Nonhost Angiosperm Volatiles and Verbenone Protect Individual Ponderosa Pines from Attack by Western Pine Beetle and Red Turpentine Beetle (Coleoptera: Curculionidae, Scolytinae)

Christopher J. Fettig, Christopher P. Dabney, Stephen R. McKelvey, and Dezene P.W. Huber

ABSTRACT

Nonhost angiosperm volatiles (NAV) and verbenone were tested for their ability to protect individual ponderosa pines, *Pinus ponderosa* Dougl. ex. Laws., from attack by western pine beetle (WPB), *Dendroctonus brevicomis* LeConte, and red turpentine beetle (RTB), *Dendroctonus valens* LeConte (Coleoptera: Curculionidae, Scolytinae). A combination of (−)-verbenone and eight NAVs [benzyl alcohol, benzaldehyde, guaiacol, nonanal, salicylaldehyde, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol] (NAVV) significantly reduced the density of WPB attacks and WPB successful attacks on attractant-baited trees. A significantly higher percentage of pitchouts (unsuccessful WPB attacks) occurred on NAVV-treated trees during two of three sample dates. In addition, significantly fewer RTB attacks were observed on NAVV-treated trees during all sampling dates. The application of NAVV to individual ponderosa pines significantly reduced tree mortality, with only 4 of 30 attractant-baited trees dying from bark beetle attack while 50% mortality (15/30) was observed in the untreated, baited control. To our knowledge, this is the first report establishing the effectiveness of NAVs and verbenone for protecting individual ponderosa pines from WPB attack.

Keywords: *Pinus ponderosa*, *Dendroctonus brevicomis*, *Dendroctonus valens*, pest management, tree protection

The western pine beetle (WPB), *Dendroctonus brevicomis* LeConte (Coleoptera: Curculionidae, Scolytinae), is a major cause of ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws., mortality in much of the western United States and, particularly, in California (Furniss and Carolin 1977). Under certain conditions, this species can attack and kill apparently healthy trees of all ages and size classes (Miller and Keen 1960). Currently, techniques for managing WPB infestations are limited to tree removals (thinning) that reduce stand density and presumably host susceptibility (Fettig et al. 2007a) and the application of insecticides to protect individual trees (Fettig et al. 2006a). In many cases, these options are not viable because of regulatory and social constraints (Wood et al. 1985). In addition, sufficient markets or labor sources may be lacking in some areas.

The red turpentine beetle (RTB), *Dendroctonus valens* LeConte, is a common bark beetle species found throughout much of North America. Usually, attacks are confined to basal portions of previously stressed, weakened, or dead and dying trees (Furniss and Carolin 1977) or those under attack by other bark beetles such as WPB (Hall 1983, Fettig et al. 2004). Typically, attacks are not considered a significant threat to tree health. However, tree mortality was attributed to RTB in a 17-year-old ponderosa pine plantation in northern California (Rappaport et al. 2001), for several trees in stands where logging residues were chipped and retained on site in northern California (Fettig et al. 2006b), and of *Pinus tabuliformis* Carriere in China (Li et al. 2001). In recent years, there has been an interest in developing semiochemical-based management tools for RTB (Rappaport et al. 2001; Sun et al. 2003; Fettig et al. 2005b, 2007b; Gillette et al. 2006). The species has become one of the most economically important forest pests in China and effective control measures are urgently needed (Li et al. 2001, Sun et al. 2003, Zhang et al. 2006).

Studies have shown that insects concentrate host searching in areas of high host concentrations (e.g., Andow [1990]). To reproduce, bark beetles must successfully locate and colonize suitable hosts while avoiding nonhosts. In mixed forests, rejection of nonhosts may occur, in flight, on the basis of absence of host cues or presence of nonhost cues such as green leaf volatiles or angiosperm bark volatiles, collectively termed nonhost angiosperm volatiles (NAV; Borden [1997]). NAVs have been the focus of several recent studies that established these compounds as capable of reducing aggregation in *Dendroctonus* spp., including WPB, southern pine beetle, *Dendroctonus frontalis* Zimmerman, mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, and Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Zhang and Schlyter 2004). For many bark beetle species, mass attack on suitable hosts is mediated by aggregation pheromones that are biosynthesized from de novo pathways or host tree precursors (Seybold et al. 2000) in combination with host kairomones (Borden 1985). For example, after initiation of attack, female WPB produce *exo*-brevicomin, which in

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Christopher J. Fettig (cfettig@fs.fed.us), Christopher P. Dabney (cdabney@fs.fed.us), and Stephen R. McKelvey (srmckelvey@fs.fed.us), Pacific Southwest Research Station, US Forest Service, Davis, CA 95616. Dezene P.W. Huber (huber@unbc.ca), Ecosystem Science and Management Program, College of Science and Management, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada. *The authors thank R. Borys (Pacific Southwest Research Station, US Forest Service), M. Patterson (University of Nevada-Reno), and D. Cluck (Forest Health Protection, US Forest Service) for technical assistance. They also thank S. Smith (Forest Health Protection, US Forest Service) and A. Vasquez (Lassen National Forest, US Forest Service) for locating the study site. This research was supported, in part, by a US Western Bark Beetle Initiative grant (2005-3).*

combination with the host monoterpene myrcene is highly attractive to conspecifics (Bedard et al. 1969). Frontalin, produced by male WPB (Kinzer et al. 1969), enhances attraction.

Poland et al. (1998) were the first to examine the disruptive effect of NAVs on WPB attraction, but their study was limited in scope to green leaf volatiles only and was conducted at the periphery of the beetle's native range (Wood 1982). The aldehyde, (*E*)-2-hexenal, and two alcohols, (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol, significantly reduced numbers of male WPB caught in attractant-baited traps. (Z)-2-hexen-1-ol also reduced numbers of female WPB captured (Poland et al. 1998).

Verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) is an antiaggregation pheromone of several *Dendroctonus* spp., including WPB (Borden 1997, Skillen et al. 1997). In 1970, verbenone was shown to elicit a negative response on tethered, flying female WPBs (Hughes and Pitman 1970). Bedard et al. (1980a) showed that verbenone reduced the number of WPB trapped at a baited source. Trap catches were reduced further by higher release rates of verbenone (Bedard et al. 1980a, 1980b; Tilden and Bedard 1988). In a more recent study, verbenone significantly reduced WPB attraction to attractant-baited traps, but no significant difference was observed between 4 and 50 mg/24-hour release rates (Fettig et al. 2005a). It is assumed that verbenone reduces intraspecific competition by reducing crowding of developing brood within the host (Byers et al. 1984).

In western North America, the use of verbenone to mitigate bark beetle-caused tree mortality has concentrated on small-scale (i.e., less than 5 ha) stand protection, primarily from MPB infestations in lodgepole pine, *Pinus contorta* Dougl. ex. Loud, forests (Amman et al. 1989, 1991; Lindgren et al. 1989; Gibson et al. 1991; Shea et al. 1992; Shore et al. 1992; Lindgren and Borden 1993; Progar 2003; Bentz et al. 2005). Results have been favorable but inconsistent at times (Bentz et al. 1989, 2005; Gibson et al. 1991; Progar 2005), which may be caused by, in part, photoisomerization of verbenone to behaviorally inactive chrysanthenone in the presence of UV light (Kostyk et al. 1993) or other factors (Zhang and Schlyter 2004). Verbenone alone does not appear to be effective for reducing WPB-caused tree mortality. For example, the 5-g verbenone pouch (50 mg/24-hour release rate) applied at 125 U/ha was ineffective for protecting ponderosa pine stands from WPB attack in northern California (Fettig 2005). A sprayable formulation of verbenone failed to protect individual ponderosa pines from WPB attack (Gillette et al. 2006). Bertram and Paine (1994) reported that application of ipsdienol and verbenone significantly reduced both numbers of WPB landing on ponderosa pines and the density of attacking beetles. In their study, paired treated and untreated trees were baited with aggregation pheromones to stimulate mass attack, but tree mortality rates were not determined. Lister et al. (1990) reported that verbenone was ineffective for protecting individual ponderosa pines from MPB attack.

Fettig et al. (2005a) examined the effect of several bark volatiles (benzyl alcohol, benzaldehyde, *trans*-conophthorin, guaiacol, nonanal, and salicylaldehyde), green leaf volatiles [(*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol], and a blend of these NAVs on WPB attraction in trapping bioassays. The NAV blend did not significantly affect the response of WPB to attractant-baited traps; however, NAV augmented the disruptive effect of 4 and 50 mg/24-hour (−)-verbenone to levels significantly below that of verbenone alone. Additional work revealed that *trans*-conophthorin was not essential to the efficacy of this blend. The revised NAVV blend [benzyl alcohol, benzaldehyde, guaiacol, nonanal, salicylaldehyde, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and verbenone (82%-(−); 50 mg/24-hours)] reduced trap catch by 87% compared with the attractant-baited control. Both males and females were equally affected (Fettig et al. 2005a). The authors suggested that applications of NAVV to ponderosa pine may reduce WPB colonization rates and presumably subsequent levels of tree mortality (Fettig et al. 2005a).

Others have shown that blends of NAVs, with or without antiaggregation pheromones, may disrupt aggregation of bark beetles on individual host trees and in forested stands (Wilson et al. 1996, Borden et al. 1998, Huber and Borden 2001, Jakus et al. 2003, Zhang and Schlyter 2004). The effectiveness of NAVs to protect individual trees from WPB attack has not been established but is promising given recent identification of an inhibitory blend in trapping bioassays (Fettig et al. 2005a) and positive results with other coniferophagous bark beetles. The objective of this study was to document the efficacy of NAVV to protect individual ponderosa pines from attack by WPB and RTB.

Methods

Study Site

This study was conducted adjacent to Butte Lake Road, Eagle Lake Ranger District, Lassen National Forest, Lassen County, California (41.60°N, 121.28°W; 1,760-m elevation) from July 2005 to July 2006. Site selection was based on surveys indicating that WPB was causing significant amounts of tree mortality in this area (Bohne and Rios 2005). The cover type was Ponderosa-Jeffrey (Yellowpine) series (mean diameter at 1.37 m [dbh] ± SEM = 27.9 ± 1.5 cm, all species; Smith [1994]). The stand was dominated by ponderosa pine (dbh ± SEM = 29.0 ± 1.8 cm) growing on soils of volcanic origin. Mean stand density was 20.5 m^2 of basal area per hectare of which 54.6% was ponderosa pine (11.2 ± 2.4 m^2/ha), 33.7% Jeffrey pine, *Pinus jeffreyi* Grev. & Balf. (6.9 ± 5.1 m^2/ha), 11.2% white fir, *Abies concolor* (Gond. and Glend.) Hildebr. (2.3 ± 1.1 m^2/ha), and 0.5% quaking aspen, *Populus tremuloides* Michx. (0.1 ± 0.1 m^2/ha). Mean crown cover was 25%. The topography was mainly flat. Ponderosa pine was the only host of WPB present in these stands (Miller and Keen 1960).

Experimental Design and Treatments

The experimental design was completely randomized with two treatments and 30 replicates (trees) per treatment. Treatments included baited and otherwise untreated ponderosa pine (mean dbh = 41.5 ± 0.9 cm) and baited NAVV-treated ponderosa pine (mean dbh = 38.2 ± 0.6 cm). NAVV components were formulated in four separate bubblecap bands (Table 1) based on similarity in chemical structure [i.e., alcohols, aldehydes, guaiacol (a phenol), and (−)-verbenone (a ketone)] and applied at a rate of 1 U/10 cm circumference around the bole of each tree beginning at 3 m in height in a manner similar to Huber and Borden (2001). Cumulative release rates for NAVV components varied in direct proportion to tree diameter. For example, a 38.2-cm diameter (measured at ~3 m in height) NAVV-treated tree received 12 bubblecap units per tree (22.8, 97.2, 61.2, 39.6 mg/24-hour cumulative release rate for alcohol, aldehyde, guaiacol, and verbenone bands, respectively; Table 1). Adjacent bands were separated by 20 cm. To rigorously test the efficacy of these treatments, the spacing between adjacent experimental trees was greater than 100 m to increase the likelihood that

Table 1. Description of semiochemicals used in a tree protection study (Lassen National Forest, Lassen County, California, 2005–2006).

Semiochemical band[a]	Components	Source[b]	Purity (%)	Release device	Release rate (mg/24 hr)[c]
Alcohols	(*E*)-2-hexen-1-ol	Bedoukian	98	Phero Tech bubblecap	0.6 (20° C)
	(*Z*)-2-hexen-1-ol	Bedoukian	95		0.8 (20° C)
	Benzyl alcohol	Fisher Scientific	98		0.5 (20° C)
Aldehydes	(*E*)-2-hexenal	Bedoukian	97	Phero Tech bubblecap	2.8 (20° C)
	Benzylaldehyde	Fisher Scientific	99		2.9 (20° C)
	Nonanal	Sigma-Aldrich	95		1.5 (20° C)
	Salicylaldehyde	Sigma-Aldrich	99		1.9 (20° C)
Guaiacol	Guaiacol	Sigma-Aldrich	98	Phero Tech bubblecap	5.1 (20° C)
Verbenone	Verbenone [82%-(−)]	Phero Tech	97	Phero Tech bubblecap	3.3 (20° C)
WPB tree bait	Frontalin (racemic)	Phero Tech	98	250 μl Eppendorf vial	3.0 (24° C)
	exo-Brevicomin (racemic)		97	250 μl Eppendorf vial	3.0 (24° C)
	Myrcene		90	1.8 ml × 2 Eppendorf vials	18.0 (24° C)

[a] Band applied at rate of 1 bubblecap U per 10-cm circumference (e.g., 12 U for 38-cm diameter at 3-m height).
[b] Bedoukian Research, Danbury, Connecticut; Fisher Scientific International, Inc., Hampton, New Hampshire; Sigma-Aldrich Canada Ltd., Oakville, Ontario, Canada; Phero Tech, Inc., Delta, BC, Canada.
[c] Measured in the laboratory at specified temperature after 10 days. Overall release rate of each bubblecap is the addition of individual components.

sufficient numbers of beetles would be in the vicinity of each tree. All trees were baited with one WPB tree bait (Phero Tech, Inc., Delta, British Columbia, Canada; Table 1) at approximately 3.5 m in height on the northern aspect between the second (aldehydes) and third (guaiacol) bubblecap bands and were checked weekly for evidence of WPB attack. Baits were removed from all trees after 28 days when significant numbers of attacks (more than 50/m^2) were recorded on untreated, control trees (Shea et al. 1984) and when natural pheromone production was likely occurring on trees under mass attack (Bedard et al. 1969, Kinzer et al. 1969, Wood et al. 1976).

For each tree (treated and untreated; $N = 60$), we nondestructively sampled, using head lamps and hand lens, the number of WPB successful attacks (i.e., oxidized phloem material present in pitch tubes or points of attack containing phloem boring dust and/or dry frass) and unsuccessful attacks (i.e., pitch tubes without oxidized phloem material) in 625 cm^2 (25 × 25 cm) sample windows at approximately 1.5 and 4 m in height at northern and southern aspects. These locations corresponded to bole regions directly above and below NAVV bands in that treatment. Destructive sampling (i.e., the removal of bark) to determine the success of egg laying and brood production was not possible without compromising the experiment. Therefore, as indicated previously, we define individual "successful attacks" as those attacks indicative of the phloem being reached by colonizing WPB, which is where egg laying and early instar feeding occur (Furniss and Carolin 1977). A significant proportion of beetles that initiate host selection are "pitched-out" by drowning or immobilization in resin before reaching or feeding on the phloem (Vité and Wood 1961). These were classified as "unsuccessful attacks." In addition, the total number of RTB attacks that occurred below 1.5 m in height was recorded for each tree. Data were collected at 14 days (Aug. 12, 2005), 28 days (Aug. 26, 2005), and 42 days (Sept. 9, 2005) after baits were applied. A test of normality was performed and appropriate transformations were used when data deviated significantly from a normal distribution (square root [attacks] and arcsine square root [% pitchouts]; Sokal and Rohlf 1995). *t*-Tests were performed on the density of WPB attacks, density of WPB successful attacks, percent of WPB pitchouts (unsuccessful attacks), and total number of RTB attacks using alpha = 0.05 (SigmaStat version 2.0; SPSS, Inc., Chicago, Illinois).

Final assessments of tree mortality were conducted in early July 2006. This period of time (more than 11 months) was sufficient for crowns to "fade," an irreversible symptom of pending tree mortality. A chi-square test was used to assess differences in tree mortality between treatments (SigmaStat version 2.0; SPSS, Inc.).

Results and Discussion

The density of WPB attacks and WPB successful attacks was significantly lower for NAVV at 14 days (df = 1, 58; $t = -3.409$, $P < 0.001$; $t = -3.195$, $P = 0.002$), 28 days (df = 1, 58; $t = -5.738$, $P < 0.001$; $t = -5.956$, $P < 0.001$), and 42 days (df = 1, 58; $t = -7.050$, $P < 0.001$; $t = -6.864$, $P < 0.001$) after treatment (Figure 1, A and B). At 42 days, we observed a 68% reduction in total attacks and a 76% reduction in successful attacks in the NAVV treatment. The percentage of pitchouts (unsuccessful WPB attacks) was significantly greater for the NAVV treatment at 28 days (df = 1, 55; $t = 4.162$, $P < 0.001$) and 42 days (df = 1, 54; $t = 4.566$, $P < 0.001$). No significant difference was observed at 14 days (df = 1, 50; $t = 1.731$, $P = 0.09$; Figure 1C). During initial phases of host colonization (e.g., 14-day sample), the percentage of pitchouts may not be an appropriate measure of treatment efficacy. Few beetles enter the bark and, typically, trees are capable of covering these wounds and encapsulating beetles (Bedard et al. [1985]; Figure 1, A–C). However, during mass attack (e.g., 28- and 42-day samples) resin flow and pressure per attack site also is a function of attack density and therefore likely a more effective measure of treatment efficacy. Successful colonization of living host trees requires overcoming tree defenses, which only can be accomplished by recruitment of a critical minimum number of beetles (Wood 1972). This varies with changes in host vigor (Fettig et al. 2007a). If a tree does not sustain a threshold number of attacks, it likely will retain the ability to defend itself by pitching out arriving beetles (Raffa and Berryman 1983).

Borden et al. (1998) reported that a combination of nonhost bark volatiles and verbenone significantly reduced MPB attack densities on attractant-baited trees. In another study, Borden et al. (2003) reported no significant difference in the attack density of MPB (attacks per square meter at eye level) among pheromone-baited *P. contorta* treated with and without NAVs and verbenone. However, the proportion of mass attacked trees (greater than 17.5-cm dbh) was significantly lower in treatments containing high release rates of verbenone and NAVs.

Fewer RTB attacks were observed on NAVV-treated trees at 14 days (df = 1, 58; $t = -6.721$, $P < 0.001$), 28 days (df = 1, 58; $t = -7.372$, $P < 0.001$), and 42 days (df = 1, 58; $t = -8.248$, $P <$

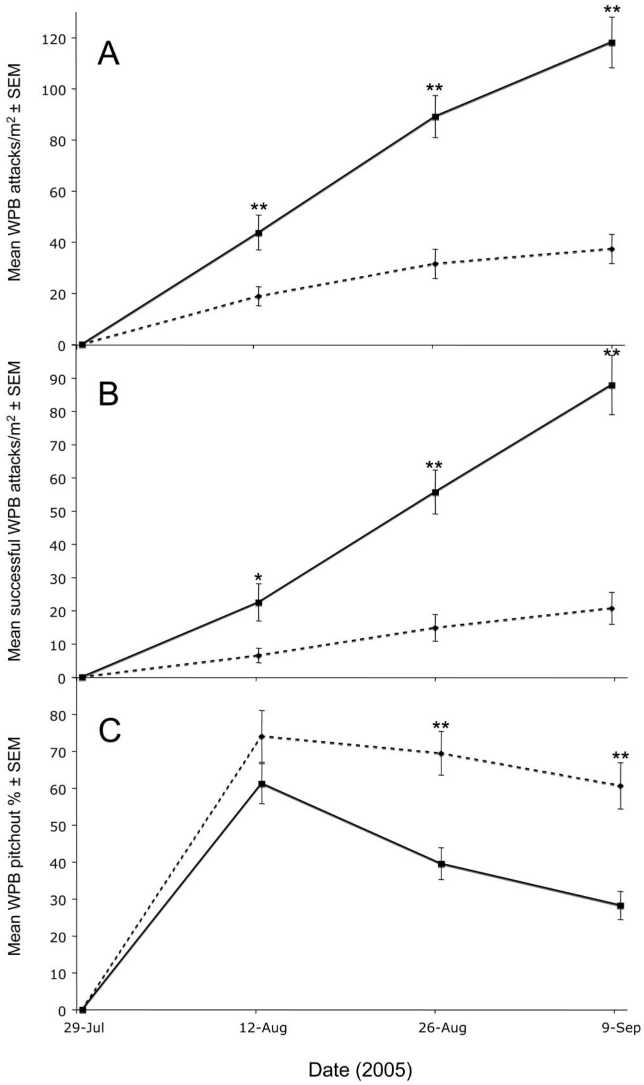

Figure 1. Mean density (±SEM) of WPB (*D. brevicomis* LeConte) (A) attacks, (B) successful attacks, and (C) percentage of pitchouts (unsuccessful attacks) occurring on attractant-baited ponderosa pine (*P. ponderosa* Dougl. ex. Laws.) treated with (dashed line, n = 30) and without (solid line, n = 30) NAV and (−)-verbenone (NAVV) at 14, 28, and 42 days after treatment (Lassen National Forest, Lassen County, California, 2005–2006). Asterisks denote a significant difference between treatments on that date (*t*-test; *P < 0.01 and **P < 0.001).

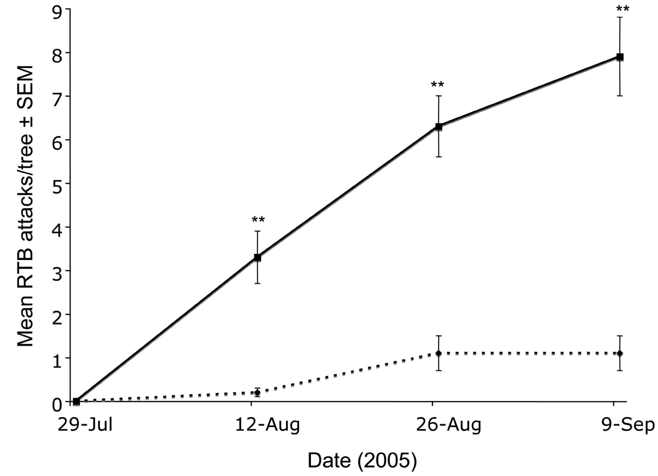

Figure 2. Mean number (±SEM) of RTB (*D. valens* LeConte) attacks per tree (below 1.5-m height) on ponderosa pine (*P. ponderosa* Dougl. ex. Laws.) treated with (dashed line, n = 30) and without (solid line, n = 30) NAV and (−)-verbenone (NAVV) at 14, 28, and 42 days after treatment (Lassen National Forest, Lassen County, California, 2005–2006). Asterisks denote a significant difference between treatments on that date (*t*-test; **P < 0.001).

0.001) after treatment (Figure 2). Although pheromones have not been identified for RTB, studies have shown that verbenone is present in the frass (Grégoire et al. 1991) and hindgut (Yan et al. 2004) and that verbenone disrupts the response of RTB to host volatiles (Rappaport et al. 2001, Sun et al. 2003, Fettig et al. 2007b). Both enantiomers appear equally effective in this regard (Zhang et al. 2006). In a recent field study, Gillette et al. (2006) treated individual *P. contorta* with a suspension of DISRUPT Micro-Flake Verbenone [Hercon Environmental, Emigsville, Pennsylvania; (−)-verbenone] in water and reported significantly fewer RTB and MPB attacks on treated trees. All trees were baited with MPB aggregation pheromones immediately after treatment. Two similar efforts proved ineffective for protecting individual ponderosa pines from WPB attack (Gillette et al. 2006).

Although we observed significantly fewer RTB attacks on NAVV-treated trees, our primary objective was to analyze the effect on WPB. This influenced the experimental methods used in this study. We caution readers that the NAVV effect observed here concerning RTB responses to attractant-baited trees warrants further investigation, but may simply be an artifact of the reduction in WPB attack densities on NAVV-treated trees. RTB attacks often occur on trees colonized by WPB. It is thought that RTB responds to monoterpenes released from host trees (Hobson et al. 1993) on attack by WPB and presumably other congenerics (Fettig et al. 2004). The most probable source of these monoterpenes is oleoresin present in pitch tubes (Fettig et al. 2004). Although verbenone (Rappaport et al. 2001, Sun et al. 2003, Fettig et al. 2007b) and other semiochemicals (Fettig et al. 2005b) have been shown to reduce RTB attraction to baited sources, we cannot isolate the confounding effects of differences in WPB attack rates on treatment effects observed in this study.

Bertram and Paine (1994) concluded that although applications of verbenone and ipsdienol did not prevent WPB from attacking baited trees, their effectiveness in reducing attack density may allow some trees to survive. Similarly, the reduction of attacks on NAVV-treated trees by both bark beetle species likely had an effect on tree mortality. In our study, the application of NAVV to individual ponderosa pines significantly reduced tree mortality (chi-square = 7.5, df = 1, and P = 0.006). Only 4 of 30 attractant-baited ponderosa pines died from bark beetle attack while 50% mortality (15 of 30) was observed in the untreated control. To our knowledge, this is the first published account of the successful application of semiochemical treatments for reducing WPB-caused tree mortality in ponderosa pine.

We have established the effectiveness of a blend of eight NAVs and verbenone for reducing WPB colonization densities and associated levels of tree mortality. Others have shown similar effects in other systems (Huber and Borden 2001, Jakus et al. 2003, Zhang and Schlyter 2004). There continues to be considerable interest in development of such tools. The potential use of NAVV for single tree protection likely will be most significant in residential, recreational (i.e., campgrounds), or administrative sites, similar to settings in which insecticides are used (Fettig et al. 2006a). Tree losses in these environments generally result in undesirable impacts such as reduced shade, screening, and aesthetics (Helm and Johnson 1995). Dead trees also pose potential hazards to public safety (Johnson 1981). In addition, NAVV may be of use in small, ecologically unique or sensitive areas where applications of insecticides are not permissible. Additional studies are required to determine the minimum release rate necessary to achieve adequate levels of efficacy, to potentially reduce the total number of compounds in our blend, to determine optimal spacing and formulation on individual trees, to determine the influence of WPB population density on treatment efficacy, and to determine the potential of NAVV for stand protection.

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