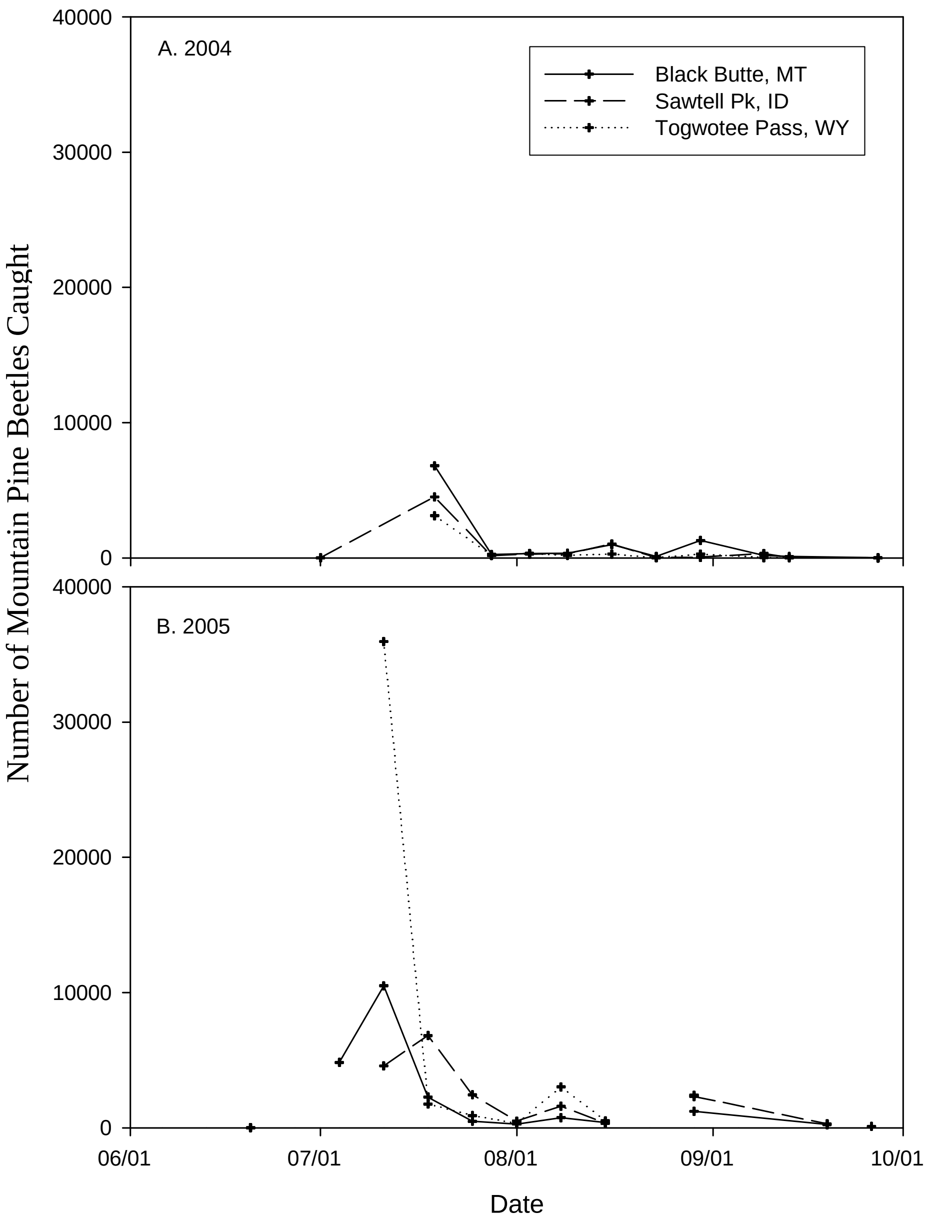

Fig. 1. A. Number of mountain pine beetle caught in aggregant-baited funnel traps at three whitebark pine sites in 2004. Each site contained 16 traps with four traps associated with each replicate. B. Number of mountain pine beetle caught in aggregant-baited traps at whitebark pine sites in 2005. Togwotee Pass and Sawtell Peak contained 48 traps per site with four, three-trap clusters associated with each replicate. Black Butte contained 36 traps per site with three replicates of trap clusters in each replicate.

2005. Pretreatment conditions were similar at all three sites with respect to in-plot diameter, beetle pressure, and the number of living whitebark pine. However, the number of living trees of all species varied significantly among sites (F = 19.06; df = 2, 27.64; p <0.0001). Togwotee Pass contained the greatest number of trees of all species per 0.25-hectare when compared to both Black Butte (t = -4.55; df = 2, 27.3; p = 0.0003) and Sawtell Peak (t = -5.78; df = 2, 27.357; p < 0.0001). Clump membership also varied significantly among the three sites (F = 7.25; df = 2, 24.92; p = 0.0033). Sawtell Peak contained significantly fewer trees that were members of clumps than both Black Butte (t = 3.02; df = 2, 25.38; p = 0.0155) and Togwotee Pass (t = -3.49; df = 2, 25.59; p = 0.0050). Additionally, the number of whitebark pine varied significantly by treatment perimeter (F = 20.05; df = 2, 3.98; p = 0.0351) with VNHV perimeters containing significantly more whitebark pine than the T+VNHV treatment perimeters (t = -2.49; df = 2, 19.96; p = 0.0546).

There were no significant differences among treatment and control plots in proportion of trees attacked by mountain pine beetle when all sites were analyzed together. However, treatment was significant in explaining mountain pine beetle attack in plot perimeters (F = 4.57; df = 2, 15.60; p = .0274). Plot perimeters containing the baited funnel traps (T+VNHV) contained the highest proportion of attacked trees when compared to control (t = 3.02; df = 2, 16.53; p = 0.0213) perimeters. The number of trees attacked one and two years prior to treatment in and surrounding the treated and control plots was significant in explaining the proportion of 2005 attacked trees only within plots (F = 6.29; df = 1, 16.15; p = 0.0232).

When analyzed by site, there were no significant differences between treatments and the control either within the treated plots or in the 25 meter perimeters at Sawtell Peak. At Togwotee Pass, the proportion of attacked trees within plots varied significantly by treatment (F= 9.29; df = 2, 7; p = 0.0107). Control plots contained significantly more attacked trees than the VNHV treatment (t = 3.37; df = 2, 7; p = 0.0323). Control plots also contained more attacked trees than the T+VNHV treatments, although the relationship was not significant (Table 4). Additionally, diameter (F = 14.88; df = 1, 7; p = 0.0062) was a significant factor in explaining mountain pine beetle attacks within plots. Treatment was also a significant factor in proportion of trees attacked in the perimeters (F = 9.65; df = 2, 7; p = 0.0097). Perimeters surrounding the T+VNHV treatments contained significantly higher proportions of attacked trees than did perimeters surrounding the control plots (t = 3.67; df = 2, 7; p = 0.0191) (Table 5). Although the relationship was not significant, T+VNHV perimeters also contained higher proportions of attacked trees than did VNHV perimeters (Table 5). Mountain pine beetles attacked significantly larger diameter trees within perimeters surrounding plots (F = 9.15; df = 1, 7; p = 0.0192).

Table 4. Host and nonhost metrics within treated and control plots (0.25-hectare each) at three whitebark pine (WBP) sites in 2005. Sawtell Peak and Togwotee had 4 replicates for each treatement and control and Black Butte had 3 replicates. All trees with DBH > 7.6 cm included in metrics. Treatments were verbenone plus nonhost volatile pouches (VNHV) and verbenone plus nonhost volatile pouches and baited funnel trap clusters (T+VNHV). Perimeters extended 25 meters outward from the plot boundaries. Proportion trees attacked among treatments within site by year with different letters significantly different at p=0.05 based on Tukey's Honestly Significant Difference test.

Treatment	**Mean (±SE) number WBP**	**Mean (±SE) number trees (all species)**	**Mean (±SE) DBH WBP**	**Mean (±SE) number WPB previously attacked***	**Mean (±SE) proportion WPB attacked in 2005within treated plots**
Black Butte					
T+ VNHV	87 (±16.1)	103 (±16.3)	26.4 (±1.3)	4.7 (±3.7)	21.9 (±10.6)^{a}
Control	87 (±20.2)	171 (±49.4)	29.6 (±4.8)	14.3 (±14.3)	16.7 (±11.1)^{b}
VNHV	130 (±37.2)	163 (±28.2)	26.9 (±3.9)	4.3 (±2.2)	9.3 (±2.0)
Sawtell Peak					
T+ VNHV	71 (±8.3)	123 (±21.9)	32.0 (±2.3)	0.5 (±0.3)	1.6 (±1.6)
Control	81 (±20.5)	127 (±28.4)	29.2 (±3.0)	2.7 (±2.4)	0 (±0)
VNHV	113 (±19.6)	128 (±13.6)	28.0 (±2.9)	2.2 (±0.7)	2.4 (±0.8)
Togwotee Pass					
T+ VNHV	164 (±31.8)	294 (±27.6)	29.1 (±1.2)	2.0 (±1.3)	2.0 (±0.7)
Control	106 (±17.1)	249 (±22.6)	27.7 (±0.8)	5.0 (±1.5)	5.2 (± 3.7)^{a}
VNHV	134 (±26.0)	254 (±34.2)	30.6 (±2.6)	5.5 (±3.6)	2.4 (±1.8)^{b}

*Previously attacked trees were defined as the total number of trees strip and mass attacked one and two years prior to treatment year with in the confines of both inside and outside perimeters of treatment and control plots (2005, 1.0-ha total size).

Table 5. Host and nonhost metrics within treated and control plot perimeters at three whitebark pine (WBP) sites in 2005. Sawtell Peak and Togwotee had 4 replicates for each treatement and control and Black Butte had 3 replicates. All trees with DBH > 7.6 cm included in metrics. Treatments were: verbenone pouches only (VERB), and verbenone pouches and baited funnel traps (T+VERB). Proportion trees attacked among treatments within a site with different letters are significantly different at p=0.05 based on Tukey's Honestly Significant Difference test.

Treatment	**Mean (±SE) number WBP**	**Mean (±SE) DBH WBP**	**Mean (±SE) number WPB previously attacked**	**Mean (±SE) proportion WPB attacked in 2005 in plot perimeters**
Black Butte				
T+ VNHV	147 (±33.3)	26.1 (±3.3)	4.7 (±3.7)	31.9 (±15.6)
Control	150 (±39.5)	31.9 (±4.0)	14.3 (±14.3)	28.3 (±14.4)[a]
VNHV	239 (±101.0)	26.4 (±6.1)	4.3 (±2.2)	19.2 (±4.4)[b]
Sawtell Peak				
T+ VNHV	179 (±30.9)	30.9 (±1.0)	0.5 (±0.3)	3.4 (±1.5)
Control	215 (±61.0)	28.9 (±3.0)	2.7 (±2.4)	0.9 (±0.5)
VNHV	272 (±49.8)	26.1 (±2.1)	2.2 (±0.7)	2.2 (±0.5)
Togwotee Pass				
T+ VNHV	267 (±24.9)	30.7 (±1.8)	2.0 (±1.3)	8.3 (±1.2)[a]
Control	241 (±12.9)	28.9 (±1.5)	5.0 (±1.5)	3.5 (±3.2)[b]
VNHV	322 (±27.6)	28.5 (±1.2)	5.5 (±3.6)	3.7 (±0.9)

*Previously attacked trees were defined as the total number of trees strip and mass attacked one and two years prior to treatment year with in the confines of both inside and outside perimeters of treatment and control plots (2005, 1.0-ha total size).

At Black Butte, treatment was significant in explaining the proportion of trees attacked within plots (F = 21.18; df = 2, 4; p = 0.0074) and in the plot perimeters (F = 67.92; df = 2, 4; p = 0.0008). Within the treated areas, T+VNHV treatment plots contained significantly higher proportions of attacked trees than the control plots (t = 3.65; df = 2, 4; p = 0.0464) (Table 4). Although not significant, T+VNHV plots also contained higher proportions of attacked threes than VNHV plots (Table 4). In the perimeters, T+VNHV perimeters had significantly higher proportions than both the control (t = 8.00; df = 2, 4; p = 0.0029) and VNHV (t = 4.06; df = 2, 4; p = 0.0331) perimeters (Table 5). VNHV perimeters contained significantly fewer attacks than did the control (t = -4.06; df = 2, 4; p = 0.0325) and T+VNHV perimeters (not significant; Table 5). Beetle pressure was significant in explaining differences in proportions of trees attacked both among treatment and control plots (F = 29.70; df = 1, 4; p = 0.0055) and perimeters (F = 78.84; df = 1,4; p = 0.0009). Significantly larger diameter trees were attacked in the perimeters surrounding all plots (F = 70.62; df = 1, 4; p = 0.0011). No other covariate tested explained differences in attacks within the treated plots or the 25-meter perimeter surrounding each plot.

At the three sites combined, there was a total of a 191 living whitebark within approximately 9 meters of the funnel trap cluster. Thirty-seven trees (19%) of those trees were attacked. Of these, three trees had been treated with verbenone pouches. The majority of trees attacked were between 6 and 9 meters from the funnel trap and were not treated with verbenone. Contrary to results in 2004, the proportion trees attacked increased as distance from the trap increased, although not significantly. The presence of verbenone pouches did not protect trees surrounding baited funnel trap clusters from mountain pine beetle attack.

When data from all sites were pooled, the number of mountain pine beetles caught in passive traps did vary significantly among sites (F = 18.11; df = 2, 28; p = <0.0001). Black Butte passive traps caught significantly more beetles (963) than at the Togwotee Pass (t = 4.09; df = 2, 25.52; p = 0.0009) and Sawtell Peak (t = 5.92; df = 2, 28; p

<0.0001) sites (243 and 122 beetles, respectively). Togwotee passive traps caught more beetles when compared to Sawtell traps, although not significantly more. The number of mountain pine beetles in traps (pooled data) did not vary significantly among treatments, and there was not a clear trend in proportion trapped within each treatment among the sites. We hypothesized that passive traps in plots treated with verbenone and NHVs would catch fewer mountain pine beetle than traps in control plots. This trend was observed at the Togwotee Pass site, where the greatest proportion of beetles was caught in control plots (53%) and the least in VNHV (15%). However, at Black Butte the greatest proportion of beetles were caught in passive traps in T+VNHV (43%) plots and the least in control plots (23%), and at Sawtell Peak traps in the VNHV plots caught the greatest proportion (74%) relative to T+VNHV (9%). At Black Butte, mountain pine beetles were caught two weeks longer in the T+VNHV and VNHV treatment passive traps than in the control passive traps (Figure 2a). At Togwotee Pass, beetles were caught in control and T+VNHV passive traps slightly longer than in the VNHV passive traps (Figure 2c).

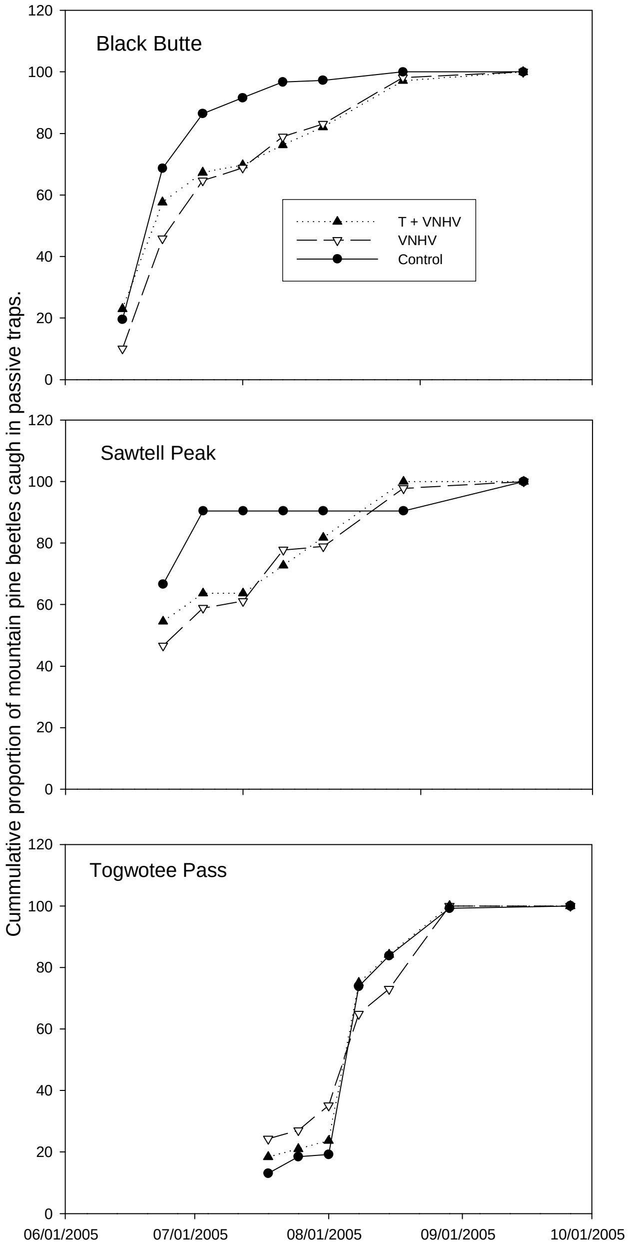

Fig. 2. A comparison of the cumulative proportion of mountain pine beetle caught in passive-traps among two treatments and controls and in aggregant-baited funnel traps at three whitebark pine sites in 2005; A) Black Butte, B) Togwotee Pass, and C) Sawtell Peak .

Mountain pine beetles were caught in baited funnel trap clusters from late June to early October (Figure 1b), with peak trap-catch in mid-July, similar to results in 2004. Funnel traps at Togwotee Pass absorbed a greater number of beetles than traps at both Sawtell Peak and Black Butte, although only significantly so when compared to Sawtell Peak (t = -4.05; df = 2, 7; p = 0.0118). In 2005, clusters of three funnel traps replaced the single traps used in 2004, although each year the same number of aggregant pheromone baits were deployed at each site (1 per trap in 2004 and 1 per cluster in 2005). At all sites, significantly more mountain pine beetle were caught in 2005 than 2004, including a 10-fold increase at the Togwotee site (Table 6). The relative contribution of increasing mountain pine beetle population size and increased efficacy of a trap cluster relative to a single trap is unclear.

Table 6. Mean (±SE) mountain pine beetle trap-catch in aggregant-baited funnel traps at three whitebark pine sites during 2004 and 2005. In 2004 single baited funnel traps were deployed at each site, 4 traps per replicate and 4 replicates per site (16 traps and 16 baits per site). In 2005 a cluster of three funnel traps with a single bait were deployed, 12 traps per replicate and 4 replicates per site (48 traps and 16 baits per site). In 2005, only 3 replicates were installed at the Black Butte site.

SITE	**2004***	**2005***
Black Butte	2600.5 (±430.9)^{a}	6966.3 (±679.7)^{b}
Sawtell Peak	1685.5 (±68.2)^{a}	4711.5 (±566.1)$^{b, x}$
Togwotee Pass	1105.0 (±437.0)^{a}	11235.7 (±1279.9)$^{b, y}$

*Contrasting superscripts consisting of ‘a’ and ‘b’ represent significant statistical differences between years. Superscripts ‘x’ and ‘y’ represent significant statistical differences between sites within the same year. All differences measured at p=0.05 based on Tukey’s Honestly Significant Difference test.

DISCUSSION

High-dose verbenone pouches and mountain pine beetle aggregant-baited funnel traps were tested in a push-pull strategy at three high elevation whitebark pine sites within the GYE in 2004. The proportion trees attacked by mountain pine beetle in verbenone treated plots, when compared to control plots, was significantly lower at only one site, Black Butte. At this same site, the number of mountain pine beetle attacked trees within a verbenone treated area surrounded by baited funnel traps (e.g., a push-pull strategy) was also reduced relative to the control, although not significantly. Of the three sites, Black Butte had the highest surrounding mountain pine beetle population as measured by baited funnel traps and number of trees attacked the previous one and two years within treated and control plots and 20-meter perimeters. At both other sites, too few attacks were observed in treatment and control plots to adequately evaluate treatment efficacy. In 2005, the proportion trees attacked by mountain pine beetle in verbenone treated plots, when compared to control plots, was significantly lower at only one site, Togwotee Pass. At this same site, the number of mountain pine beetle attacked trees within a nonhost volatile-verbenone treated area surrounded by baited funnel trap cluster (e.g., a push-pull strategy) was also reduced relative to the control, although not significantly. Of the three sites, Togwotee Pass had the highest surrounding mountain pine beetle population as measured by baited funnel trap clusters.

The lack of consistent treatment efficacy in this study may result from an array of different factors. Although in an operational trial aggregant baits would not be used to lure mountain pine beetle into treated areas, baits are typically used when semiochemicals are evaluated to ensure beetle pressure (Lindgren et al. 1989, Borden et al. 2003, Kegley et al. 2003). Mountain pine beetle aggregant baits were not used within plots in this study due to the sensitive nature of the high elevation whitebark sites. Following treatment, many replicates had too few attacks in control and treated plots for adequate statistical analyses. This was particularly true at the Sawtell Peak and Togwotee Pass sites in 2004. Another possible explanation for reduced treatment efficacy is that verbenone and NHVs eluted from release devices prior to conclusion of flight (Kegley and Gibson 2004, 2009) and/or photoisomerized into antenally inactive chrysanthenone (Kostyk et al. 1993). At our sites, although small numbers of beetle continued to fly through September, the majority of emergence occurred in mid-July, after pouches had been deployed for only a month and a half, suggesting that elution timing would not have been an issue.

Although pretreatment stand conditions including the number of living trees of all species (2004 and 2005), clump membership (2005), and the number of living whitebark pine in treatment perimeters (2005) were significantly different between sites and treatments (respectively), they were not significant in describing differences in proportion of trees attacked. This could be due to the small amount of variation among plots and sites in density measures including SDI and basal area. However, structure may have affected pheromone plume distribution. The heterogeneous and open nature of the whitebark pine stands may have diluted the pheromone plume through atmospheric turbulence, thereby losing any manipulative effect (Thistle et al. 2004). Additionally, the semiochemical diversity hypothesis, wherein mixed species forests have greater semiochemical diversity and fewer insect outbreaks (Zhang and Schlyter 2004) may help explain reduced proportion of trees attacked at the Togwotee Pass site, despite the large number of beetles caught in traps. The Togwotee Pass site had the largest diversity in tree species.

Passive traps were used in 2005 to measure non-directed mountain pine beetle flight through treated and control plots. We hypothesized that we would see a reduction in beetle movement through treated areas when compared to control plots. Only in one replicate at Togwotee Pass were the number of mountain pine beetle caught in passive traps fewer in treated compared to control plots, suggesting that the treatments did not deter mountain pine beetle dispersal into areas with verbenone and NHVs.

Aggregant-baited funnel traps were evaluated in a strategy to ‘pull’ mountain pine beetle that were being ‘pushed’ from verbenone and NHV treated plots. Although all funnel traps caught beetles, there was not a consistently significant reduction in the number of attacked trees in treated areas, relative to controls. In 2005, passive traps at the Black Butte site caught significantly more beetles than passive traps at either Togwotee pass or Sawtell Peak. However, this same year significantly more beetles were caught in aggregant-baited funnel traps at the Togwotee site than either Black Butte or Sawtell Peak. These results suggest that although a significant reduction in attacked trees in verbenone and NHV-treated areas was not observed, a large number of beetles were absorbed in the pheromone traps at the Togwotee site (relative to passive trap catch). Vandygriff et al. (2000) also observed that the ‘pull’ (aggregant semiochemicals) portion of the push-pull strategy may be more efficacious than the ‘push’ (repellant semiochemicals).

Although funnels traps may absorb significantly more beetles than trap trees (baited or standing), one potential trade-off is large numbers of attacked trees near the trap (Laidlaw et al. 2003) as was observed in our study. In 2004, 16% of whitebark pine within 5 meters of aggregant-baited funnel traps were attacked by mountain pine beetle, and 68% of these attacked trees had been treated with verbenone. In 2005, 5% (a single tree) of whitebark pine within 5 meters of aggregant-baited funnel trap clusters was attacked by mountain pine beetle, and was treated with verbenone. It is important to note that in 2004 64% of the total whitebark pine surrounding baited funnel traps fell within the five meter radius, whereas only 9% of the total whitebark pine surrounding baited funnel trap clusters fell within the 5-meter radius in 2005. Kegley and Gibson (2009) found that two high-dose verbenone pouches, replaced once during the summer, protected individual whitebark, lodgepole, and ponderosa pines from mountain pine beetle attack 80% of the time. Our results suggest that when a strong attractant is within 5 meters, the repellant effects of verbenone may be diminished thereby reducing its effectiveness for individual tree protection. The active range of verbenone is believed to be about 5 meters (Huber and Borden 2001), and may be overpowered by aggregation pheromones that have longer attractive ranges (Pureswaran and Borden 2003, Laidlaw et al. 2003). Due to issues with potential spillover attacks surrounding baited funnel traps, felled trap trees or standing trap trees that have been baited with aggregant pheromones may be the best option for reducing the number of beetles in an area (Borden et al. 1987, Laidlaw et al. 2003). The addition of whitebark pine oleoresin to existing baits, which were developed for mountain pine beetle in lodgepole, may also provide more effective trap bait (Pureswaran 2003, Borden et al. 2008). Naturally baited traps also result in significantly fewer spillover attacks than synthetic lures (Hansen et al. 2006) and could be used where baiting and/or felling host trees is not desirable.

Significantly more beetles were caught in funnel traps in 2005 compared to 2004. Although the same number of aggregant baits were used each year, in 2005 a cluster of three funnel traps was used compared to a single trap in 2004. One reason for such increases is that there were simply greater numbers of beetles in and around treated and control plots. Another explanation is that clustered traps are more effective as ‘sinks’ than single traps (Laidlaw and Wieser 2002).

Although not consistent among years or sites, areas with greater beetle pressure (e.g., number of trees attacked by mountain pine beetle one and two years prior to treatment) and larger diameter trees were more likely to have more attacked trees, similar to results from previous studies in whitebark pine (Kegley et al. 2003, Kegley et al. 2004, Bentz et al. 2005). Size of the surrounding beetle population, however, was not a good predictor of treatment efficacy.

CONCLUSION

Whitebark pine is a long-lived species that is restricted to higher elevations in western North America. Direct effects of climate warming on mountain pine beetle outbreak dynamics and the exotic pathogen white pine blister rust are believed to be two significant contributors to decline of whitebark pine in recent years (Logan and Powell 2001, McKinney and Tomback 2007). Due to the isolated nature of many whitebark pine ecosystems, direct control measures such as silvicultural manipulation are often not possible. High-dose verbenone pouches have shown promise for protection of individual whitebark pine (Kegley and Gibson 2009), and verbenone-releasing laminated flakes for stand-level protection (Gillette et al. 2009). We tested a push-pull strategy wherein aggregant-baited funnel traps were deployed in an effort to absorb dispersing beetles from verbenone and NHV-treated areas. As has been previously found with semiochemicals tested for stand level protection against mountain pine beetle, our results were inconsistent among sites and years. Although a large number of beetles were absorbed by funnel traps, significant differences in number of attacked trees in semiochemical-treated areas relative to control areas were not observed. One potential alternative is to try different patterns of trap dispersion and lure content that are specific to mountain pine beetle in whitebark pine. Additional research on methods to provide population ‘sinks’ without incurring substantial spillover of attacks on nearby host trees are also needed. Because annual removal or disposal of infested trees, in conjunction with semiochemical strategies, is a suggested integrated pest management strategy for mountain pine beetle (Borden et al. 2006), additional research on de-barking and burning infested trees in remote locations may prove useful. Furthermore, additional research on mountain pine beetle phenology at high elevation sites would ensure that semiochemical treatments are applied at the appropriate time.

Dendroctonus fossils were found in lake sediment cores associated with time periods of abundant whitebark pine during the Holocene (Brunelle et al. 2008) and tree-ring analyses suggest that mountain pine beetle was responsible for significant whitebark pine mortality during the late 1920s (Perkins and Swetnam 1996). However, the ecological role of mountain pine beetle in high elevation pine ecosystems relative to low elevation ecosystems remains unclear and warrants additional research. Active involvement in restoration programs such as presented in Mahalovich and Dickerson (2004) is needed to ensure the future existence of whitebark pine.

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