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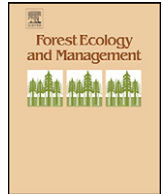
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Aerially applied verbenone-releasing laminated flakes protect *Pinus contorta* stands from attack by *Dendroctonus ponderosae* in California and Idaho

N.E. Gillette^{a,*}, N. Erbilgin^{b,h}, J.N. Webster^c, L. Pederson^d, S.R. Mori^a, J.D. Stein^{e,1}, D.R. Owen^f, K.M. Bischel^{g,h}, D.L. Wood^h

^a USDA Forest Service, PSW Research Station, Berkeley, CA 94701, United States

^b Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3, Canada

^c Total Forestry, Anderson, CA 96007, United States

^d USDA Forest Service, Forest Health Protection, Coeur d'Alene, ID 83815, United States

^e USDA Forest Service Forest, Health Technology Enterprise Team, Morgantown, WV 26505, United States

^f California Department of Forestry and Fire Protection, Redding, CA 96002, United States

^g Opus Environmental, Palo Alto, CA 94301, United States

^h Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, United States

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ABSTRACT

We tested a new formulation of verbenone, an antiaggregation pheromone of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae: Scolytinae), for area-wide protection of lodgepole pine (*Pinus contorta* Douglas ex Loudon) stands in the western United States. Helicopter applications of verbenone-releasing laminated flakes were made at the rate of 370 g of active ingredient/ha to two sites, one in California and one in Idaho, during summer 2005. Each site consisted of five 20.23-ha treated plots and five matching 20.23-ha untreated plots. We assessed *D. ponderosae* flight into study plots using traps baited with aggregation pheromones and we tallied *D. ponderosae* attack rates on *P. contorta* trees in treated and control plots before and after application. There were no significant differences between numbers of *D. ponderosae* trapped on treated and control plots. However, a significantly smaller proportion of *P. contorta* trees was attacked in treated plots than in control plots at both sites; the attack rate in untreated stands was roughly three times that of treated stands in both California and Idaho, even at this low application rate. Furthermore, attack rate in 2004 was a significant explanatory variable for the response in 2005 regardless of treatment in both California and Idaho. There was no significant treatment effect at either site on attraction of *Temnochila chlorodia* (Coleoptera: Trogositidae) Mannerheim, a key predator of *D. ponderosae*, to the prey aggregation pheromone.

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1. Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the most damaging insect pest of lodgepole pine, *Pinus contorta* Douglas ex Loudon, throughout its range in western North America (Furniss and Carolin, 1977; Wood et al., 2003) (Fig. 1), and outbreaks are increasing in response to changing climate (Logan and Powell, 2001; Hicke et al., 2006). For example, a current epic outbreak in British Columbia, Canada, has affected over 9.2 million hectares

(British Columbia Ministry of Forests and Range, 2007) and has breached the Continental Divide, spilling over into interior North America (Wilent, 2005). This outbreak, the largest ever documented, is expected to continue until either the host is depleted or severe cold weather reduces beetle populations (Ebata, 2004). Outbreaks of this magnitude can convert large regions of boreal and temperate forest from carbon sinks to carbon sources, exacerbating global warming (Kurz et al., 2008). *D. ponderosae* could infest millions of hectares of jack pine (*Pinus banksiana* Lamb.) in the vast boreal forests of Canada and the north central United States, and climate change may favor *D. ponderosae* range extensions into this habitat (Logan and Powell, 2001; Carroll et al., 2003; Ono, 2004). *D. ponderosae* also attacks other economically important pine species, such as sugar pine (*Pinus lambertiana* Douglas), ponderosa pine (*Pinus ponderosa* Douglas ex P. and C. Lawson), and western white pine (*Pinus monticola* Douglas ex D. Don) as well as ecologically important pines such as whitebark

* Corresponding author at: USDA FS, PSW Research Station, P.O. Box 245, Berkeley, CA 94701 USA. Address for courier deliveries: USDA FS, PSW Research Station, 800 Buchanan Street, West Annex, Albany, CA 94710, USA. Tel.: +1 510 559 6474; fax: +1 510 559 6440.

E-mail address: ngillette@fs.fed.us (N.E. Gillette).

¹ Retired.

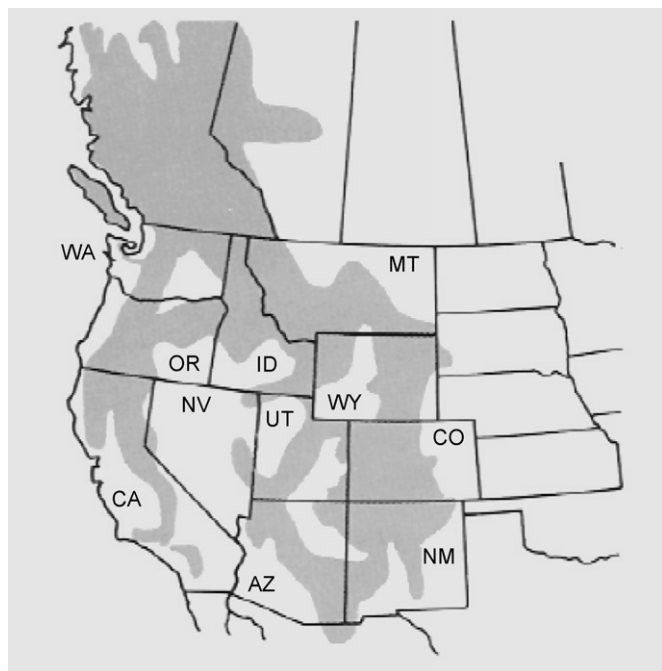


Fig. 1. Approximate distribution of *Dendroctonus ponderosae* in North America (reprinted from Amman et al., 1990).

pine (*Pinus albicaulis* Engelm.), foxtail pine (*Pinus balfouriana* Balfour), limber pine (*Pinus flexilis* James) and pinyons (Furniss and Carolin, 1977; Wood et al., 2003). There is good evidence that elevated stand density and basal area, fire, drought, and air pollution contribute to tree stress and thereby increase levels of bark beetle damage (Jones et al., 2004; Breshears et al., 2005). Heavily stocked or old-growth stands are particularly at risk (Wood et al., 1985; Shore et al., 2000), with extensive outbreaks predicted for many locations in the western United States (Krist et al., 2007; Hicke and Jenkins, 2008). Forest managers have therefore sought methods to mitigate the effects of this pest.

Several *D. ponderosae* management techniques have been tested, including silvicultural treatments to reduce stand density and/or basal area (Wood et al., 1985; Amman and Logan, 1998; Fettig et al., 2006a), sanitation (McMullen et al., 1986), insecticides (Haverty et al., 1998; Naumann and Rankin, 1999; Fettig et al., 2006b), and pheromone-based strategies including aggregation pheromones deployed in trap-out, trap tree, or concentration approaches (Gray and Borden, 1989; Gibson and Weber, 2004; Borden et al., 2006) and antiaggregants to interrupt colonization of hosts (Wilson et al., 1996; Huber and Borden, 2001; Borden et al., 2003, 2004, 2006; Kegley et al., 2003; Gibson and Kegley, 2004; Progar, 2005; Bentz et al., 2005; Gillette et al., 2006). As suggested above, reducing stand basal area may be the single most effective treatment (Johnstone, 2002; Safranyik et al., 2004; Whitehead and Russo, 2005; Zausen et al., 2005), but forest management objectives, particularly on public lands, often require preservation of large old-growth trees for wildlife habitat (Andrews et al., 2005). Insecticides are likewise frequently ruled out because of adverse effects on nontarget organisms.

The advantages of pheromone-based insect control strategies, especially where insecticides and silvicultural treatments are not practicable, have motivated research on the development of attractant and repellent pheromones for bark beetle control (Lindgren and Borden, 1993; Cook et al., 2007). S-(–)-Verbenone [(1S,5S)-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one], an antiattractant pheromone for *D. ponderosae*, has been tested for decades for both individual tree protection and area-wide control in various

release formulations (Borden, 1997). Verbenone is produced *in vivo* by some insects and is found in a variety of plants; it was approved by the Food and Drug Administration as a food additive (Syracuse Environmental Research, Inc., 2000) and is currently registered by the United States Environmental Protection Agency (EPA) as a biopesticide for use in forestry. Earlier work with verbenone targeting the southern pine beetle, *Dendroctonus frontalis* Zimmerman, indicated promise for such pheromone-based approaches, and operational treatments were subsequently developed for *D. frontalis* (Payne and Billings, 1989; Payne et al., 1992; Salom et al., 1995; Borden, 1997; Clarke et al., 1999). More recently, a variety of approaches have been tested with verbenone targeting *D. ponderosae* (Lindgren and Miller, 2002; Kegley et al., 2003; Progar, 2003; Gibson and Kegley, 2004; Kegley and Gibson, 2004; Bentz et al., 2005; Progar, 2005; Gillette et al., 2006). Lister et al. (1990) found that a verbenone bubblecapsule ("bubblecap") formulation was ineffective for single tree protection, but the bubblecap release devices used in their study may not have had sufficiently high release rates. Similarly, an earlier polyolefin bead formulation was shown to release too rapidly to provide protection throughout the beetle flight periods (Holsten et al., 2000), probably explaining the inconsistent results seen with that formulation in field trials (Shea et al., 1992). We speculated that many small, point-source, reservoir type releasers with longer-lasting release periods, such as pheromone-releasing laminated flakes, might provide better pheromone dispersal and could better simulate natural beetle release in a forest stand, giving better efficacy than larger releasers such as pheromone-releasing plastic pouches and bubblecaps (Thistle et al., 2004). Such a dispersible formulation also lends itself to area-wide application using rotary or fixed-wing aircraft, opening the possibility of large-scale treatments targeting larger outbreaks.

We chose to assess efficacy of DISRUPT[®] Micro-Flake Verbenone (Hercon Environmental, Emigsville, PA, USA), a verbenone-releasing laminated plastic flake formulation. A similar formulation has been used for decades with a different pheromone in the USDA Forest Service's "Slow-the-Spread" program to control the invasive gypsy moth (Sharov et al., 2002). We selected this system because of its longevity of release with this and other beetle pheromones (Gillette et al., 2006, 2009), its favorable regulatory status (it was already registered for other forest pests) and its ease of application with pods and hoppers adapted for fixed-wing aircraft and helicopters. Our study design incorporated large plots (20.2 ha) because of the potential for edge effects, which may have been responsible for some inconsistent results in previous tests.

2. Materials and methods

2.1. Study locations and timing

We installed the study in early 2005 at two sites, one in northern California and one in Idaho. The California study was carried out northeast of Mt. Shasta in northern California (122°5'58.96" W and 41°28'9.39" N). The plots were widely scattered on broad, high-elevation (1700–1850 m) flats dominated by *P. contorta* among rolling hills mixed with some steep broken cinder cones, in the areas of Military Pass and Stephens Pass. The area has a Mediterranean climate with long, dry summers. Frost pockets where cold air accumulates are common landscape features. The majority of the precipitation in the study area falls as snow. The soils are volcanic in origin, dominated by sand and ash. The forest composition in the area is primarily *P. contorta* in frost pockets with white fir [*Abies concolor* (Gord. & Glend.)] and Shasta red fir (*Abies magnifica* var. *shastensis*) occupying steeper north slopes, and ponderosa pine dominating south-facing slopes.

Table 1

Stand structure characteristics and pre- and post-treatment attack rates in treated and control plots in California and Idaho, measured in 2005.

	Mean (S.E.) total basal area (m ² /ha) ^a	Mean (S.E.) <i>P. contorta</i> basal area (m ² /ha) ^a	Mean (S.E.) DBH (cm) ^a	Mean (S.E.) number stems/ha ^a	Mean (S.E.) number <i>P. contorta</i> stems/ha ^a	Mean (S.E.) trees/ha attacked, 2004 ^a	Mean (S.E.) trees/ha attacked in 2005 ^a
(A) California							
Control	29.1 (2.0)a	24.4 (1.3)a	24.7 (0.7)a	459.8 (33.9)a	399.5 (23.0)a	2.8 (1.1)a	5.1 (1.6)a
Treated	28.8 (1.9)a	24.8 (2.5)a	27.8 (1.6)a	411.5 (19.7)a	362.6 (15.5)a	3.8 (1.5)a	1.6 (0.7)b
(B) Idaho							
Control	25.6 (3.1)a	19.2 (2.6)a	24.9 (0.5)a	496.1 (83.0)a	391.5 (69.6)a	1.1 (0.5)a	4.6 (1.9) a
Treated	26.3 (1.4)a	24.7 (2.3)a	26.6 (1.5)a	515.2 (87.0)a	487.2 (99.6)a	1.7 (0.9)a	1.6 (0.7) a

Means in the same column followed by the same letter are not significantly different at experiment-wise error rate, $\alpha = 0.05$.^a S.E., standard error.

The Idaho study was carried out 5–18 km east of the Historic Red Ives Historic Ranger Station in the headwaters of the St. Joe River along the Idaho and Montana state borders in the Bitterroot Mountains (115°13' 54.08" W, and 47° 4' 26.32" N). The nearest town is St. Regis, Montana, about 22 air km to the north-northeast. We installed plots in two areas, one east of Red Ives Peak and the other southeast of Cascade Peak, with elevations ranging from 1650 m to 1950 m. The landscape is a steeply dissected topography of glacial origin, and it was not uncommon for the elevation to vary by 70 m or more within a plot. The climate is characterized by dry summers and cold winters, with most precipitation falling as snow during the fall, winter and spring. The geology of the area is primarily stacked slabs of sedimentary bedrock. The forests are dominated by *P. contorta* across the entire landscape. Other species that are found on the plots, depending on aspect and elevation, are Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], sub-alpine fir [*Abies lasiocarpa* (Hook) Nutt.], mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.], western larch [*Larix occidentalis* Nutt.] and Engelmann spruce [*Picea engelmannii* Parry].

At each location we selected ten 20.2-ha plots, at least 400 m apart, with similar stand stocking levels and existing rates of *D. ponderosae* infestation (Table 1). We then randomly assigned the pheromone treatment to half of the plots, reserving the remaining half as untreated controls. A core plot of 10.1 ha was established in the center of each of the 10 plots so that treatment effects (beetle flight and rate of attack on trees) could be measured while avoiding possible edge effects.

2.2. Pheromone formulation

Verbenone-releasing flakes were formulated to contain 15% verbenone in a central layer of plastisol bounded by two thin layers of rigid polymer laminate. This laminated formulation, which is prepared in large sheets and then cut into small square “flakes”, releases verbenone only at the perimeter (not from the upper and lower surfaces) of each 3.2 mm × 3.2 mm flake. Each flake thus represents a small reservoir of verbenone with limited pheromone-releasing surface-to-volume ratio, resulting in sustained release of the pheromone over time.

2.3. Application rate and timing

The pheromone was applied in Idaho on 16 June 2005 and in California on 24 June 2005 at the rate of 370 g AI/ha (2.47 kg of formulated pheromone/ha). This application rate is equivalent to ca. 9.7 flakes/m². Application was made using a Bell 47-G3B2A turbine helicopter equipped with two side pods, each equipped with slot augers feeding a hydraulic spinner to achieve even distribution of flakes. The airspeed during application was 72.5 km/h. Evenness and precision of application were assessed by playing four pieces of 1 m × 1 m cardboard per plot, each sprayed with a tacky substance to catch dispersing flakes; flakes were counted immediately following application.

2.4. Stand structure and beetle flight measurements

We established four fixed east-west transect lines on each core plot for strip cruises and fixed-radius plot cruises, with all transects equidistant from one another and each spanning the 10.1-ha core plot (Fig. 2). Two fixed-plot centers were marked along each transect, with plot centers equidistant. We conducted a 0.4-ha fixed-radius plot cruise at each fixed-plot center of all trees equal to or larger than 10 cm DBH, the size range that is susceptible to attack by *D. ponderosae*, documenting the species and DBH of each tree. These 0.4-ha plots were used to estimate the total number of trees, number of target trees (i.e. by species susceptible to beetle attack), total basal area, and target basal area for the corresponding transects. With such large plots (experimental units) it is not feasible to measure stand structure by complete census, so we chose to use these smaller plots to estimate stand structure. We also conducted a 15.2-m wide strip cruise along each of the four transects to assess attack rates in 2004 and 2005 (the sum of the areas of the four transects equaled about one-fifth of the total core plot area). For each strip cruise, we examined all trees within the transect for signs of bark beetle attack. We conducted this cruise once during spray week to document pre-existing beetle populations, and then again at the end of the season to document new attacks after treatment. New attacks, including mass attacks, strip attacks and pitch-outs, were identified by the presence of pitch tubes and red boring dust, with attacks primarily in the lower bole of the tree (Furniss and Carolin, 1977).

Immediately after the treatments, we placed four Intercept panel traps (Advanced Pheromone Technologies, Marylhurst, OR, USA) in each 10.1-ha core plot, with one trap in the NW, SW, NE and SE corner). Traps were suspended at a height of 2 m as far away

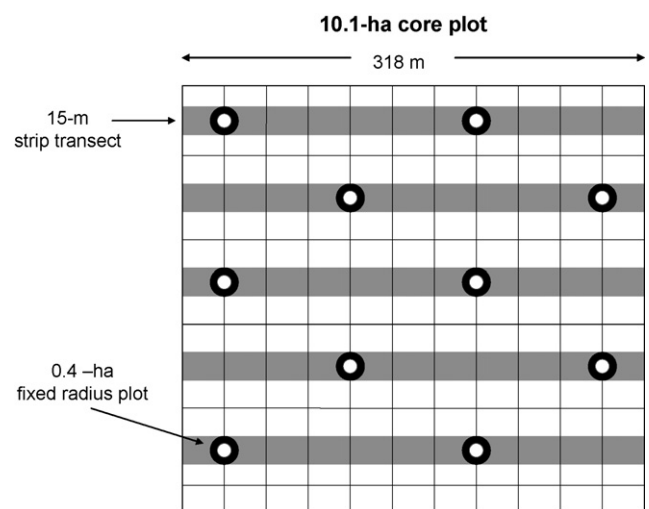


Fig. 2. Timber cruise sampling scheme (gray bands indicate strip-cruise transects; black circles indicate fixed-radius plots).

as possible from any host trees. The traps were baited with mountain pine beetle aggregation pheromone (Phero Tech International, Delta, British Columbia, Canada); pheromones were replaced twice during the post-treatment assessment period, at 1-month intervals following pheromone application. Two insecticide-releasing plastic strips (Hercon Environmental) were placed in each trap collection cup to avoid predation. We collected the beetles caught in these traps at roughly 1-month intervals in California and biweekly in Idaho for 2 months following pheromone application. Beetles were identified and counted at the University of California, Berkeley. We also counted trapped *Temnochila chlorodia* Mannheim (Coleoptera: Trogositidae) beetles, an important bark beetle predator species, in order to assess possible treatment effects on this important nontarget insect.

2.5. Statistical analysis

The experimental design is a completely randomized design with plots as experimental units and transects nested in plots as pseudo-replicated experimental subunits. The number of attacked trees per transect nested in plot in 2005 (post-treatment) was analyzed with a Poisson regression model for over-dispersed Poisson-distributed responses, which belongs to the family of generalized linear models, to address the discrete nature of the response (counts) and the variability associated with plot (McCulloch and Searle, 2001). Stand structure covariates (basal area, DBH, and/or stand density) were assessed using Akaike's Information Criterion (AIC) (Venables and Ripley, 1997), but these covariates did not improve the model, so only treatment and pre-existing attack rate were used as explanatory variables. The logarithm of the estimated mean number of *P. contorta* trees in each transect was used as an offset to estimate the proportion of attacked trees per hectare. The regression model:

$$\text{Expected}[\text{attack2005}_{i,t(\text{plot})} | \varepsilon_{\text{plot}}] = e^{T_i + b * \text{attack2004}_{t(\text{plot})} + \log(\text{trees}_{t(\text{plot})}) + \varepsilon_{\text{plot}}}$$

where “attack2005” is the number of attacked trees in 2005 in the transect t nested in plot, $t = 1, 2, 3, 4$; T_i is the treatment effect ($i = 1$ control, $i = 2$ treated); b is the regression coefficient for number of trees attacked in 2004; $\log(\# \text{ trees})$ is the logarithm of the estimated number of trees from the fixed-radius plots in the transect t nested in plot; and ε is the over-dispersion error due to plot variability, and “|” means “conditioned to”. The number of trees attacked in 2005 per transect was assumed to have an over-dispersed Poisson distribution with mean equal to the expected value modeled above.

Since the logarithm of the estimated number of trees is used as an offset in the above model, the proportion of attacked trees (attack rate) in 2005 per transect can be obtained from the model above; therefore this model is equivalent to:

$$\frac{\text{Expected}[\text{attack2005}_{i,t(\text{plot})} | \varepsilon_{\text{plot}}]}{\text{trees}_{t(\text{plot})}} = e^{T_i + b * \text{attack2004}_{t(\text{plot})} + \varepsilon_{\text{plot}}}$$

The parameters were estimated using the maximum likelihood estimation and generalized estimating equations techniques (McCulloch and Searle, 2001) with the SAS (v. 9.1.3) GENMOD procedure (SAS Institute, 1997). The Wald Chi-square statistic was used to compare contrasts, and the experiment-wise error rate was 0.05.

The number of beetles trapped in 2005 in each plot corner was also analyzed with a Poisson regression model for over-dispersed Poisson-distributed responses to address both the discrete response and the variability associated with multiple traps in each plot through time (two sampling periods for California and four sampling periods for Idaho) (McCulloch and Searle, 2001).

Explanatory variables were treatment (control vs. treated) and sampling period. The regression model:

$$\text{Expected}[\text{beetle count}_{i,j,c,\text{plot}} | \varepsilon_{c(\text{plot})}] = e^{T_i + \text{Time}_j + \varepsilon_{c(\text{plot})}},$$

where beetle count is the number of trapped beetles; T_i is the treatment effect ($i = 1$ control, $i = 2$ treated); Time_j is the time effect ($j = 1, 2$; 2 periods for California or 1, 2, 3, 4; 4 periods for Idaho); $\varepsilon_{c(\text{plot})}$ is the random effect (over-dispersion error) accounting for variability due to location, $c = 1, 2, 3, 4$ corners, and “|” means “conditioned to”. The number of beetles trapped in 2005 in each plot corner was assumed to have an over-dispersed Poisson distribution with mean equal to the expected value modeled above. The Wald Chi-square statistic was used to estimate parameters and compare treatments (SAS Institute, 1997).

3. Results and discussion

There were no significant differences between treatment and control plot stand structures and pre-treatment beetle attack rates at either site (Table 1). Mean basal areas for all tree species combined were 29.1 m²/ha in control plots vs. 28.8 m²/ha in treated plots in California, and 25.6 vs. 26.3, respectively, for Idaho. The values for total mean stems per hectare were 459.8 and 411.5 for control vs. treated plots in California and 496.1 vs. 515.2 in Idaho. Mean basal areas for *P. contorta*, the only host in either area for *D. ponderosae*, were 24.4 m²/ha vs. 24.8 m²/ha for control vs. treated plots, respectively, in California, and 19.2 m²/ha vs. 24.7 m²/ha in Idaho. Mean *P. contorta* stems per hectare were 399.5 vs. 362.6 in California and 391.5 vs. 487.2 in Idaho. Tree diameters were also similar in control and treated plots at both sites, with mean DBHs of 24.7 cm and 27.8 cm for control and treated plots, respectively, in California and 24.9 cm and 26.6 cm, respectively, in Idaho. Pre-existing beetle attack rates were likewise similar, with rates of 2.8 trees/ha in control plots and 3.8 trees/ha in treated plots in California, and 1.1 vs. 1.7 in Idaho. There were no significant differences in stand structures or pre-treatment attack rates at either site, but post-treatment attack rates were significantly different in California, but not in Idaho. In California, control plots had 5.1 trees attacked/ha for the control plots vs. 1.6 trees/ha for treated plots, and in Idaho control plots averaged 4.6 attacked trees/ha vs. 1.6 trees/ha in treated plots, or a roughly threefold difference between the control and treated plots at both sites. These differences in post-treatment attack rates were significant in California ($P = 0.004$) but only approached significance in Idaho ($P = 0.063$). We note that these values are not adjusted for stand density; when proportional attack rate is assessed (below) there is a significant treatment effect at both sites.

The attack ratio (estimated proportion of trees attacked in control plots:estimated proportion of trees attacked in treated plots) in 2005 in California was 2.7:1 ($P = 0.048$) and in Idaho the attack ratio was 3.7:1 ($P = 0.041$) (Table 2 and Fig. 3), indicating a significant treatment effect at both sites. The level of beetle attack in 2004 was a significant factor in the 2005 attack rate in both California ($P < 0.0001$) and Idaho ($P = 0.032$) (Table 2).

The rate of increase in attack rates from 2004 to 2005 was steeper in Idaho than in California, but at both sites the verbenone treatments reduced the level of attack to about one third that in untreated plots (Fig. 3). Beetle populations, as measured by 2004 attack rate, were much lower in Idaho than in California to begin with, but had reached nearly the same level overall by 2005 (Table 1).

There were no significant differences between trap catches of *D. ponderosae* in treated and control plots at either site, but in general slightly more beetles were trapped in control plots at both sites

Table 2

Estimates of the regression coefficients for previous year (2004) attack rate and treatment comparisons in California and Idaho, 2005.

Parameter	Estimate	Lower 95% CI	Upper 95% CI	P-value
(A) California				
2004 attack coefficient	0.2057	0.1257	0.2857	<0.0001
Ratio of attack rates, control/treated ^a	2.7	1.0	7.0	0.048
(B) Idaho				
2004 attack coefficient	0.3584	0.0304	0.6865	0.0322
Ratio of attack rates, control/treated ^a	3.7	1.1	13.0	0.041

^a Ratio of proportion of control trees attacked to proportion of treated trees attacked.

(Figs. 4 and 5). This result is understandable inasmuch as the aggregation pheromone for *D. ponderosae* is an extremely strong behavioral cue, so baited traps may attract more beetles than do host trees, even in the presence of high levels of the antiattractant verbenone. As expected, trap catches declined as the season progressed. Although the attack rate in 2004 was much higher in California than in Idaho (Table 1), the 2005 beetle populations in Idaho, as assessed by beetle trap catches (Figs. 4 and 5), were nearly 10-fold higher than in California, perhaps indicating a growing outbreak there.

Responses to treatments by *T. chlorodia* were different at the two sites, with higher levels of *T. chlorodia* in treated plots in California and lower levels of *T. chlorodia* in treated plots in Idaho. Both treated and controls plots in California, however, had higher levels of *T. chlorodia* overall than did Idaho plots (e.g. an average of more than 15 per trap in California vs. fewer than 2 per trap in Idaho). Stated another way, the prey: predator ratio in control plots in California was roughly 1:1, whereas in Idaho it was roughly 100:1 at the first sampling date. Such differences may play a role, along with host stress and stand composition, in the development

of an outbreak. In addition, Erbilgin et al. (2007) showed that verbenone interrupted *T. chlorodia* response to the aggregation pheromone of *Dendroctonus brevicomis* LeConte in a ponderosa pine stand, but other studies (Erbilgin et al., 2003; Erbilgin and Raffa, 2004) indicate that differences in either release rate of the aggregation pheromones deployed or host volatiles emanating from the stand may explain differences in response by predators. The use of baited pheromones in traps for monitoring purposes, therefore, may have affected beetle responses differently at the two sites because of differences in elution rates and/or differences in host volatiles.

We recommend use of a modification of the post-treatment sampling scheme in future studies to assess stand structure and pre-existing attack rate, because we feel that the combined strip cruise with fixed-radius plot cruise did not provide sufficient spatial linkage between beetle attack data (derived from strip cruises) and stand structure (derived from fixed-radius plots) (Fig. 2). In retrospect, we believe that a cruise design using large (i.e. 1 ha) circular plots around the fixed-radius plots might have better captured the relationship between basal area and susceptibility to beetle attack. Alternatively, a 100% cruise could be made of smaller core plots.

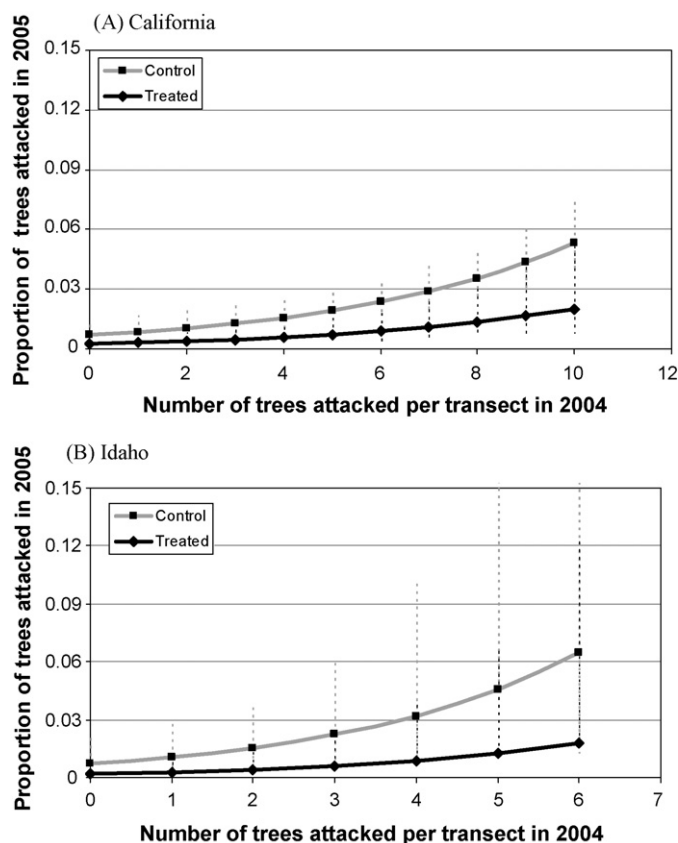


Fig. 3. Attack rate in 2005 (with 95% CI) in California and Idaho as function of 2004 *D. ponderosae* attack rates, with 95% confidence intervals shown as dashed lines.

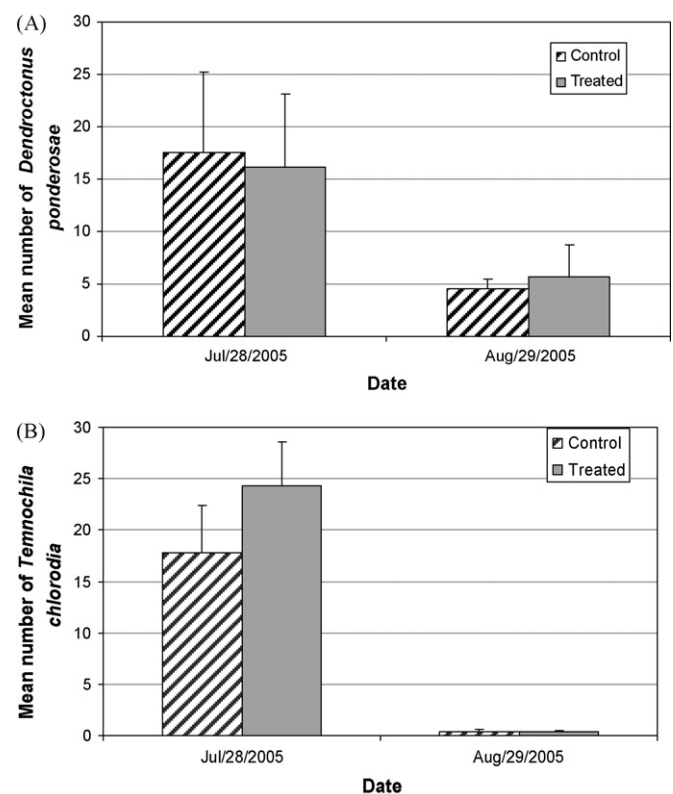


Fig. 4. Response of *Dendroctonus ponderosae* (A) and *Temnochila chlorodia* (B) to traps baited with mountain pine beetle aggregation pheromone, California, 2005.

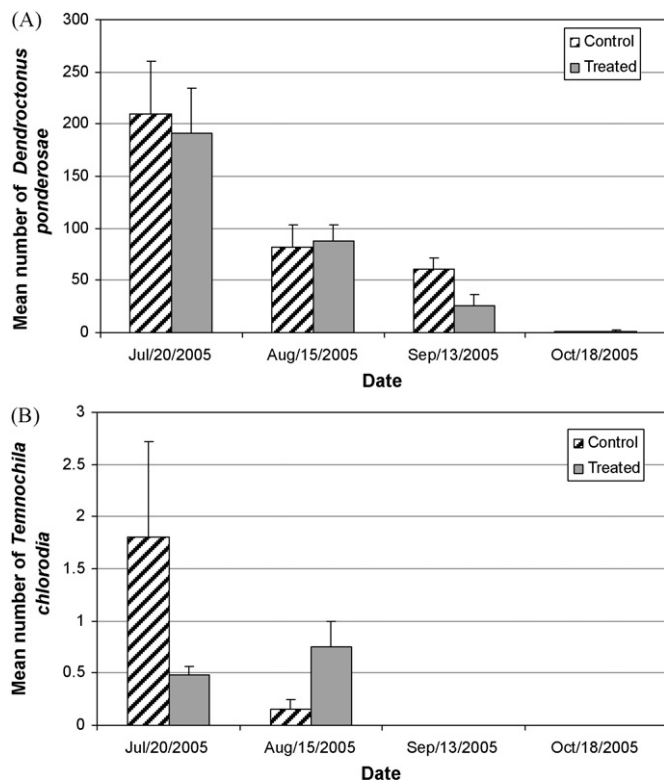


Fig. 5. Response of *Dendroctonus ponderosae* (A) and *Temnochila chlorodia* (B) to traps baited with mountain pine beetle aggregation pheromone, Idaho, 2005.

4. Conclusions

Although verbenone has often been shown to be effective for bark beetle management, results have sometimes been inconsistent, especially in cases where beetle populations were high and stands were highly susceptible. For example, Progar (2005) reported that verbenone pouches manually attached to individual trees initially reduced bark beetle-induced pine mortality in central Idaho, but that their efficacy declined after 5 years of repeated treatment of the same plots. By the end of that study, however, stand basal area was dramatically reduced by beetle activity in both the control and untreated stands surrounding the small treated plots, rendering the comparison problematic. Bentz et al. (2005) found that deployment of verbenone pouches in lodgepole and whitebark pine stands significantly reduced rate of attack by mountain pine beetle for up to 3 consecutive years, but they reported that some treated plots, particularly those with large emerging beetle populations, showed higher attack rates than controls. In these cases, higher levels of verbenone (Miller et al., 2006) or use of a combined “push–pull” strategy employing baited traps (e.g. Cook et al., 2007) may have been needed to overcome the effect of high levels of tree stress (i.e. drought) and/or large beetle populations.

Treatments using hand-applied antiattractant pouches (Borden et al., 2003, 2004) or attractant-baited lures in trap-out and concentration approaches (Gray and Borden, 1989; Borden et al., 2006) are promising for small, high-value stands, but are too labor-intensive to be used over large areas. In addition, many of the stands requiring protection from *D. ponderosae* are steep and/or remote, presenting difficulties for deployment of hand-applied tree protection treatments. Furthermore, beetle flight begins when roads in many areas are impassable, making alternatives such as an aerially applied treatment highly desirable in order to achieve timely applications early in the season.

In our tests in both California and Idaho, a significantly smaller proportion of trees was attacked in stands treated with aerially applied verbenone-releasing flakes than in control stands, with a threefold reduction in attack rate even with a relatively low application rate of 370 g/ha (≈ 9.7 flakes/m²). This rate is the maximum allowable for experimentation before a new pheromone is registered. For comparison, a verbenone risk assessment prepared at the request of the USDA Forest Service (Syracuse Environmental Research Associates, Inc., 2000) assumed application rates of 800–1200 g AI/ha using pouch release devices. This new laminated flake formulation of verbenone was recently registered by the US EPA with maximum application rates more than three times higher than the rate we tested in the current study, so it can now be tested at higher rates. It is clear both intuitively and from our results (Fig. 3) that higher pre-existing beetle populations present a greater challenge for mitigating damage, and we therefore recommend testing at higher application rates, especially when beetle populations are high. This formulation could be applied when beetle populations have erupted, but could also be applied preemptively when stands are expected to be vulnerable because they are stressed by drought, thinning, fire, pollution, disease, or overstocking. This approach might be useful both with aerial application in larger landscapes and with ground applications employing fertilizer-spreaders and/or paint-ball applicators in special-use sites such as campgrounds, ski resorts, and administrative sites. For example, campgrounds that are at risk because of a combination of prolonged drought and high stand basal area could be protected for a few consecutive years while facilities were established in less vulnerable sites. Likewise, stands rendered vulnerable by wildfire or prescribed fire could be treated until stand susceptibility had subsided. These possibilities warrant further testing.

In addition to the applications described above, pheromone-releasing flakes may also prove useful in protecting high-elevation, remote stands of limber pine, *P. flexilis*, and whitebark pine, *P. albicaulis*, as well as other ecologically important conifers. These important western pine species are currently threatened by a combination of infection by white pine blister rust (*Cronartium ribicola* J.C. Fischer) and attack by *D. ponderosae* (Tomback et al., 2001; Schoettle and Sniezko, 2007). The outlook for these two species is so dire that some important seed sources in high-elevation stands (some of them rust-resistant, some not) are currently being treated with insecticides to preserve seed sources for reforestation following the extensive mortality that is underway (Schoettle, personal communication). Helicopter applications of pheromone-releasing flakes may offer an appealing alternative to the use of insecticides in such environments.

This study assessed use of a single antiaggregation pheromone to protect *P. ponderosa* stands as a “push” (repellent) strategy, but even better efficacy may be achieved with this technique used in conjunction with the aggregation pheromone deployed in a trap-out strategy, with attractant-baited traps surrounding the area treated with antiaggregation pheromones (“push–pull”) (Borden et al., 2006; Cook et al., 2007). Push–pull strategies have typically been deployed on a fairly modest scale in western North America because of logistical constraints associated with previous pheromone release devices. With the advent of newer, dispersible release systems, we recommend the testing of a large-scale push–pull strategy in western North America because increasing climate warming and drying is likely to result in even more frequent and long-lasting bark beetle outbreaks. The use of attractant and repellent pheromones, when deployed in release devices and traps appropriate to the scale of these outbreaks, may prove to be effective in “herding” bark beetles into baited traps, baited live trees, or even baited, recently killed dead trees. The latter possibility is particularly attractive because it would not entail

the risk of producing yet another generation of bark beetles to exacerbate existing outbreaks.

Further testing is recommended to determine the optimum application rate, assess other potential active ingredients, and confirm the efficacy of verbenone flakes for higher beetle populations. Trends in climate change (Breshears et al., 2005) and forest stand conditions (Hessburg et al., 2000), however, suggest a continuing need for this type of area-wide treatment for bark beetle management. While we recognize the value of reducing basal area to minimize stand susceptibility to *D. ponderosae*, thinning of stands is time-consuming and is sometimes contraindicated by management objectives, especially on public lands. Pheromones, which can reach the target pest more effectively than contact insecticides, often have the further advantage of low toxicity toward nontarget organisms, including other insects, and especially natural enemy complexes (Erbilgin et al., 2007). Aerial verbenone treatments may prove useful for rapid response to *D. ponderosae* outbreaks in periods following prolonged drought, wildfire and thinnings when stands are temporarily vulnerable to attack. They may also be useful for protecting old-growth pine stands that are susceptible to bark beetle attack but must be managed at higher than optimal basal areas in order to provide valuable habitat for endangered wildlife species. The demonstrated efficacy of verbenone-releasing flakes for *D. ponderosae* control offers the hope of a rapid, area-wide treatment in the face of these explosive and widespread bark beetle outbreaks.

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