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Verbenone-releasing flakes protect individual *Pinus contorta* trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae)

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Abstract

1 In a study site in interior northern California, twenty individual lodgepole pines *Pinus contorta* were sprayed with a suspension of DISRUPT Micro-Flake® Verbenone (4,6,6-trimethylbicyclo(3.1)hept-3-en-2-one) Bark Beetle Anti-Aggregant flakes (Hercon Environmental, Emigsville, Pennsylvania) in water, with sticker and thickener, from ground level to a height of 7 m. Twenty trees sprayed with just water, sticker and thickener served as controls. All trees were baited immediately after spraying with mountain pine beetle *Dendroctonus ponderosae* aggregation pheromone lures, and lures were refreshed after 4 weeks.

2 Trees treated with verbenone had significantly lower attack density by *D. ponderosae* than controls at 2, 4, 6 and 8 weeks after application of flakes.

3 None of the treated trees was attacked by red turpentine beetle *Dendroctonus valens*, whereas control trees averaged nearly two *D. valens* attacks per tree, 8 weeks after treatment.

4 A dry frass index, used to predict ultimate tree mortality, was significantly higher in control trees than treated trees for all four sampling intervals. This index proved to be a significant predictor of ultimate tree mortality.

5 Ten months after application, treated trees showed significantly lower mortality than control trees.

Keywords Individual tree protection, lodgepole pine, mountain pine beetle, pheromones, Pinaceae, red turpentine beetle, Scolytinae, Scolytidae, semiochemicals, 4,6,6-trimethylbicyclo(3.1)hept-3-en-2-one.

Introduction

The mountain pine beetle *Dendroctonus ponderosa* Hopkins is the most important pest of lodgepole pine *Pinus contorta* Douglas ex Loudon throughout its range in North America (Furniss & Carolin, 1977; Wood *et al.*, 2003). *Dendroctonus ponderosae* typically erupts in large, episodic outbreaks. A current infestation in British Columbia, Canada has already reached over 11 million hectares in size and has breached the Continental Divide, spilling over into interior North America (Wilent, 2005). There is concern that *D. ponderosae* will colonize millions of acres of jack pine *Pinus banksiana* Lamb. in the vast boreal forests of Canada and the north central U.S.A., and that global climate change will favour *D. ponderosae* range extensions into this habitat (Logan & Powell, 2001; Wilent, 2005). Indeed, jack pine and another boreal pine, *Pinus flexilis* James, have been shown to be adequate hosts for *D. ponderosae* (Cerezke, 1995). *Dendroctonus ponderosae* also attacks other economically important pines, such as ponderosa pine *Pinus ponderosa* Douglas ex P. & C. Lawson (Furniss & Carolin, 1977; Wood *et al.*, 2003) and ecologically important pines such as whitebark pine *Pinus albicaulis* Engelm. (Keane, 2001; Tomback *et al.*, 2001; Schwandt & Kegley, 2004). It has been suggested that factors such as elevated stand density, fire, drought and air pollution contribute to tree stress and thereby increase levels of bark

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beetle attack (Waters, 1985a; Amman & Logan, 1998; McHugh *et al.*, 2003; Elkin & Reid, 2004; Jones *et al.*, 2004; Safranyik *et al.*, 2004).

Models and stand hazard rating systems have been developed to predict *P. contorta* susceptibility to *D. ponderosae* (Amman & Logan, 1998; Shore *et al.*, 2000; Smith *et al.*, 2002; Perkins & Roberts, 2003; Negron & Popp, 2004; Wulder *et al.*, 2004), and many attempts have been made to develop silvicultural (Fiddler *et al.*, 1989; Johnstone, 2002) and chemical (Taylor *et al.*, 1997; Haverty *et al.*, 1998; Naumann & Rankin, 1999) means to manage *D. ponderosae* damage in pine stands. Although maintenance of stand health through silviculture is arguably the most durable and effective method of protecting trees from bark beetle outbreaks (Wood *et al.*, 1985; Whitehead & Russo, 2005; Zausen *et al.*, 2005), such treatments can be difficult to implement in remote, steep or environmentally sensitive pine stands. Silvicultural treatments, such as thinning to reduce basal area in heavily stocked stands, are labour-intensive and can present regulatory hurdles (Waters, 1985a; Wood *et al.*, 1985). Proximity of infested stands to human activities, such as parks, campgrounds and wildland–urban interfaces, can severely limit the use of pesticides. Because silvicultural and pesticide treatments can be used only under somewhat limited conditions, considerable effort has been made to develop semiochemical approaches for the control of bark beetles in pine stands.

S-(−)-verbenone, [(1S,5S)-4,6,6-trimethylbiclo[3.1.1]hept-3-en-2-one], a beetle-produced anti-aggregation pheromone also found in pines (Kainulainen & Holopainen, 2002) and a wide variety of angiosperms (Molyneux *et al.*, 1980; Guillen & Cabo, 1996; Fournier *et al.*, 1997; Buttery *et al.*, 2000; Umano *et al.*, 2000; Pintore *et al.*, 2002; Sefidkon *et al.*, 2002; Ghannadi & Zolfaghari, 2003; Robles *et al.*, 2003), can be effective in limiting damage to pines by *Dendroctonus* spp. bark beetles (Payne & Billings, 1989; Payne *et al.*, 1992; Salom *et al.*, 1995; Borden, 1997; Clarke *et al.*, 1999; Lindgren & Miller, 2002; Kegley *et al.*, 2003; Progar, 2003; Gibson & Kegley, 2004; Kegley & Gibson, 2004; Bentz *et al.*, 2005; Progar, 2005). Although verbenone has often been shown to be effective, the results obtained have not been entirely consistent. Progar (2005) reported that verbenone pouches initially reduced bark beetle-induced pine mortality in central Idaho, U.S.A., but that the effect did not last for the entire 5-year treatment period. However, in that study, the same plots were treated every year, and stand basal area was dramatically reduced by beetle activity in both the controls and surrounding untreated stands relative to 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 three consecutive years, but they reported that some treated plots, particularly those with large emerging beetle populations, showed higher attack rates than controls. In the two latter cases, greater concentrations of verbenone may have been needed to overcome high concentrations of aggregation pheromones released from large beetle populations. In other earlier studies, failures may have resulted from photoisomerization of verbenone to chrysanthenone (Kostyk *et al.*, 1993), but more recent formulations have stabilizers to prevent isomerization. Lister *et al.* (1990) found that verbenone bubblecaps were ineffective for single tree protection, but the bubblecap release devices used in their study may have release properties, such as rate and distribution of release, that are not optimal for protection from scolytid attack. For example, 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 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 pouches and bubble-caps. In addition to potentially superior release characteristics, the flakes represent a less concentrated source of the active ingredient than do plastic pouch and bubble cap formulations, and may present less of a risk from tampering. The latex sticker used in the application provides excellent adhesion over several months (N. E. Gillette *et al.*, unpublished data), so there is extremely little risk of accidental removal by wildlife brushing up against the treated trees. In some cases, discrete, removable devices may have regulatory advantages over small, highly dispersed release devices such as flakes. However, most discrete, removable devices that have been developed for use in managing bark beetles require placement at a height of 5 m above ground, making removal (as well as deployment) an operational challenge. Although the flakes, unlike pouches and bubble caps, are not discrete removable devices, each flake contains only a small quantity of active ingredient and they are firmly glued to the bark, making it difficult to conceive that wildlife or park visitors would remove enough of them to present a hazard. If desired, sprays could even be applied above the reach of children. We used a hydroseeder for our applications to achieve a high level of consistency, which limited our study sites to roadside treatments. However, in an operational setting, other application methods, such as paint-balls and aerial sprays, would open up the possibility of this type of treatment for steep and remote areas.

Other chemicals, such as green leaf volatiles and nonhost angiosperm volatiles, may increase the efficacy of verbenone in protecting pines from attack by bark beetles (Wilson *et al.*, 1996; Huber & Borden, 2001; Borden *et al.*, 2003; Pureswaran & Borden, 2004; Fettig *et al.*, 2005). However, in these studies, at least eight additional components were required to achieve significant control of mountain pine beetle (Huber & Borden, 2001), and only a nine-component blend added to verbenone performed better than high-release verbenone alone for control of western pine beetle *Dendroctonus brevicomis* LeConte (Fettig *et al.*, 2005). Each additional component must undergo regulatory evaluation, including an array of fish, avian, invertebrate, plant and mammalian toxicity tests, for it to be registered for use in pest control. That process might be prohibitive for such complex blends.

We hypothesized that a single-component pheromone could be effective if deployed in a release system with the proper release characteristics (i.e. sustained, high release lasting throughout the beetle flight period). Such a single-component release system has obvious regulatory and marketing advantages, which are often crucial for product development for forestry uses. We selected verbenone as the active ingredient because of its demonstrated efficacy as an anti-aggregation pheromone for a wide variety of species in the genus *Dendroctonus*, and in particular *D. ponderosae* (Borden, 1997). We chose a laminated flake release device with the expectation that such a formulation, in which the active ingredient is held largely within the release device, might have superior release characteristics that would provide sustained levels of verbenone in a stand throughout the beetle flight period, normally late May to August in interior northern California (Furniss & Carolin, 1977; Waters, 1985a). In the summer of 2004, we field-tested a laminated 'flake' formulation of verbenone (DISRUPT Micro-Flake® Verbenone Bark Beetle Anti-Aggregant, Hercon Environmental, Emigsville, Pennsylvania) similar to one used for decades in the Gypsy Moth *Lymantria dispar* Linnaeus 'Slow-the-Spread' program (Sharov *et al.*, 2002).

We report the results of tests of the verbenone flake formulation applied to individual pine trees for protection from attack by *D. ponderosae*. The red turpentine beetle *Dendroctonus valens* LeConte, a secondary pest that sometimes attacks trees weakened by previous *D. ponderosae* attacks (Wood *et al.*, 2003), was also present in our study site and we therefore exploited the opportunity to assess efficacy against this pest too. This is the first report of a laminated flake formulation for protection of forest trees from bark beetle attack.

Materials and methods

Study location

The study was installed on 12 August 2004 on industrial forestry lands in Section 31, Siskiyou County, California (122°7′24.88W, 41°31′42.24N, approximately 5.6 km northeast of the peak of Mt. Shasta), T43N, R3W, Section 36, at an elevation of 2240 m. The site is in the rain shadow of the southern Cascade Range on the edge of the Basin and Range Province, and is characterized by cool, dry summers and very cold winters. The forest consists of secondary growth natural stand composed of interior lodgepole pine with a small component of Shasta red fir *Abies magnifica* var. *shastensis* Lemm. The site was chosen because it has a history of *D. ponderosae* infestations and is characteristic of much of industrial forestry land in the western U.S.A. (i.e. basal area and competing vegetation levels are lower than in most publicly managed lands). The flight periods of both *D. ponderosae* and *D. valens* typically begin 2–3 months before applications were made (Wood *et al.*, 2003); thus, we baited trees with aggregation pheromones to ensure high levels of attack by *D. ponderosae*. Earlier tests (N. E. Gillette *et al.*, unpublished data) indicated that trees under attack by *D. ponderosae* are likely to be attacked by *D. valens* as well. Because there is no known aggregation pheromone for *D. valens*, we relied on existing host volatiles cues to attract *D. valens*.

Pheromone formulation

(S)-(−)-verbenone (Bedoukian Research, Connecticut) was formulated as the active ingredient (AI) in a polyvinyl chloride resin layer sandwiched between two impermeable polymer layers (Hercon Environmental) at the rate of 15% wt/wt AI (i.e. 150 g AI/kg flake material). The sheets of laminate were cut into 3 × 3 mm squares, which were suspended in a solution of distilled water with 4.0% (v/v) Gelva sticker (Hercon Environmental) and 5.72 g/L guar gum (Hercon Environmental) as thickener. A solution of the formulation, identical except for the absence of flakes, was prepared for application to control trees.

Application

Application was made on 12 August 2004 using a modified hydroseeder seed/mulch spraying apparatus (Hercon Environmental) at the rate of 11.4 L/tree carrying 100 g/tree of flakes and 15 g/tree of AI. Flake and control formulations were sprayed onto trees in a single strip, approximately 30 cm wide, on a single side of each tree from ground level to a height of 7 m. Laboratory pheromone release data provided by the manufacturer showed that the flakes release verbenone at the rate of approximately 1 mg/day per gram of product, and we estimate that each tree therefore released approximately 100 mg verbenone/day during beetle flight. Immediately after treatment, each tree was baited at breast height with a mountain pine beetle lure (Phero Tech, Inc., Canada) containing *trans*-verbenol and *cis*-verbenol, in a ratio of 87 : 13, plus *exo*-brevicomin. Each lure was taped over half of its surface with duct tape to reduce the release rate of lure components because previous experience indicated that full strength aggregation pheromone lures were probably too strong a cue. Lures were refreshed 4 weeks after treatment, and were left in place over the winter because early snowstorms blocked access to the site after the 8-week sampling interval. The site remained inaccessible for 9 months after the last sampling interval.

Experimental design, sampling and statistical analysis

Forty trees of similar size (as measured by diameter at breast height; d.b.h.) and live crown ratio were selected from among all accessible (i.e. roadside) trees in the stand. Hydroseeders must be towed by an all-terrain vehicle, and therefore not all trees within the stand were accessible for treatment. Trees selected for the study were a minimum of 50 m apart. Twenty trees were selected at random for treatment from among the 40 trees, and the remainder served as controls. Both d.b.h. and live crown ratio are thought to be correlated with tree susceptibility to *D. ponderosae* attack, with larger trees and trees with lower ratios of live crown to total tree height being considered more susceptible to attack (Waters, 1985b). Competition among trees, as measured by basal area of tree surface per hectare, is also thought to contribute to susceptibility to bark beetle attack (Wood *et al.*, 1985). Trees were therefore measured for d.b.h., live crown ratio and basal area, and these traits were subjected to a chi-square test to ensure that there was no inadvertent bias in the random selection of trees for treatment vs. control categories. There were no significant differences in d.b.h., basal area, or live crown ratio between treated and control trees (Table 1).

A 30-cm band was demarcated on the bole of each tree, with the base of the band centred at breast height. At 2, 4, 6 and 8 weeks after treatment, counts were made of the number of resinous pitch tubes (*D. ponderosae* attacks) within each of these 30-cm bands. At the same time intervals, counts were also made below the bottom of the 30-cm base of the number of *D. valens* attacks per tree and the number *D. ponderosae* attacks producing dry frass. The latter number was coded as a dry frass index (0 = no dry frass; 1 = one to ten attacks with dry frass; 2 = more than ten attacks with dry frass). These categories were intended to provide a prediction of ultimate tree mortality because trees that have many attacks with dry frass (as opposed to highly resinous pitch tubes) are considered likely to have depleted their defensive resources and are more likely to succumb to bark beetle attack. We assumed that no trees in category 0 would ultimately die, some in category 1 would die, and all in category 2 would die. At 11 months after treatment, trees were inspected and ranked into one of three categories: (1) obviously dead, (2) obviously alive, or (3) uncertain status. The obviously living trees had deep green foliage overall, whereas the obviously dead trees had lime-green ('fading') to yellow, orange or brown foliage. Trees placed in the 'uncertain' category still had deep green foliage but had evidence of reduced resin flow (many dry frass tubes), or individual branches with brown foliage. There can be some spatial overlap on tree boles between attacks by *D. ponderosae* and *D. valens*, but *D. valens* normally produces much more resinous pitch tubes that are located lower on the bole than *D. ponderosae* pitch tubes. However, when the species of attacking beetle was uncertain, we later removed bark in the area of the pitch tubes to examine beetle galleries, which are clearly diagnostic for the two species (Furniss & Carolin, 1977).

The numbers of *D. ponderosae and D. valens* attacks per unit area of bark (attack density) were analysed with generalized linear models for over-dispersed Poisson distributed responses for counts with repeated measures (McCulloch & Searle, 2001) offset by the log of the area of tree trunk measured for rate of attack. The dry frass index was analysed with the Pearson's chi-squared test for independence for a three-way contingency table (Agresti, 1996) and graphically displayed using Mosaic plots (Friendly, 1994). The final dry frass indices were fitted with the proportional odds model (Collett, 1991). The score chi-square statistic was used to compare treatment effect vs. control for each sampling interval. This test is based on the generalized score function (Rotnitzky & Jewell, 1990; Boos, 1992). A GENMOD procedure (SAS Institute, 1997) was used for fitting over-dispersed Poisson generalized linear model. A LOGISTIC procedure was used for fitting proportional odds model to the frass index, and R XTABS routine with R MOSAICPLOTS routine (Development Core Team, 2004) were used for the Pearson's chi-squared test. The tree mortality status was also assessed by the R XTABS routine using the Pearson chi-squared test for independence.

Table 1 Stand characteristics of treated and control trees

Stand	d.b.h. (cm)	Live crown ratio (%)	Basal area (m^2/ha)
Treated	31.25 ± 4.20^a	70.75 ± 15.58^a	29.02 ± 15.50^a
Control	34.30 ± 5.68^a	68.25 ± 17.04^a	28.69 ± 15.17^a

Means ± SD in the same columns followed by the same superscript letter are not significantly different at $\alpha = 0.05$, Chi-square test

d.b.h., Diameter at breast height; live crown ratio, ratio of height of tree to live crown to total height of tree, expressed as a percentage; basal area, square meters of tree trunk per ha ($P > 0.05$ for each of the three comparisons).

Results

Treated trees had significantly lower attack rates by *D. ponderosae* at 2, 4, 6 and 8 weeks after application of flakes (Fig. 1), with mean attack densities reduced to near zero for treated trees at each sampling interval ($P < 0.0001$). No single treated tree was attacked by *D. valens*, whereas control trees averaged nearly two *D. valens* attacks per tree, 8 weeks after treatment, resulting in a significant treatment effect for this pest species too (Fig. 2) ($P < 0.0001$). The dry frass index, used to predict ultimate tree mortality, was significantly higher in control trees than treated trees for all sampling intervals ($P < 0.0001$) (Fig. 3) and, at week 8, the proportional odds model showed that the control trees had a significantly poorer prognosis than treated trees ($P < 0.0001$). Ten months after application, treated trees showed significantly lower mountain pine beetle mortality than control trees (Fig. 4) ($P < 0.0001$), with no mortality in treated trees and no definite survivors in untreated trees. The dry frass index was a highly reliable indicator of ultimate tree mortality (Fig. 5) ($P < 0.0001$), indicating that this measurement may provide a useful short-term predictor for long-term survival of trees under attack by bark beetles.

Discussion

Several previous studies have demonstrated efficacy of other verbenone formulations for protection of both individual trees and forest stands from attack by *D. ponderosae* (Lindgren & Miller, 2002; Kegley *et al.*, 2003; Progar, 2003; Gibson & Kegley, 2004; Kegley & Gibson, 2004). Those studies utilized pouch or bubble cap release devices applied singly to trees and resulting in a rate of 800 mg AI/tree for bubble caps and 4.65 g/AI/tree for pouches, compared with 15 g/AI/tree for the flake formulation. The reduction in rate of attack by *D. ponderosae* and *D. valens* in the present study was rather striking and was significant at each sampling interval, lasting for at least 8 weeks (Figs 1, 2). This result was considerably better than in some previous studies using both bubble caps and pouches (Lister *et al.*, 1990; Progar, 2005). The improved efficacy observed with the flake formulation in the present study may be simply a result of higher application rates/tree using flakes, or may result from improved pheromone distribution with release of pheromone from

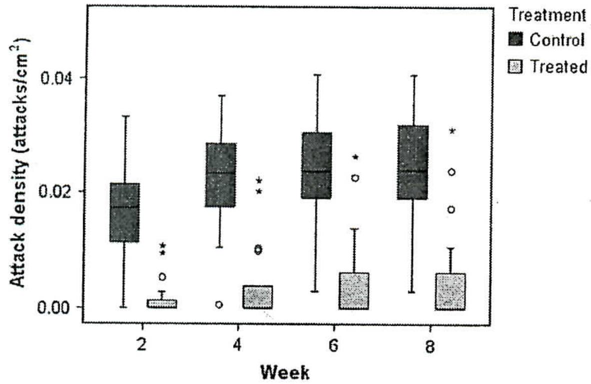

Figure 1 Mean density of attack by *Dendroctonus ponderosae* (number of attacks/cm² of bark) at 2-week intervals after treatment. Shaded boxes represent the interquartile range; whiskers represent the range excluding outliers and extreme values; outliers are shown as open circles, and extreme values are shown as asterisks. Rate of attack on treated trees was significantly different from controls ($P < 0.0001$) for every sampling interval (score chi-square statistic).

many point-sources over a much larger surface area (i.e. 2.1 m^2 for flakes vs. 0.070 m^2 for bubble caps). Bentz *et al.* (2005) suggest that higher emerging beetle populations may overwhelm the standard verbenone pouch treatment, but further research will be needed to determine whether the increased verbenone release rate or the more dispersed pheromone release pattern was responsible for the improved efficacy observed in the present study.

The increased rate of attack by *D. valens* in untreated trees vs. treated trees may have resulted from: (1) an increase in host attractants released by *D. ponderosae* attacks in those untreated trees (Hobson *et al.*, 1993); (2) pheromones released by attacking *D. ponderosae*; or (3) the anti-aggregation effects of the verbenone treatment itself. Verbenone was

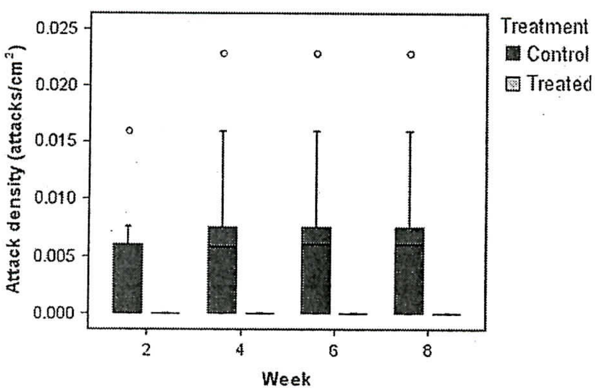

Figure 2 Mean density of attack by *Dendroctonus valens*/tree (number of attacks/cm² of bark) at 2-week intervals after treatment. Shaded boxes represent the interquartile range; whiskers represent the range excluding outliers, and outliers are shown as open circles. Rate of attack on treated trees was significantly different from controls ($P < 0.0001$) for each sampling period (score chi-square statistic).

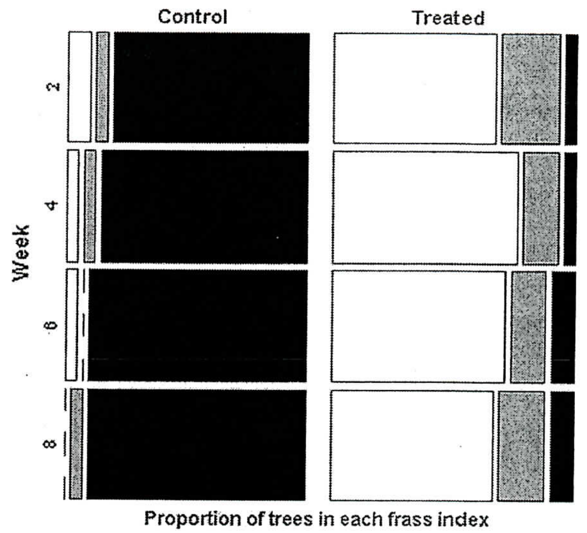

Figure 3 Contingency table representation of dry frass indices for four sampling intervals after treatment. White, no dry frass; grey, one to ten attacks with dry frass; black, more than ten attacks with dry frass. Treatment had a significant effect on dry frass indices (Pearson's chi-squared test, $P < 0.0001$).

previously shown to inhibit attraction of *D. valens* to its hosts (Rappaport *et al.*, 2001; Sun *et al.*, 2003), and we believe that this outcome is probably a result of both the verbenone treatment and the induction of other semiochemicals, such as frontalin, exo-brevicomin and *cis*- and *trans*-verbenol, by attacking congeners (Pureswaran *et al.*, 2000), as has been shown for *D. valens* after attacks by *D. brevicomis* LeConte (D. R. Owen, unpublished data). Indeed, Sánchez Martínez & Wagner (2002) reported that *D. valens* was an indicator of unmanaged stands in a ponderosa pine ecosystem in northern Arizona, U.S.A., suggesting that the effect may be reflective of increased tree stress and subsequent changes in the semiochemical environment.

The proportion of trees with 10 or more attacks with dry frass increased slightly over time in both the control and treated trees, but reached a plateau at four weeks in only treated trees (not controls) (Fig. 3), suggesting that an effective dose of verbenone was released from flakes during this

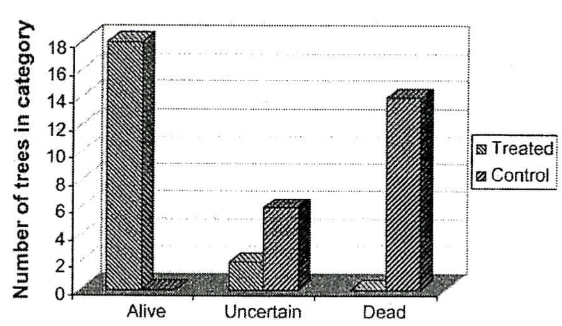

Figure 4 Frequency distribution of trees in mortality categories. Categories are Alive, Uncertain and Dead (as defined in the text). There was a significant treatment effect on mortality categories (Pearson's test, $P < 0.0001$).

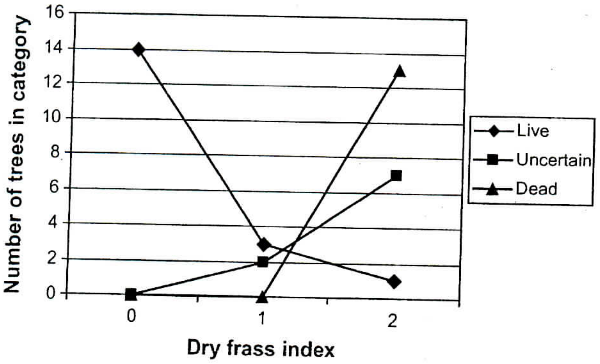

Figure 5 Numbers of trees in mortality categories plotted against dry frass index (dry frass categories: 0 = no dry frass; 1 = one to ten attacks with dry frass; 2 = more than attacks with dry frass) (Pearson's chi-squared test of independence, $P < 0.0001$).

eight week portion of beetle flight. A related study of aerially applied Verbenone DISRUPT® flakes, conducted nearby during the same year, indicated that the flakes continued to emit behaviorally significant amounts of verbenone for at least 14 weeks following treatment (Gillette et al., unpublished data), lending support to that conclusion. The dry frass index may prove to be very useful as an early indicator for assessing the effects of other tree-killing bark beetle species, as well. This method facilitates estimates of ultimate tree mortality shortly following bark beetle attack, without waiting a year or more for obvious tree death and without resorting to destructive sampling methods such as removal of tree bark to examine the status of bark beetle galleries.

The final tree mortality counts (Fig. 4) revealed a striking treatment effect, with treatment dramatically improving the chance of survival for a tree. Ninety percent of treated trees were alive, 10% of treated trees were of uncertain status and none were dead, whereas 70% of control trees were clearly dead, 30% of control trees were of uncertain status and none were alive. The treated trees clearly suffered a few beetle attacks (Figs 1, 2), but were able to defend themselves by pitching out the beetles with resin. These results, indicating that verbenone DISRUPT® flakes were able to inhibit aggregation to a very strong cue, are quite promising. By the time of the final tree mortality count, the flakes were apparently depleted because there was evidence of fresh (spring or early summer of 2005) beetle attacks on treated trees, but the trees were producing copious resin and were effectively repelling the attacks. In addition to the immediate tree mortality data, which show a clear and strong treatment effect, we noted that there were four 'spill-over' attacks on trees adjacent to trees baited with aggregation pheromone. All four of the spill-over attacks occurred adjacent to control trees, and none of them occurred next to treated trees. There is thus some evidence of an analogous spill-over protective effect of the verbenone flakes, which is encouraging in view of the desirability of achieving an area-wide protective effect.

Pouch and bubble cap release devices, when effective, are particularly useful in situations where access is easy and terrain smooth. On the other hand, flakes are amenable to aerial application, and thus have advantages in remote areas. The flake formulation is one of the few new release devices for verbenone in the last decade. Shea *et al.* (1992) reported one success using a polyolefin bead formulation of verbenone, but they report that they were unable to replicate that success. Holsten *et al.* (2000) later showed that the bead formulation released verbenone for only 2 weeks after application to forest stands, which may explain the inconsistent results achieved with that formulation. Sun *et al.* (2003) showed efficacy of a sprayable, microencapsulated formulation of verbenone for protection of Chinese pine *Pinus tabuliformis* Carrière for protection from *D. valens* attack, but that formulation is no longer commercially available.

The results of the present study suggest that either a higher release rate or a larger release surface may provide better protection than some previous formulations, but further studies must be conducted, especially considering the inconsistent results obtained in some previous studies with verbenone (Shea *et al.*, 1992; Progar, 2005). It is promising that this single-component release system has shown efficacy for one important forest pest, *D. ponderosae*, and one secondary pest, *D. valens*, which occasionally acts as a primary tree-killer (Sun *et al.*, 2003; Eaton & Rodriguez Lara, 1967; Rappaport *et al.*, 2001). Although multiple component formulations using verbenone with ipsdienol (Bertram & Paine, 1994) or angiosperm or green-leaf volatiles may provide enhanced efficacy over verbenone alone for some beetle species (Huber & Borden, 2001; Borden *et al.*, 2003; Pureswan & Borden, 2004), each additional component poses further regulatory and manufacturing obstacles that may limit product development in what is widely considered to be a 'niche' market. On the other hand, many of the nonhost volatiles are considerably cheaper than verbenone, a factor that may outweigh the costs of nontarget testing and maintenance of regulatory approval for multiple component formulations. Single component products, to the extent that they provide effective control with minimal regulatory effort, are nevertheless obviously advantageous. The evidence presented herein suggests that the efficacy of verbenone for management of bark beetles may be considerably enhanced simply by deploying it at higher release rates and/or from different types of release devices. However, it would be a simple matter to include adjuvant flakes in cases where verbenone alone does not provide sufficient protection. Verbenone is an interruptant for a wide range of *Dendroctonus* spp. (Skillen *et al.*, 1997; Rappaport *et al.*, 2001), and this broad activity makes it especially promising as a candidate for managing bark beetles. On the other hand, it should be noted that we conducted two similar trials of the flake formulation for individual tree protection against attack by *D. brevicomis*, with no treatment effect whatsoever (N. E. Gillette *et al.*, unpublished data). Although the individual tree protection tests using verbenone flakes with *D. brevicomis* were not promising, recent aerial application tests of the flakes for *D. brevicomis* control in *P. ponderosa* stands were very encouraging (N. E. Gillette *et al.*, unpublished data). The verbenone flake formulation is one of only two new bark beetle pheromone formulations in more than a decade with the potential for aerial as well as ground application (Sun *et al.*, 2003), and the release device is already registered for use with pheromones of forest Lepidoptera (Sharov *et al.*, 2002). Although more testing is clearly required to confirm the efficacy shown in this study, changing forest stand conditions (Hessburg *et al.*, 2000) and climate trends (Logan & Powell, 2001; Breshears *et al.*, 2005; Wilent, 2005) suggest a continuing need for large, area-wide treatments for bark beetle management.

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