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Verbenone Decreases Whitebark Pine Mortality Throughout a Mountain Pine Beetle Outbreak

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Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) have been killing pines on millions of ha throughout the western United States since 2000. One species being affected is whitebark pine (*Pinus albicaulis* Engelm.), a five-needle pine already experiencing a number of other threats. Whitebark pine is a keystone species providing a variety of values including watershed protection and food and habitat for wildlife. An increasingly used method of protecting pines from mountain pine beetles involves the antiaggregation pheromone verbenone, but no studies have evaluated the ability of verbenone applied annually to protect whitebark pines throughout mountain pine beetle outbreaks. We applied verbenone pouches annually for 7 years until an outbreak ended. Probabilities that whitebark pines survived through the end of the outbreak were 0.34 ± 0.15 for control trees and 0.68 ± 0.17 for trees treated with verbenone once per year. Evidence from a second verbenone treatment that was discontinued before the end of the outbreak suggested that applying verbenone twice, as opposed to once, per year may more effectively protect trees. Increased survival did not appear to vary with tree size (i.e., dbh). We believe increased survival of the magnitude we observed could reduce risks to threatened whitebark pine populations.

Keywords: *Dendroctonus ponderosae,* pheromone, *Pinus albicaulis,* tree protection

Whitebark pine (*Pinus albicaulis* Engelm.) is a five-needle pine of high-elevation ecosystems occurring throughout western North America. It is valued for watershed protection, soil stabilization, and snowpack retention (Arno and Hoff 1989, Farnes 1989). The large, nutritious seeds are an important food source for wildlife including Clark's nutcrackers (*Nucifraga columbiana* Wilson, family Corvidae), the primary seed disperser of whitebark pine seed, and grizzly (*Ursus arctos horriblis*) and black bears (*Ursus americanus*) (Kendall 1983, Mattson and Jonkel 1990, Zhang and Schlyter 2004). In addition, whitebark pine ameliorates harsh environmental conditions (e.g., reduces wind exposure) for other tree species, thus facilitating succession (Arno and Hoff 1989, Callaway 1998, Tomback et al. 2014).

Whitebark pine is currently experiencing threats from white pine blister rust caused by the exotic fungus *Cronartium ribicola* (Schoettle and Sniezko 2007, Maloney et al. 2012) as well as fire in some areas (Jenkins et al. 2014), succession in some community types (Arno and Hoff 1989, Campbell and Antos 2003), and perhaps climate change (Romme and Turner 1991, Creeden et al. 2014, Maloney 2014). In addition, mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae; MPB), the insect species considered most damaging to whitebark and all other western North American pines (Furniss and Carolin 1977, Meddens et al. 2012), is currently causing heavy losses of whitebark pine (Bentz et al. 2010, Macfarlane et al. 2013). Recent outbreaks have occurred from northern British Columbia to southern Colorado and resulted in the death of millions of whitebark pines as well as pines of other species (Gibson et al. 2008). The combined threats to whitebark pine have led to its listing as a Candidate Species under the Endangered Species Act (Federal Register 2011).

A number of strategies are being used to conserve whitebark pine. Seeds collected and stored in nurseries administered by the federal government are being used in restoration projects and in efforts to identify white pine blister rust-resistant strains for gene conservation and breeding programs (Mahalovich and Dickerson 2004, Schoettle and Sniezko 2007). Also, tree thinning is being used to reduce competition (Keane et al. 2012) and the high fuel levels that lead to fire mortality.

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; grams (g) 1 g = 0.035 oz; hectares (ha): 1 ha = 2.47 ac.

Other efforts to protect whitebark pine are focusing on preventing and reducing MPB attacks. Mass attacks of pines by MPB are regulated by visual cues and a complex system of semiochemicals recently reviewed by Progar et al. (2014). MPBs typically attack mature, reproductive-aged trees, although smaller trees are also sometimes attacked (Cole and Amman 1980). Outbreaks typically last 8–12 years in individual stands before most suitable hosts are depleted and MPB populations decline (Roe and Amman 1970, Cole and Amman 1980, Perkins and Swetnam 1996). However, cold weather and natural enemies can curtail outbreaks before host populations are depleted (Safranyik and Carroll 2006, Bentz et al. 2010). The cool, high-elevation environments of whitebark pine have historically led to slow, asynchronous MPB growth and adult emergence from trees, thereby moderating MPB outbreaks (Amman 1973, Logan and Bentz 1999). Furthermore, although mountain pine beetle epidemics have been documented in whitebark pine in the past (Ciesla and Furniss 1975, Perkins and Swetnam 1996, Perkins and Roberts 2003), tree mortality during the ca. 2000 to current outbreak is thought by some to be more widespread than in previous outbreaks (Gibson et al. 2008). Warmer temperatures, perhaps as a consequence of climate change, are producing conditions more conducive to MPB development (Logan and Powell 2001, Bentz et al. 2010, 2014).

Insecticides are one tool that appear to be useful for protecting whitebark pine from MPB (Jorgensen 2010), although replicated studies have not been conducted to quantify the effects of insecticides reducing whitebark pine mortality. Replicated insecticide studies have been conducted on other species and have sometimes caused impressive reductions in mortality. For example, a single application of carbaryl-based insecticide applied to boles of lodgepole pine (*Pinus contorta* Douglas) nearly eliminated MPB-induced mortality for 2 years (Gibson and Bennett 1985, Grosman et al. 2010). Unfortunately, because motorized equipment is needed for insecticide applications, insecticide treatments are often infeasible in the remote, high-elevation areas where whitebark pine generally occurs (Tomback and Achuff 2010).

In addition to insecticides, verbenone (4,6,6-trimethylbicyclo [3.1.1]-hept-3-en-2-one), a semiochemical instrumental in regulating mass attacks, has also been used in attempts to protect pines (Borden et al. 2003, Kegley et al. 2003, Bentz et al. 2005, Progar 2005, Progar et al. 2013). Verbenone is an antiaggregation semiochemical that in sufficient aerial concentrations discourages bark beetles from infesting susceptible pine trees. In nature, verbenone is produced in three ways: as an allomone produced by pines through oxidation of monoterpenes (e.g., α-pinene) occurring in the phloem (Hunt et al. 1989, Flechtmann et al. 1999); as a pheromone produced by bark beetles directly (Rudinsky et al. 1974); and by conversion of verbenols by microorganisms (primarily yeasts) associated with adult bark beetles (Hunt and Borden 1989). In whitebark pine studies, trees receiving pouches containing synthetic formulations of verbenone have generally had greater survival than trees not receiving pouches during the year the pouches were attached (Kegley et al. 2003, Kegley and Gibson 2004, Fettig et al. 2012), and this has tended to be the case with other pine species as well (Borden et al. 2003, Bentz et al. 2005, Progar 2005, Negron et al. 2006, Borden et al. 2007, Progar et al. 2013). In addition to protecting trees receiving the pouches, Bentz et al. (2005) found that verbenone pouches attached to equally spaced trees increased survival across entire stands. Similarly, Gillette et al. (2012) found that verbenone flakes applied once on an area-wide basis provided some protection of whitebark stands during the year of application.

All past whitebark pine studies have applied verbenone for only a single year. Therefore, it has been unclear whether verbenone can protect whitebark pine throughout a typical, multiyear MPB outbreak. Progar (2005) and Progar et al. (2013) found that verbenone applied annually increased the survival of lodgepole pine throughout a multiyear MPB outbreak, and this suggests that multiyear treatments may be effective for whitebark pine as well. For managers, the decision to use verbenone to protect whitebark pines requires information about its efficacy throughout the entire course of outbreaks. Managers also require information derived from naturally occurring MPB outbreaks, but unfortunately, except for the single-year study of Fettig et al. (2012), all past verbenone studies in whitebark pine have used attractant pheromones to artificially inflate beetle numbers to the levels needed to test verbenone. The objective of this study was to determine whether verbenone pouches applied annually to individual whitebark pines could protect the trees throughout a naturally occurring, multiyear MPB outbreak.

Methods

Study Area

Our study area was a broad flat ridge top at ~2,865 m elevation on Bureau of Land Management-administered lands in the Sawtooth-Salmon River region of Central Idaho (latitude 44.288 and longitude −114.373). The semiarid study site was dominated by whitebark pine with few subalpine fir (*Abies lasiocarpa* Hook) and lodgepole pine. Soils were coarse and well drained, derived from Ordovician and Cambrian quartzite and Ordovician shale. Stand basal areas and tree diameters were characteristic of whitebark pine stands susceptible to MPB (Perkins and Roberts 2003). Whitebark pine basal area was ~12 m^2 ha^{-1}, and excluding trees of <13 cm dbh, mean whitebark pine dbh was 22 cm. MPB populations began increasing in 2003 and had greatly declined by 2012.

Experimental Protocol

In 2005, seven transects (300–1,000 m) were established throughout the study area. Every 40 m along each transect, the nearest whitebark pine tree of >20 cm dbh was marked. When the nearest tree had multiple stems, the largest diameter stem was marked. A total of 149 trees were marked, and the dbh of each marked tree was recorded.

Trees were randomly assigned either a no verbenone control (n = 41) or one of two verbenone treatments, A (n = 50) or B (n = 58). In both treatments and in all years (i.e., 2005–2011), two pouches containing verbenone were stapled to tree boles, one facing northeast and the other facing northwest, just before adult MPB emergence, which occurred in late June to late July. The verbenone doses supplied by the pouches, which varied by year owing to changes in commercial availability, are provided in Table 1. In treatment B, the original 5-g pouches were replaced with new 5-g pouches in mid-August because of concerns raised by Kegley and Gibson (2004) that 5-g pouches applied early in the year may not omit sufficient verbenone concentrations throughout the period of beetle activity (Table 1). However, this replacing of pouches occurred only in 2005 and 2006. In 2007, the 5-g pouches used in 2005 and 2006 became commercially unavailable, and only 7.5-g pouches were sold (Table 1). Therefore, in 2007, we used 5-g pouches we had purchased in 2006 to maintain treatment A unchanged. In treatment B in 2007, two 7.5-g pouches were applied in late June, and our decision to not

Table 1. Doses and approximate times of verbenone applications to individual whitebark pine trees in a study evaluating the ability of verbenone to protect whitebark pine from mountain pine beetle.

Year	Treatment A	Treatment B
2005	10 g mid-July	10 g mid-July; 10 g mid-August
2006	10 g late June–early July	10 g late June–early July; 10 g mid-August
2007	10 g late June	15 g late June
2008	15 g mid-July	15 g mid-July
2009	15 g late July	15 g late July
2010	15 g late July	15 g late July
2011	15 g mid-July	15 g mid-July

In all cases, the listed doses were split between two pouches that were stapled to the trees.

replace these pouches was based on an indication from the manufacturer that a single application of two of the larger pouches would provide sufficient verbenone concentrations for the entire year. After 2007, treatment A and B trees were identical, with each treated tree receiving one verbenone application per year consisting of two 7.5-g pouches (Table 1). Respectively, the manufacturers of the 5- and 7.5-g pouches were PheroTech (acquired by Contech Enterprises, Inc., Delta, BC, Canada) and Synergy Semiochemicals Corporation (Burnaby, BC, Canada).

Tree mortality was evaluated each fall in mid-October after MPB flight. A tree was recorded as "live" if it had no evidence of beetle attack or was attacked on small portions of the bole (Kegley et al. 2010). A tree was recorded as "dead" when the circumference of the bole was riddled with pitch tubes and frass was present in bark crevices and around the base of the tree. Monitoring of foliage color in July through October of the year following MPB attacks verified that trees recorded as dead had died and trees recorded as live had survived.

Data Analysis

To estimate the effects of treatments on whitebark pine survival probabilities, we applied the probit model for binary data (Albert and Chib 1993)

$$\Pr(y_i = 1) = \Phi(\alpha_{j(i)} + \beta x_i) \quad (1)$$

where $\Phi()$ denotes the normal distribution function with its single argument being the mean and the SD being 1.0. The response, y_i, equals 1 if a tree i died and 0 otherwise. The (3×1) vector a contains parameters controlling for the effects of treatment A, treatment B, and the no verbenone control, and the indicator function $j(i)$ maps treatments to trees. The parameter β controls for dbh, and x_i is the dbh of tree i standardized to mean 0.0 and SD 1.0. The model was fit to the 2006 data to determine whether replacing verbenone pouches in treatment B in the first 2 years of the study (i.e., 2005–2006) increased whitebark pine survival. In addition, the model was fit to the 2011 data to determine whether verbenone protected whitebark pine until the end of the MPB outbreak. The model was fit using Bayesian statistics with noninformative (i.e., uniform) priors assigned to all parameters. A Gibbs sampling algorithm written in Fortran was used to estimate the model parameters (Albert and Chib 1993, Intel Corporation 2013).

Results

Although a higher proportion of verbenone-treated trees survived than controls, mortality increased in both treated and control trees from 2004 to 2007 (Figure 1). Point estimates from Equation 1 of probabilities of survival after 2 years of verbenone application (i.e., the end of 2006) are 0.63, 0.76, and 0.92 for the control, treatment A, and treatment B, respectively (Figure 2). Whitebark pine survival through 2006 was significantly greater with two verbenone applications per year (i.e., treatment B) than for the control ($P < 0.0001$), and weak evidence suggests greater survival with one application per year (treatment A) than in the control as well ($P = 0.10$) (Figure 2). Trees receiving two applications per year had greater survival through 2006 than those receiving one application per year ($P = 0.02$).

Survival differences between treatments A and B diminished rapidly after treatment B trees stopped receiving two verbenone applications per year; i.e., after 2006 when trees of both treatments began to receive one verbenone application per year (Table 1; Figure 1). Beetle densities appeared to become too low to cause further mortality after 2009 (Figure 1), but we continued with treatments and data collection through 2011. By 2011, when the MPB outbreak

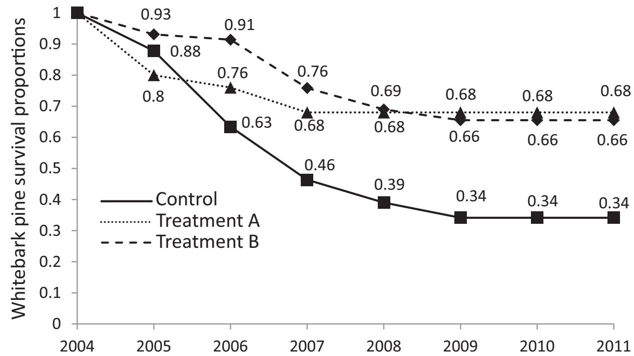

Figure 1. Survival proportions of whitebark pines treated (treatment A and treatment B) and not treated (control) with verbenone each year through the course of an MPB outbreak. In 2005 and 2006, verbenone treatments consisted of one (treatment A) or two (treatment B) verbenone applications per year. From 2007 on, both treatments consisted of one verbenone application per year.

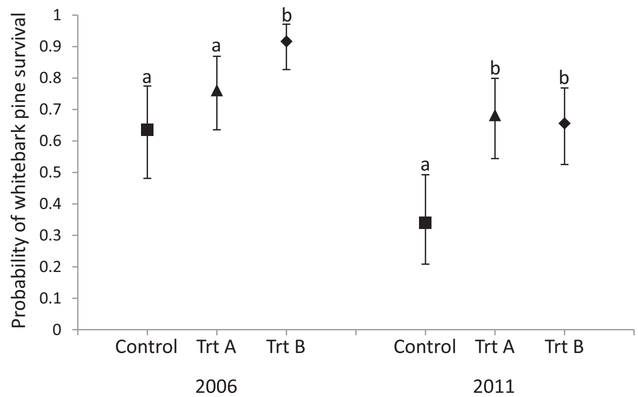

Figure 2. Point estimates (symbols) and 95% confidence intervals from a binary regression (i.e., probit) model used to estimate survival probabilities of whitebark pines that received verbenone treatments (Trt A and B) or were not treated (control). The two response variables were tree status (i.e., live or dead) in 2006 and 2011. In 2005 and 2006, verbenone treatments consisted of one (treatment A) or two (treatment B) verbenone applications per year. From 2007 on, both treatments consisted of one verbenone application per year. Bars with different letters are statistically different ($P < .05$).

had clearly ended, there was no evidence of survival differences between treatments A and B (Figure 2). Verbenone increased whitebark pine survival through 2011, with point estimates suggesting 68 and 66% survival for treatments A and B, respectively, compared with 34% survival for the control.

The 95% confidence intervals on the parameter β, which estimates the effect of dbh on survival, were 0.005 ± 0.24 and 0.12 ± 0.25 for 2006 and 2011, respectively. Thus, because these confidence intervals greatly overlap zero, there is no evidence for a relationship between whitebark pine size and mortality probability. We also tested verbenone treatment $\times$ dbh interaction terms in the model, and confidence intervals on the corresponding parameters provided no evidence that verbenone efficacy varied with tree size.

Discussion

Our results contribute to a growing body of evidence indicating that verbenone applied once per year can increase survival of pines throughout MPB outbreaks (Progar et al. 2013). In addition, our results illustrate that applying verbenone twice, as opposed to once, per year can more effectively protect whitebark pines from MPB for 2 years. Compared with one application per year, two applications per year may more effectively protect whitebark pines throughout outbreaks, but our study did not test this because we stopped applying verbenone twice per year before the outbreak ended. To our knowledge, the only other study to compare single with multiple verbenone applications per year was Kegley and Gibson (2004), but, in addition to the number of applications, the types of pouches differed between treatments in their study (i.e., slow- versus fast-release pouches). In light of the increased survival we documented in 2005 and 2006, it may be useful to conduct additional research comparing single and multiple verbenone applications per year throughout an MPB outbreak. However, any advantage of multiple applications may diminish as verbenone formulations and delivery mechanisms improve and become more effective at maintaining high aerial concentrations of verbenone for longer time periods (Progar et al. 2014).

Our results resembled those of short-term studies with lodgepole pine. Specifically, after 2 years in our study, MPB had mass attacked/killed 37, 24, and 9% of control, treatment A, and treatment B trees, respectively (Figure 1). In other studies, where verbenone was applied to lodgepole pine for 1 year along with baits to ensure high MPB densities, mass attack percentages for bait alone versus bait plus verbenone, respectively, were 24 versus 7% (Amman et al. 1989), 13 versus 5% (Lindgren et al. 1989), 22 versus 2%, 15 versus 3%, 11 versus 3%, and 10 versus 2% (Bentz et al. 2005). At sites where baits were not used, MPB mass attacked 17 versus 3% (Bentz et al. 2005) and 21 versus 11% (Lindgren et al. 1989) of control and verbenone-treated lodgepole pine, respectively.

In a 1-year study of whitebark pine that employed baits, Bentz et al. (2005) reported that 70 and 20% of control and verbenone-treated trees were mass attacked, respectively. Whereas these values illustrate greater efficacy of verbenone than our short-term findings, they roughly resemble our long-term results, and this may be because baiting accelerated mortality rates in the Bentz et al. (2005) study. In another 1-year study that did not apply baits, MPB mass attacked 28% (control) and 5% (verbenone) of whitebark pine (Fettig et al. 2012), and these values are consistent with our short-term findings. In addition, the proportion of trees with mass attacks in the 2-year study of Kegley and Gibson (2004) closely resembles the proportion of trees mass attacked and killed by the end of year 2 of our study. Specifically, where Kegley and Gibson (2004) applied verbenone pouches twice per year, they observed mass attack rates of 42 and 5% for untreated and treated trees, respectively, and we observed comparable attack/mortality rates of 37 and 8% in the treatment where we applied pouches twice per year. Combined with our long-term results, results from short-term studies suggest that verbenone can consistently provide protection to whitebark pines over the short and long term.

Beyond our study, long-term studies of verbenone are lacking in whitebark pine. Conversely, long-term studies have been conducted in lodgepole pine (Progar 2003, 2005, Progar et al. 2013), and the degree of similarity between our long-term results and long-term results from lodgepole pine varies by site. For example, 3–7 years after starting annual verbenone treatments at five sites, survival percentages in untreated and verbenone-treated plots, respectively, were 88 and 95%, 18 and 78%, 62 and 78%, 42 and 58%, and 5 and 50% for lodgepole pines of >33 cm dbh (Progar et al. 2013). Whitebark pine survival estimates from the final year of our study were 34% for untreated trees and 66% for treated trees. Thus, although the effects of verbenone on lodgepole pine survival have varied widely by site, the increase in percent survival we observed for whitebark pine is in the range of values observed for lodgepole pine by Progar et al. (2013). Our long-term data and the long-term data on lodgepole pine both suggest that verbenone tends to be a better option than no management for protecting pine trees from MPB.

The use of semiochemicals for forest pest control remains an active area of research, and recent advances in formulations and delivery systems are encouraging. Formulations composed of verbenone combined with nonhost volatiles (e.g., angiosperm green-leaf and angiosperm bark volatiles) provide a more diverse array of sensory cues for signaling unsuitable habitats, and compared with verbenone alone, verbenone combined with these nonhost volatiles may sometimes more effectively discourage bark beetles from infesting pines (Zhang and Schlyter 2004, Shepherd et al. 2007, Progar et al. 2014). However, in a Montana study of whitebark pine, Kegley and Gibson (2009) failed to detect a difference between verbenone alone and verbenone combined with nonhost volatiles. Future research comparing verbenone alone with verbenone with different combinations of nonhost volatiles in varied proportions may reveal treatments that perform more effectively than verbenone alone. A new controlled-release verbenone product in a wax emulsion called SPLATVerb, (Specialized Pheromonone & Lure Application Technology; ISCA Technologies, Inc., Riverside, CA) has been applied with caulk guns to tree boles. Results in lodegepole pine are promising (C.J. Fettig, A. Mafra-Neto, and A.S. Munson, unpubl. data, Jan. 15, 2013; Progar et al. 2014). This product was registered for use in the United States in 2013. Aerially delivered verbenone-impregnated flakes have reduced mortality of whitebark and lodgepole pine and are an efficient, potentially cost-effective tool for treating large areas (Gillette et al. 2006, 2012). By demonstrating that semiochemicals can protect whitebark pine throughout an MPB outbreak, we believe our results will help encourage further development of formulations, additives, and delivery methods.

Maintaining seed sources is essential to natural and assisted regeneration and postdisturbance recovery of whitebark pine (Kegley and Gibson 2004, Schwandt 2006). In our study, verbenone roughly doubled whitebark pine survival. This magnitude of survival increase could allow whitebark pine populations to more quickly recover from MPB outbreaks, which can cause 20–90% loss of whitebark pine basal area (Safranyik and Carroll 2006). Integrating verbenone with other management actions may further boost whitebark pine survival. In particular, verbenone might be effectively integrated with tree thinning to reduce competition from other tree species (Schwandt 2006, Keane et al. 2012). In areas where beetle populations are building, combining verbenone treatments with removal of MPB-infested trees has been suggested as a tool to protect pines (Progar 2005, Borden et al. 2007, Progar et al. 2013), but no data on this strategy are available yet.

In the future, verbenone and other semiochemicals may play an important role in conserving whitebark pines with desirable genetic traits. Specifically, verbenone could be used to protect trees identified as resistant to white pine blister rust. To evaluate heritability, trees tested and verified as having a level of blister rust resistance, as well as untested trees that are relatively or completely asymptomatic, must be kept alive until their offspring are evaluated for rust resistance (Kegley and Gibson 2004, Mahalovich and Dickerson 2004, Schwandt 2006). Those trees whose progeny exhibit resistance may prove extremely important as sources of seed and scion material for establishing rust-resistant seed orchards (Mahalovich and Dickerson 2004) and generating resistant populations in natural settings. Verbenone and other semiochemicals, as well as other tools capable of protecting trees identified as particularly genetically valuable, may become increasingly important as managers work to develop whitebark pine genetic stock capable of withstanding the threats currently facing the species.

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