The Push–Pull Tactic for Mitigation of Mountain Pine Beetle (Coleoptera: Curculionidae) Damage in Lodgepole and Whitebark Pines

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ABSTRACT   In an attempt to improve semiochemical-based treatments for protecting forest stands from bark beetle attack, we compared push–pull versus push-only tactics for protecting lodgepole pine (*Pinus contorta* Douglas ex Loudon) and whitebark pine (*Pinus albicaulis* Engelm.) stands from attack by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in two studies. The first was conducted on replicated 4.04-ha plots in lodgepole pine stands (California, 2008) and the second on 0.81-ha plots in whitebark pine stands (Washington, 2010). In both studies, *D. ponderosae* population levels were moderate to severe. The treatments were 1) push-only (*D. ponderosae* antiaggregant semiochemicals alone); 2) push–pull (*D. ponderosae* antiaggregants plus perimeter traps placed at regular intervals, baited with four-component *D. ponderosae* aggregation pheromone); and 3) untreated controls. We installed monitoring traps baited with two-component *D. ponderosae* lures inside each plot to assess effect of treatments on beetle flight. In California, fewer beetles were collected in push–pull treated plots than in control plots, but push-only did not have a significant effect on trap catch. Both treatments significantly reduced the rate of mass and strip attacks by *D. ponderosae*, but the difference in attack rates between push–pull and push-only was not significant. In Washington, both push–pull and push-only treatments significantly reduced numbers of beetles caught in traps. Differences between attack rates in treated and control plots in Washington were not significant, but the push-only treatment reduced attack rates by 30% compared with both the control and push–pull treatment. We conclude that, at these spatial scales and beetle densities, push-only may be preferable for mitigating *D. ponderosae* attack because it is much less expensive, simpler, and adding trap-out does not appear to improve efficacy.

KEY WORDS   *Pinus albicaulis*, *Pinus contorta*, semiochemicals, verbenone, green leaf volatiles

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the principal insect pest of pines in western North America, particularly lodgepole pine, *Pinus contorta* Douglas ex Loudon (Furniss and Carolin 1977, Wood

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et al. 2003). Lodgepole pine is a geographically widespread conifer species spanning a north–south range from the Yukon Territory to Baja California and from the Pacific Ocean in the west to the Black Hills of South Dakota in the east (Lotan and Critchfield 1990). Lodgepole pine forests recently have been devastated by expansive *D. ponderosae* outbreaks that threaten to turn boreal forest carbon sinks into carbon sources (Logan and Powell 2001, Kurz et al. 2008).

More recently, *D. ponderosae* attacks in whitebark pine (*Pinus albicaulis* Engelm.) stands also have escalated drastically (Logan and Powell 2001, Perkins and Roberts 2003, Gibson 2006). Whitebark pine is an ecologically important subalpine conifer that serves as a keystone species in high-elevation areas of the Cascade Ranges, the northern Rocky Mountains, and the Sierra Nevada regions of the northwestern United States and western Canada (Tomback et al. 2001, Schwandt 2006). Whitebark pine seeds are an important source of overwintering nourishment for grizzly bears (*Ursus arctos horribilis* Ord.), and studies have

shown them to be crucial for the survival of gestating cubs and other wildlife (Pease and Mattson 1999, Robbins et al. 2006). Whitebark pines are facing a double threat, however, from the combination of an introduced pathogen, white pine blister rust (*Cronartium ribicola* A. Dietr), and *D. ponderosae* (Tomback et al. 2001). Trees infected with blister rust appear to be more susceptible than uninfected trees to attack by *D. ponderosae* when beetle populations are low (Schwandt and Kegley 2004), and although *D. ponderosae* preferentially attacks older whitebark pines, blister rust is particularly damaging to seedlings. Thus, both the seed-bearing older trees and the new regeneration are suffering heavy losses. Furthermore, warming climates have resulted in a shift in high-elevation *D. ponderosae* voltinism from semivoltine to univoltine (Bentz and Schen-Langenheim 2007), so outbreaks of *D. ponderosae* in whitebark pines, which were once rare, are now common (Schwandt 2006). Regeneration of this species is so severely compromised by the combination of beetles, disease, and warming climate that a petition has been filed with the U.S. Fish and Wildlife Service to list it as an endangered species (Federal Register, http://www.fws.gov/mountain-prairie/species/plants/whitebarkpine/TempFR07192010.pdf). To help maintain whitebark pine populations, recent efforts have focused on collection of seeds from rust-resistant trees for screening for propagation in seed orchards (Schoettle and Sniezko 2007). In spite of these efforts to conserve resistant genotypes, many of the naturally rust-resistant trees are at risk of being killed by *D. ponderosae* before they can be identified, screened, and incorporated into a genetic resistance program. There is therefore much interest in the development of a safe, effective method for protecting this important resource.

The environmental consequences of these outbreaks have stimulated much productive research focused on semiochemical treatments to mitigate *D. ponderosae*-caused tree mortality, but at high beetle population levels such treatments are not consistently as effective as desired (Bentz et al. 2005, Progar 2005). In an attempt to increase the efficacy of antiaggregation semiochemicals such as verbenone for protecting lodgepole pines from *D. ponderosae*, various additional methods have been investigated, including the use of concentration and containment, where beetles are lured into a discrete area and then killed, and push–pull strategies, where beetles are lured to attractant-baited traps and also repelled with antiaggregants (Borden et al. 2006). A large body of research has yielded useful approaches to deploying verbenone (Borden et al. 1983a,b; Gray and Borden 1989; Borden 1997; Kegley et al. 2003; Gibson and Kegley 2004; Kegley and Gibson 2004, 2009; Bentz et al. 2005; Gillette et al. 2006, 2009) and verbenone with nonhost volatiles (Borden et al. 2003, Kegley et al. 2010) for the protection of lodgepole and whitebark pines from *D. ponderosae.* Most of this research, however, has focused on the deployment of bubblecap and pouch release devices that must be applied by hand, which

can be particularly challenging in remote, alpine sites where snow-cover does not melt in time to permit access by ground before beetle flight occurs. More recently, aerial applications of verbenone-releasing flakes have been shown to be effective for mitigation of *D. ponderosae*-caused tree mortality in lodgepole pine (Gillette et al. 2009) and whitebark pine (Gillette et al. 2012) stands.

Although these studies showed considerable promise for the use of antiaggregants against low to moderate beetle population levels, concern has been expressed about the efficacy of this technology for outbreak beetle population levels, which typically have been difficult to control with any treatment methods that have been tested except for insecticide applications (Fettig et al. 2006). For that reason, we chose to assess a push–pull approach where an attractive lure is used in conjunction with an antiaggregant, in the hope of achieving better control than with the antiaggregation semiochemical treatments alone (Borden 1997, Cook et al. 2007). Previous push–pull or concentration approaches for mitigating bark beetle damage mostly have compared push–pull with pull-only strategies by using baited trap trees that are intended to be logged to protect adjacent antiaggregant-treated stands (Lindgren and Borden 1993, Borden et al. 2006). Although the trap-tree approach has been largely successful, on most public lands in the United States the intentional sacrifice of living trees for such purposes may be prohibited by regulation, public policy, or both. Shea and Neustein (1995) report possible success with a method using only baited traps in conjunction with antiattractant semiochemicals for control of *Ips paraconfusus* Lanier. That study, however, had unreplicated treatments and no controls and therefore did not account for the record-breaking rainfall at the outset of the study that may have mitigated beetle-caused tree mortality. Nevertheless, this approach may have promise for mitigation of *D. ponderosae* infestations without the problems associated with trap trees. We therefore chose to test the alternative of combining beetle trap-out with an antiaggregation treatment, wherein we deployed a perimeter ring of attractant-baited traps around the antiaggregant-treated stands. Instead of comparing push–pull with the use of baited trap trees, we focused on a comparison of push–pull with push-only, because this approach does not risk killing healthy trees and past studies have already documented the considerable efficacy achievable with push-only (Gillette and Munson 2009).

Materials and Methods

Semiochemical treatments consisted of nonbiodegradable plastic verbenone flakes in the first study (California 2008) and a combination of biodegradable verbenone and biodegradable GLV (green leaf volatile) flakes (1-hexanol and Z-3-hexenol) in the second study (Washington 2010). We added the GLVs in the second study because work by Kegley and Gibson (2009) and Kegley et al. (2010) indicated their prom-

Table 1. Summary description of treatments conducted at Klamath National Forest, CA in 2008 and Okanogan-Wenatchee National Forest, WA in 2010

Location, yr, and treatment (code)	Anti-aggregation semiochemical(s), rate, and type of application (aerial or ground)	Plot size	Trap spacing
CA/2008 (CT)	None	4.04 ha	45.7 m
CA/2008 (PO)	Verbenone, 1,101 g/ha (aerial)	4.04 ha	45.7 m
CA/2008 (PP)	Verbenone, 1,101 g/ha (aerial)	4.04 ha	45.7 m
WA/2010 (CT)	None	0.81 ha	14.4 m
WA/2010 (PO)	Verbenone, 741 g/ha + GLVs, 370 g/ha (ground)	0.81 ha	14.4 m
WA/2010 (PP)	Verbenone, 741 g/ha + GLVs, 370 g/ha (ground)	0.81 ha	14.4 m

CA is California, WA is Washington, CT is control, PO is push-pnly, PP is push–pull, GLV is green leaf volatiles.

ise for enhancing efficacy of verbenone. This study was not designed to compare efficacy of GLVs in combination with verbenone, so that aspect is not discussed further in this study. Because the first study failed to show sufficient added tree protection by using widely spaced (47.2 m) perimeter traps baited with *D. ponderosae* aggregation pheromones, we used smaller plots with closer trap spacing in the second study. The first study was conducted with five replicates, but funding limitations constrained us to three replicates in the second study. Beetle populations were at full outbreak levels in California and early-outbreak levels in Washington, with 44% of trees in control plots killed in the California study, and 4% (nearly 10 trees/ha) in control plots in the Washington study.

Semiochemical Formulations. The verbenone (4, 6, 6-trimethylbicyclo(3.1)hept-3-en-2-one) formulation used in California in 2008 was DISRUPT Micro-Flake Verbenone Bark Beetle Anti-Aggregant flakes (Hercon Environmental, Emigsville, PA). These consisted of verbenone-releasing flakes, 3.2 by 3.2 mm^2, formulated to contain ≈15% verbenone in a central layer of plastisol bounded by two thin layers of polymer laminate. Thus, 1 kg of flakes contained ≈150 g of verbenone. In Washington in 2010, we used a combination of DISRUPT Bio-Flake Verbenone Bark Beetle Anti-Aggregant flakes and DISRUPT Bio-Flake GLV Bark Beetle Anti-Aggregant flakes (both made of a biodegradable polymer of roughly 3.2 by 3.2 mm^2 flakes, with ≈ 15% active ingredient in the verbenone formulation and ≈ 10% of each of the active ingredients, 1-hexanol (*N*-hexyl-alcohol) and *Z*-3-hexenol (*cis*-3-hexen-1-ol), in the GLV formulation). We applied verbenone at the rate of 1,101 g/ha in California in 2008. In Washington in 2010 we applied verbenone at the rate of 741 g/ha and GLVs at 370 g/ha (Table 1).

Study Site, Experimental Design, and Pheromone Application (California 2008). The study was conducted on the Goosenest Ranger District of the Klamath National Forest in Siskiyou County, CA (41° 50′26.849″ N, 122° 13′29.25″ W, elevation 1,330 m) in a stand consisting primarily of lodgepole pine with an admixture of ponderosa pine. We selected fifteen 4.04-ha plots, at least 500 m apart, with similar stand and stocking levels and similar rates of *D. ponderosae* infestation. We then randomly assigned each of the three treatments (push-only, push–pull, and control) (Table 1) to one third of the plots, yielding five rep-

licates per treatment (see Fig. 1 for a schematic diagram of the push–pull treatment). Both push-only and push–pull treatments received the "push" (verbenone) treatment, and the push–pull treatment had an additional "pull" treatment consisting of traps baited with *D. ponderosae* aggregation pheromone. The push-only treatment consisted of an aerial application of MicroFlake Verbenone on 23 June 2008, using methods described in Gillette et al. (2009). The push–pull treatment consisted of identical pheromone applications followed by the installation of a perimeter line of Intercept panel traps (Advanced Pheromone Technologies, Marylhurst, OR) baited with the four-component *D. ponderosae* aggregation pheromone, a blend of *trans*-verbenol, *exo*-brevicomin, myrcene, and terpinolene (ConTech International, Inc., Delta, BC, Canada). The perimeter traps were spaced 45.7 m apart. We established a 2.02-ha core plot nested within each treated 4.04-ha treated or control plot for measurements of stand structure and beetle attack rates, to minimize influence of edge effects on those variables (Fig. 1).

Study Site, Experimental Design, and Pheromone Application (Washington 2010). This study was conducted on the Chelan Ranger District of the Okanogan-Wenatchee National Forest (48° 39′36.50″ N, 119° 55′33.57″ W) in a stand consisting primarily of whitebark pine with an admixture of lodgepole pine, subalpine fir, western larch, and Engelmann spruce. We selected nine 0.81-ha plots, at least 400 m apart, attempting to locate plots with similar stand stocking levels and similar rates of *D. ponderosae* infestation. We then randomly assigned each of the three treatments (push-only, push–pull, and control) to one third of the plots (see Fig. 2 for a schematic diagram of the push–pull treatment), for three replicates per treatment in total. As above, both push-only and push–pull treatments received the "push" (verbenone) treatment, and the push–pull treatment had an additional "pull" treatment consisting of traps baited with *D. ponderosae* aggregation pheromone. Biodegradable flakes were applied on 22 July 2010 by a five-person crew using broadcast spreaders with slot augers calibrated to dispense evenly and at the desired rate as a simulated aerial application (methods described in detail in Gillette et al. 2012). The perimeter traps were spaced 14.4 m apart. We established a 0.40-ha core plot nested within each treated 0.81-ha plot for measurements as described below (Fig. 2).
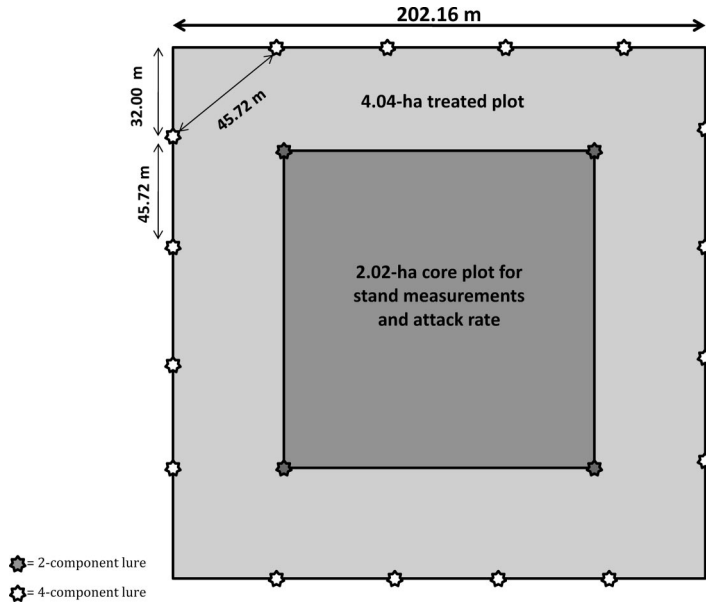
Fig. 1. Plot lay-out for push–pull treatments, Klamath National Forest, CA, in 2008. Open stars indicate traps baited with four-component *D. ponderosae* aggregation pheromone, and black stars indicate monitoring traps baited with two-component *D. ponderosae* aggregation pheromone. Central square indicates core plot for measurements of *D. ponderosae* attack rates (2007 and 2008) and stand structure and composition.

Beetle Flight, Stand Structure, and Beetle Attack Rate Measurements. Four Intercept panel traps were installed in each plot immediately after pheromone applications to monitor beetle flight into treated and untreated plots. In an effort to avoid the potential confounding effect of inducing *D. ponderosae* attack on nearby pines by the baited traps (and the consequent release of natural beetle pheromone by attacking beetles) the traps were suspended on nonhost trees or shrubs as far away from hosts as possible (no closer than 5 m). The traps were baited with *D. ponderosae* aggregation pheromone, a two-part blend of
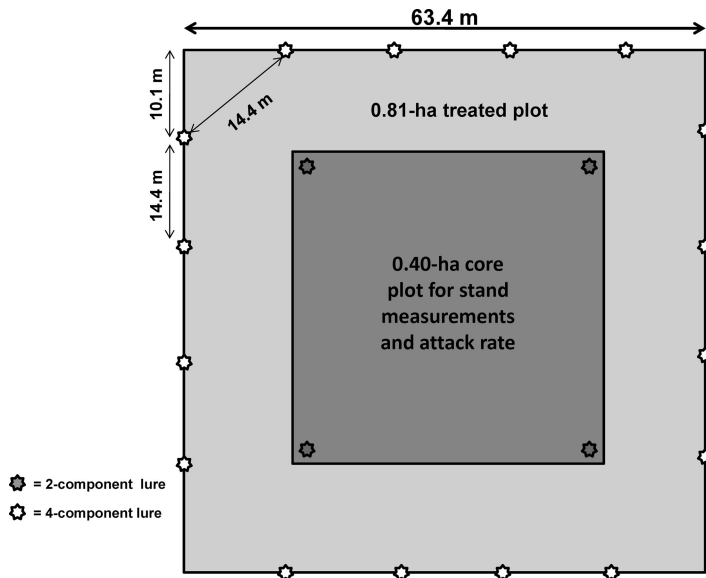

Fig. 2. Plot lay-out for push–pull treatments, Okanogan-Wenatchee National Forest, WA, in 2010. Open stars indicate traps baited with four-component *D. ponderosae* aggregation pheromone, and black stars indicate monitoring traps baited with two-component *D. ponderosae* aggregation pheromone. Central square indicates core plot for measurements of *D. ponderosae* attack rates (2009 and 2010) and stand structure and composition.

trans-verbenol and *exo*-brevicomin (ConTech International, Inc.). In an attempt to reduce the release rates of the lures and the associated potential for beetle attack on nearby host trees, bait components were placed in a semipermeable zip-lock sandwich bag with half the surface area covered with Mylar tape (3M Stationery Products Division, St. Paul, MN). Collection cups attached to the trap bottoms contained Vaportape insecticide-releasing strips (Hercon Environmental, Emigsville PA) to reduce losses of responding *D. ponderosae* to trapped predators. Trapped insects were collected weekly for 10 wk after application and were shipped to the University of California, Berkeley, for identification to species level. Voucher specimens were deposited in the Essig Museum of Entomology, University of California, Berkeley.

Stand characteristics, including posttreatment beetle attack and previous-year host mortality, were measured on 15 September 2008 in California, and on 12–13 October 2010 in Washington. All live trees ≥10.2 cm in diameter at breast height were tallied by species and measured for diameter at breast height. Attack rates were recorded for all host trees attacked by *D. ponderosae* in 2007–2008 in California and 2009–2010 in Washington. Attacked trees were classified by year of attack (current: pitch tubes and boring dust on otherwise green trees, immature brood; previous: needles ranging from pale green to brilliant orange, often with mature brood; older: needles ranging from dull orange to fallen, no live brood) and type of attack (mass: circumferential attack, strip: attack that does not girdle the tree, or pitch-out: unsuccessful attack). We assumed that mass-attacked trees ultimately would be killed by the beetle attack because they are completely girdled; this attack density therefore serves as a surrogate for tree mortality. Beetle population trends commonly are assessed using the ratio of "green-attacked" (attacked in current year, foliage still green) to "red-attacked" (attacked in the previous year, with foliage discolored), because of the overriding importance of infested brood trees to the risk of current-year *D. ponderosae* attack in a given locality (Wulder et al. 2009). This ratio was used to assess trends in beetle attack rates in the analyses.

Statistical Analysis. Tree attack rates and beetle capture rates, like most counts data, are typically overdispersed Poisson-distributed (i.e., the variance is proportional to the mean, and there are many cells with low counts) (McCulloch and Searle 2001). Newer software packages enable analysis of this type of data using the Poisson and overdispersed Poisson distributions (e.g., SAS version 9.2, Cary, NC), with this capability it is particularly important to account for the overdispersion that arises in most counts data as a random effect in the statistical models used (Warton and Hui 2011). We therefore examined each set of response data to assess whether it fit the overdispersed Poisson distribution, and because all of them did fit that distribution, we used it in the analytical models for assessment of treatment effects shown below. For the analysis of tree attack rates, it also has been shown to be important to include the previous-year attack rate as a covariate in the analysis because it serves as a measure of emerging beetle populations that are attacking nearby trees in the current year, and thus it increases the precision of the estimates (Wulder et al. 2009).

Tree Attack in California. We tested several overdispersed Poisson regression models from the family of Generalized Linear Models (GLM, McCulloch and Searle 2001) to estimate the proportion of attacked trees in 2008 for three treatment levels (Control, Push–pull, and Push-Only). The best model, based on the Akaike AIC diagnostic (Burnham and Anderson 1998), has treatment effect and percent infested trees in the prior untreated year (2007) as fixed effects. It is usually important to include the prior year infestation rate in such models because it serves as an indicator of the numbers of beetles emerging and attacking trees in the current year, which can vary among plots (Wulder et al. 2009), so using it as a covariate increases precision of the estimates. The Poisson model is as follows:

$$\frac{\text{Expected}[\#2008 \text{ attacked tress}_{ij}]}{\#2008 \text{ target trees}_{ij}}$$

$$= e^{T_i + a*\log(\text{rate2007}_{ij}) + \varepsilon_{ij}} \quad [1]$$

Where target trees are defined as *D. ponderosae* host trees of a size to be susceptible to attack; $i = 1, 2, 3$, for treatment; $1 =$ control, $2 =$ Push–pull, $3 =$ Push-Only; $j = 1, 2, 3, 4, 5$ for five plots per treatment; #2008 attacked trees = number of target trees attacked in 2008; #2008 target trees = number of target trees in 2008; rate2007 = proportion of target trees attacked in the prior year; ε is the overdispersion error to account for plot effect. We assumed #2008 attacked trees for a given plot to have the Poisson distribution with expected value given by (1). We used the SAS (version 9.2) GENMOD procedure to estimate the parameter T_i and the coefficient a. We used the Likelihood Ratio test with the Bonferroni adjustment to test pairwise comparisons between the treatment levels.

Beetle Trap Catch in California. A Mixed Generalized Linear model for overdispersed Poisson responses with plot as a random effect also was used to model the number of beetles per trap placed at the four corners of each site to compare the three treatments levels at each weekly period with the Likelihood Ratio test. SAS GENMOD procedure and the Bonferroni adjustment to test pairwise comparisons between the treatment levels were used for the estimation and comparison tests.

Statistical Model.

$$\text{Expected}[2008 \text{ beetle count}_{ijkl}]$$

$$= e^{\text{Treat}_i * \text{Date}_j + \varepsilon_{kl}} \quad [2]$$

Where 2008 beetle count$_{ijk}$ is the number of beetles trapped in 2008 on corner l of plot k, for treatment level i on day j ($j = 1,2,.,5$ sampling periods). The beetle count in plot k is assumed to have an overdis-

Table 2. Summary of stand conditions at time of treatment in 2008 and 2007 attack rates, Klamath National Forest, CA in 2008

TR	Mean stems/ ha, all spp., 2008	Mean stems/ ha, host spp., 2007	Mean stems/ ha, host spp., 2008	Mean BA all spp. 2008 m²/ha	Mean BA host spp., 2008, m²/ha	Mean % mass + strip attack, 2007	Mean % mass + strip attack, 2008	Mean DBH, all spp. 2008, cm	Mean DBH, host spp. 2008, cm
CT	259.3	183.8	158.6	16.2	9.8	37.8	55.7	26.0	26.6
PP	339.8	167.2	137.8	26.9	8.8	39.6	31.1	28.1	28.2
PO	271.0	143.8	127.1	18.6	6.5	26.5	19.2	26.8	24.1

TR is treatment, BA is basal area, DBH is diameter at breast height, CT is control, PO is push-only, PP is push–pull.

persed Poisson distribution with expected value given by (2).

Tree Attack in Washington. We used the overdispersed Poisson regression from the family of GLM models to estimate the ratio of number of attacked trees in 2010/number of attacked trees in 2009 for three treatment levels (Control, Push–pull, and Push-only). After an exploratory analysis using the Akaike AIC diagnostic, the best Poisson model was as follows:

$$\frac{\text{Expected } [\#2010 \text{ attacked trees}_{ij}]}{\text{rate2009}_{ik} * \#2010 \text{ target trees}_{ik}} = e^{T_i + \varepsilon_{ik}} \quad [3]$$

where $i = 1, 2, 3$, for treatment: $1 =$ control, $2 =$ Pull-push, $3 =$ Push-only; $j = 1$–3, for three plots per treatment; #2010 attacked trees = number of target trees attacked in 2010; #2010 target trees = number of target trees in 2010; rate2009 = proportion of target trees attacked in the prior year; ε is the overdispersion error to account for plot effect. We assume #2010 attacked trees for a given plot to have the Poisson distribution with expected value given by (3). We used SAS (version 9.2) GENMOD procedure to estimate the parameter T_i. We used the Likelihood Ratio test with Bonferroni adjustment to test pairwise comparisons between the treatment levels.

Beetle Trap Catch in Washington. A Mixed GLM model for overdispersed Poisson with plot as a random effect also was used to model the number of beetles per trap placed at the four corners of each site to compare the three treatments levels at each weekly period with the Likelihood Ratio test. We used SAS

GENMOD procedures and the Bonferroni adjustment to test pairwise comparisons between the treatment levels for the estimation and comparison tests.

Statistical Model.

$$\text{Expected}[2010 \text{ beetle count}_{ijkl}]$$
$$= e^{\text{Treat}_i * \text{Date}_j + \varepsilon_{kl}} \quad [4]$$

Where 2010 beetle count$_{ijk}$ is the number of beetles trapped in 2010 on corner l of plot k, for treatment level i on day j ($j = 1, 2, ..,$ five sampling periods). The beetle count in plot k is assumed to have an overdispersed Poisson distribution with expected value given by (4).

Results

California. None of the stand structure or previous-year *D. ponderosae* attack rate measurements were significantly different among treatments (Table 2, Suppl. Table 1) although in some cases the differences were rather large in absolute terms. Push–pull significantly reduced the number of beetles trapped in core plots as compared with the controls (Figs. 3 and 4), and although the difference between push-only and the control was not significant, it was substantial in absolute terms. The difference in trap catch between push–pull and push-only was not significant at $\alpha = 0.05$. At peak beetle flight (Fig. 3), traps in control plots caught >350 *D. ponderosae* beetles, whereas push-only caught 104 beetles and push–pull caught 25
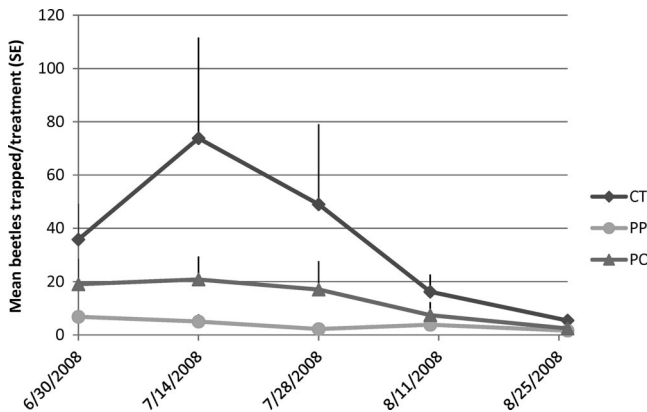
Fig. 3. Number of *D. ponderosae* beetles collected in monitoring traps (Fig. 1), Klamath National Forest, CA, in 2008. Diamonds indicate responses in control (CT) plots, triangles indicate responses in Push-Only (PO) plots, and circles indicate responses in Push–pull plots (PP). Vertical bars indicate standard errors.
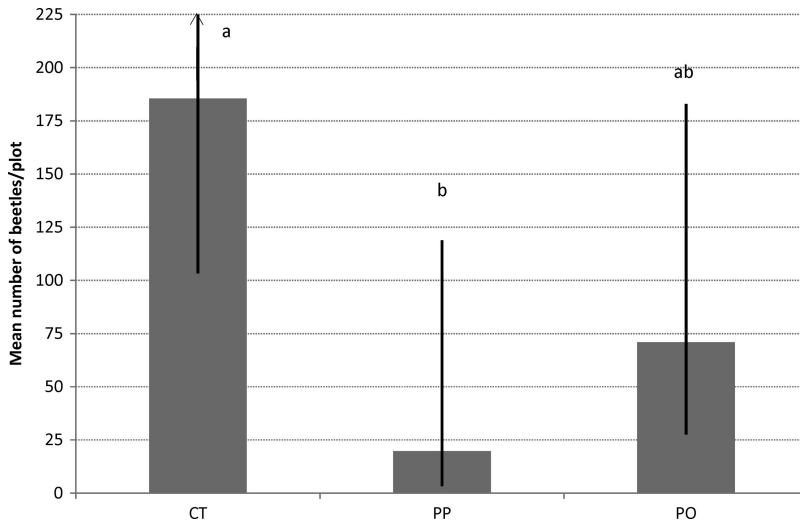
Fig. 4. Comparison of season-long *D. ponderosae* catches by treatment, Klamath National Forest, CA, in 2008, with 95% confidence intervals. Bars with the same letter are not significantly different at an experiment-wise error rate of 0.05 (CT, Control; PO, Push-Only; PP, Push–pull).

beetles. The rate of *D. ponderosae* attack in 2007 was a significant variable in the model (Table 3), as we expected. The 2008 *D. ponderosae* mass + strip attack rates for both push–pull and push-only were significantly lower, using the Bonferroni approach to maintain an experiment-wise error rate of 0.05, than that in controls (Table 4; Fig. 5), and the two pheromone treatments were not significantly different from one another. The 2007 versus 2008 attack rates per plot (Fig. 5), which is essentially the ratio of green-attacked:red-attacked trees for a range of *D. ponderosae* attack rates, indicates that at previous-year infestation levels of up to 40% of host trees, both treatments reduce *D. ponderosae* attack rate. Push-only was significantly lower than push–pull, however, effectively reducing attack rate by >50% even when nearly half the host trees were mass-attacked the previous year.

Washington. The stand conditions and previous-year attack rates were not significantly different among treatments (Table 5, Suppl. Table 2), but the differences were large even if not significant. These

differences may explain the significant plot effects for all treatments (Table 6). Both push–pull and push-only significantly reduced the number of beetles trapped in core plots compared with the control plots (Figs. 6 and 7), and there was no significant difference between the two pheromone treatments. We did not demonstrate any significant differences in *D. ponderosae* attack rates among treatments (Fig. 8), possibly because of excessive heterogeneity in stand conditions and previous-year *D. ponderosae* attack rates among treatments (Table 4, Suppl. Table 2), which was unavoidable with limited replication. Nevertheless, the *D. ponderosae* attack rate in the push-only treatment was, overall, about one third lower than that in either the push–pull or the control treatment.

Discussion

We confirmed the efficacy of DISRUPT Micro-Flake Verbenone Bark Beetle Anti-Aggregant flakes alone (in contrast to the push–pull treatment) to reduce *D. ponderosae* damage, even at the very high beetle population levels that occurred in California. Although the push–pull approach clearly reduced numbers of beetles trapped in treated plots in both California and Washington, and push-only did so as

Table 3. Regression coefficients, Klamath National Forest, CA in 2008

Parameter	Coefficient (log scale)			
	Estimate	95% lower bound	95% upper bound	*P* value
CT	−0.672	−1.089	−0.255	0.0016
PP	−1.125	−1.562	−0.687	<0.0001
PO	−1.486	−2.008	−0.963	<0.0001
Log (proportion of trees mass + strip attacked, 2007)	0.210	0.001	0.419	0.049
Overdispersion	2.479			

P value lower than 0.0167 indicates that the actual mean attack rate is significantly greater than zero; CT is control, PO is push-only, PP is push–pull.

Table 4. Comparison of attack rates among various treatments, Klamath National Forest, CA in 2008. Values of *P* lower than 0.0167 are significant at a Bonferroni-adjusted exp-wise error rate of 0.05

Comparison	Ratio	95% lower CL	95% upper CL	*P* value
CT vs PP	1.573	1.117	2.215	0.0096
CT vs PO	2.256	1.505	3.381	<0.0001
PP vs PO	1.435	0.919	2.240	0.112

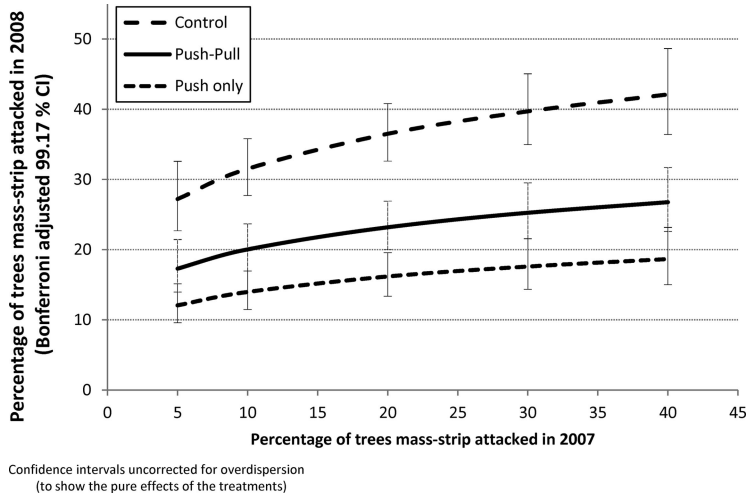CT is control, PO is push-only, PP is push–pull.

Fig. 5. Attack rate in 2008 as a function of attack rate in 2007 by treatment, with 95% confidence intervals (CT, Control; PO, Push-Only; PP, Push–pull).

well in Washington, in neither case did the addition of a perimeter row of attractant-baited traps significantly reduce the rate of attack below that in plots treated only with antiaggregants. In fact, in California, the addition of perimeter traps appears to have increased the rate of attack in push–pull treatments, even though the number of beetles trapped was slightly lower in the push–pull treatment than in the push-only treatment. We speculate, however, that the slightly higher attack rate in the push–pull treatment was a result of the slightly higher number of large trees, higher basal areas, and higher brood tree levels (i.e., 2007-attacked trees) in the push–pull plots (Table 2) rather than any result of the pheromone treatment itself.

In Washington, beetle numbers were significantly reduced by both treatments, but rate of *D. ponderosae* attack on host trees was not. The rate of *D. ponderosae* attack in push-only treated plots in Washington, although not significantly different from either the control or the push–pull treatment, was only about two thirds the rate in push–pull and control plots, whereas in push–pull plots it was actually slightly (but not significantly) higher than in the controls. These findings raise questions about the effect of such spatial attributes as plot size, trap spacing, and potential edge effects, considering the large difference (a factor of 5) in plot sizes in the two experiments. The difference in trap spacing was more than three-fold, and we had expected to see greater efficacy with closer trap spac-

ing, but in fact efficacy was worse in the study with the closer spacing, both in terms of beetles trapped and trees attacked. This outcome suggests that closer spacing of perimeter traps may, in fact, attract greater numbers of beetles into plots rather than simply trapping out larger numbers of beetles. Similarly, the smaller plots likely had larger edge effects (proportion of the plot interiors affected by conditions at plot perimeters) than the larger plots. All of these spatial variables may have played a role in the beetle trap catch and attack rate results.

To our knowledge, all of the previous published work with the push–pull approach for control of *D. ponderosae* has been conducted using baited trees rather than baited traps as the attractant treatment (Lindgren and Borden 1993, Borden et al. 2006). That approach, commonly referred to as "concentration and containment," is a subset of the push–pull approach in which the pest insects are attracted to their host plants, attack them, and then are killed when the host plant is harvested with the insects still within plant tissues. It is, in effect, an attract-and-kill approach, and was shown to be quite effective when combined with an antiaggregation pheromone and removal of infested brood trees (Lindgren and Borden 1993, Borden et al. 2006). Although this approach has been shown to work quite reliably (although not infallibly), it is appropriate only in lands that are actively managed using silvicultural treatments that are incor-

Table 5. Summary statistics for stand conditions and 2009 attack rates, Okanogan-Wenatchee National Forest, WA, in 2010

TR	Mean stems/ ha, all spp., 2010	Mean stems/ ha, host spp., 2009	Mean stems/ ha, host spp., 2010	Mean BA all spp., m²/ha 2010	Mean BA host spp., m²/ha 2010	Mean % mass + strip attack, 2009	Mean % mass + strip attack, 2010	Mean DBH all spp., 2010, cm	Mean DBH host spp., 2010, cm
CT	357.5	313.8	292.4	171.4	143.7	23.1	9.9	23.9	24.3
PP	374.8	333.6	322.1	172.4	153.8	14.0	7.4	25.0	25.5
PO	327.0	281.7	275.1	181.8	158.6	6.6	2.5	24.4	25.1

TR is treatment, BA is basal area, DBH is diameter at breast height, CT is control, PO is push-only, PP is push–pull.

Table 6.   Estimates of regression coefficients for attack rates, Okanogan-Wenatchee National Forest, WA in 2010

Treatments	Coefficient			
	Estimate	95% lower bound	95% upper bound	*P* value
CT	0.039	0.018	0.082	<0.0001
PP	0.022	0.011	0.041	<0.0001
PO	0.009	0.002	0.0387	<0.0001

P value lower than 0.0167 indicates that the actual mean is significantly greater than zero; CT is control, PO is push-only, PP is push-pull.

porated into pest management implementation. For many public lands in the United States, regulatory constraints make this approach difficult to deploy because of the need to sacrifice some of the living trees in a stand to contain beetle populations and prevent them from attacking other nearby trees.

Our study was designed to test the hypothesis that baited traps deployed in a perimeter line (surrounding the stand to be protected) might increase the efficacy of antiaggregation pheromone alone, thus achieving levels of control equivalent to those using the containment-and-concentration approach in a push–pull tactic. Our study design differed in other ways from those of previous studies insofar as those were designed to pull beetles into a central, sacrificial group of trees (concentration) rather than inhibiting them from entering the stand of interest. In either approach, the "pull" treatment risks attracting too many beetles into the area, with resulting spill-over into the stands we wish to protect. It appears that in our two projects the scale of the treatments (both plot size and trap spacing) was not adequate for effective trap-out and consequent tree protection. In addition, we speculate that baited traps may simply be insufficient to attract host-seeking beetles and to interrupt their response to living host trees, because other studies have shown sufficient interruption by using baited trees (Lindgren and Borden 1993, Borden et al. 2006). However, we speculate that baited traps may possibly trap beetles over a longer period than baited trees, because traps do not trigger release of antiaggregation pheromone as do attacked trees (Wood et al. 1985).

Another question that deserves further investigation is whether, by treating some stands with antiaggregation pheromones, we are merely herding beetles onto adjacent untreated stands. Evidence from electroantennogram studies coupled with observations of flight behavior shows that exposure to verbenone reduces muscle potential in *Dendroctonus frontalis* Zimm. (Dickens and Payne 1978), perhaps explaining the arrestment of flying beetles near traps baited with both attractants and verbenone. McPheron et al. (1997) also demonstrated that verbenone exposure significantly reduced the walking speed of another bark beetle species, *Ips paraconfusus* Lanier, in laboratory olfactometer tests. Taken together, these results support the hypothesis that verbenone may have a generalized effect on beetle locomotion that could result in arrestment rather than repellency. Many anecdotal observations of stands adjacent to treated areas support the supposition that treatments do not simply exacerbate beetle-caused tree mortality in adjacent stands (J.N.W., unpublished data). Whatever the underlying behavioral mechanism, it is clear from myriad studies that exposure to verbenone reduces the ability of *D. ponderosae* to aggregate in sufficient numbers to successfully attack its host trees (Bentz et al. 2005; Gillette et al. 2006, 2009, 2012). It would, nevertheless, be of interest to spatially characterize the behavioral responses of verbenone-exposed beetles in the field, and to determine whether they are still capable of aggregating in adjacent areas after exposure to verbenone-treated plots.

In California, the verbenone-releasing flakes consistently reduced *D. ponderosae* attack rates by roughly 50%, a level that is consistent with long-term *D. ponderosae* damage control (Coggins et al. 2011). Wulder et al. (2009), using brood tree removal as the only treatment, attempted to define a *D. ponderosae*
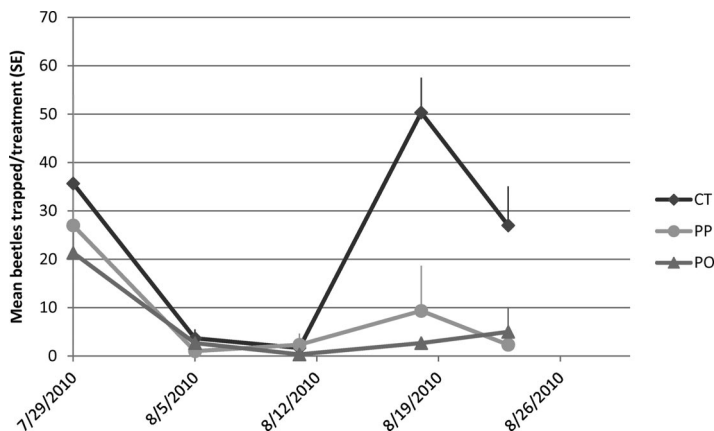
Fig. 6.   Number of *D. ponderosae* beetles collected in monitoring traps (Fig. 2), Okanogan-Wenatchee National Forest, WA, in 2010. Squares indicate responses in control (CT) plots, triangles indicate responses in Push–pull plots (PP), and circles indicate responses in Push-Only (PO) plots. Vertical bars indicate standard errors.
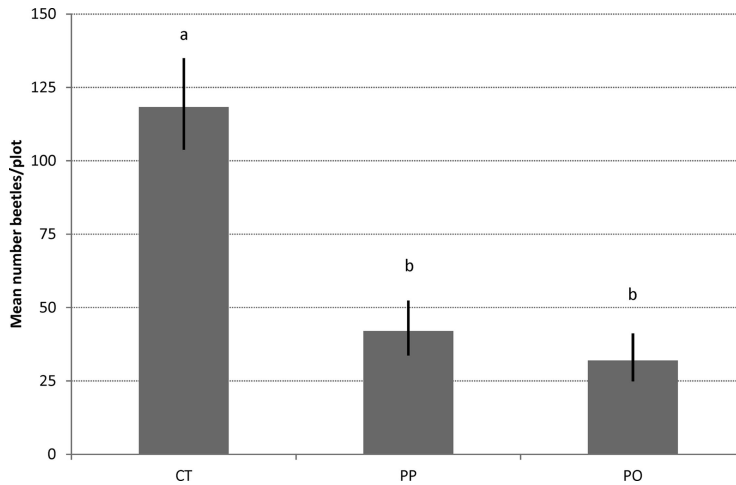
Fig. 7. Comparison of season-long *D. ponderosae* catches by treatment, Okanogan-Wenatchee National Forest, WA, in 2010, with 95% confidence intervals. Bars with the same letter are not significantly different at an experiment-wise error rate of 0.05 (CT, Control; PO, Push-Only; PP, Push–pull).

population level that represents a rough threshold or plateau beyond which treatments could be considered futile. Following on that work, Coggins et al. (2011) showed that if the *D. ponderosae* attack rates in treated stands can be kept below ≈50%, long-term control of beetle damage is feasible. Thus, our findings support verbenone-based intervention to protect lodgepole and whitebark pine stands from *D. ponderosae*-caused tree mortality. We recommend that future tests incorporate dose-range tests (Miller et al. 1995) and additional semiochemical components (Kegley and Gibson 2009, Kegley et al. 2010) to achieve greater efficacy.

In the face of the epic *D. ponderosae* outbreaks seen in western North America for the last 10 yr, there has been much discussion regarding the presumed futility of conducting any treatments at all, whether based on silvicultural prescriptions, sanitation (brood tree re-

moval), or semiochemical approaches. Our work, along with that of others, shows that these approaches can indeed mitigate losses to *D. ponderosae* and prevent the immediate and complete loss of stands. There remains the question of whether cumulative losses, over periods of years or decades, will eliminate natural stands, result in species conversions in western North America, or both, especially under the pressures of climate change. Some research suggests that susceptibility increases with host density (summarized in Amman and Logan 1998), presumably because the denser stands suffer more stress, whereas other research suggests that susceptibility decreases with host density (Borden et al. 2006, 2007), perhaps because the ratio of attacking *D. ponderosae* to target hosts is diluted in denser stands. Fettig et al. (2007) reviewed the existing literature on the effect of silvicultural manipulations on stand susceptibility to bark beetles,
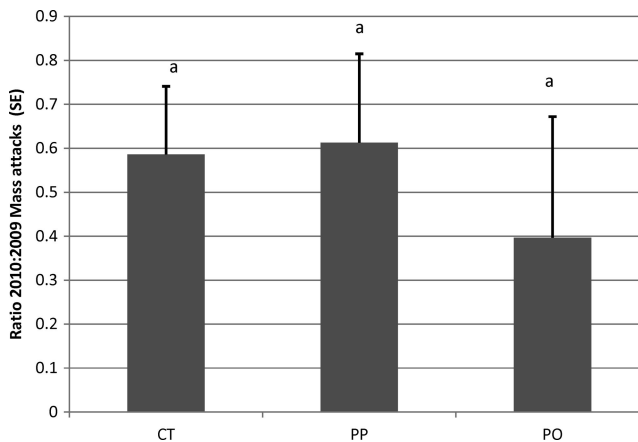

Fig. 8. Ratio of attacks in 2010 to attacks in 2009 ("green-attacked : red-attacked ratio"), with 95% confidence intervals; Okanogan-Wenatchee National Forest, WA. Means followed by the same letter are not significantly different at an experiment-wise error rate of 0.05 (CT, Control; PO, Push-Only; PP, Push–pull).

and concluded that the preponderance of evidence supports the assumption that wider tree spacing in lodgepole pine stands will help to "beetle-proof" them. To the extent that susceptibility to *D. ponderosae* decreases with reduced stand density, it is possible that by slowing the rate of beetle-caused mortality below the critical threshold described by Coggins et al. (2011), we could maintain stands at more beetle-resistant densities until the system equilibrates at a level that can be sustained for a longer period. In so doing, we would be harnessing the capacity of bark beetles to thin stands, at a more moderate rate than typically occurs in over-stocked stands subjected to long-term fire-suppression.

Acknowledgments

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