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Efficacy of verbenone and a blend of verbenone and nonhost volatiles for protecting lodgepole pine from mountain pine beetle (Coleoptera: Curculionidae)

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Abstract

1 Significant research has been devoted to the development of semiochemical repellents for mountain pine beetle *Dendroctonus ponderosae* Hopkins. Several formulations of the beetle's antiaggregation pheromone verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) are registered to protect pine trees and stands.

2 We compared the efficacy of verbenone and Verbenone Plus for protecting individual lodgepole pine *Pinus contorta* Dougl. ex Loud. and small stands of *P. contorta* from mortality attributed to *D. ponderosae*. Verbenone Plus is a blend of semiochemicals [(−)-verbenone, acetophenone, and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] originally developed to inhibit aggregation of western pine beetle *D. brevicomis* LeConte. It is the only effective semiochemical repellent that protects ponderosa pine *P. ponderosa* Dougl. ex Laws. from mortality attributed to *D. brevicomis*, but has yet to be registered or commercialized.

3 Both verbenone and Verbenone Plus were effective for protecting individual *P. contorta* and small stands of *P. contorta* from mortality attributed to *D. ponderosae*. Verbenone alone was as effective as Verbenone Plus.

4 An obstacle to the broader use of semiochemical repellents for the management of bark beetles is the relatively high cost and specificity of the semiochemicals involved. A semiochemical repellent with efficacy across multiple bark beetle species and hosts, such as Verbenone Plus, would be desirable, assuming the additional components are not cost-prohibitive or limit registration.

Keywords (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, acetophenone, *Dendroctonus ponderosae*, *Pinus contorta*, semiochemical repellents, tree protection, Verbenone Plus.

Introduction

Mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) is an important forest insect pest in North America where it colonizes several hosts, including lodgepole pine *Pinus contorta* Dougl. ex Loud. (Negrón & Fettig, 2014). Extensive levels of tree mortality associated with *D. ponderosae* outbreaks may impact timber and fibre production, water quality and quantity, fish and wildlife populations, fire risk and severity, recreation, grazing capacity, biodiversity, carbon storage, endangered species, and cultural resources, among other factors (Morris *et al.*, 2018). Several tactics are available to manage bark beetle infestations and to reduce associated levels of tree mortality. Direct control involves short-term tactics designed to address current infestations by manipulating beetle populations and often includes the use of insecticides, semiochemicals, sanitation harvests, or a combination of these and related treatments (Fettig & Hilszczański, 2015). Indirect control is preventive and designed to reduce the probability and severity of future infestations within treated areas by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and/or altering age classes and species composition.

Progar *et al.* (2014) and Seybold *et al.* (2018) synthesize knowledge of the chemical ecology of the *D. ponderosae* system, and identify factors limiting the development, effectiveness, and utility of semiochemical repellents to reduce levels of tree mortality attributed to *D. ponderosae*. *Dendroctonus ponderosae* uses a complex system of semiochemical communication for host selection, mate attraction, and conspecific aggregation to

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overwhelm host defences, and most of the primary semiochemicals involved have been identified. *Dendroctonus ponderosae* females initiate colonization of the host tree in a sequence mediated by aggregation pheromones (Pitman *et al.*, 1968, 1969; Ryker & Libbey, 1982) and host kairomones (Renwick & Vité, 1970; Borden *et al.*, 1987; Miller & Lindgren, 2000). Females are subsequently joined by males and other females, and mass attack ensues enabling *D. ponderosae* to overwhelm host tree defences. Increasing amounts of verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) are produced during the later stages of host colonization (Pitman *et al.*, 1969; Rudinsky *et al.*, 1974), which discourage additional colonization of the target tree. Verbenone is produced by auto-oxidation of the host monoterpene α-pinene (Hunt *et al.*, 1989), and through degradation of host material by microbes associated with *D. ponderosae* (Hunt & Borden, 1990).

In North America, significant research has been devoted to the development of verbenone for tree protection, and several formulations are registered for use in Canada and the U.S.A. (Seybold *et al.*, 2018). Whereas early studies demonstrated the efficacy of verbenone to reduce levels of tree mortality attributed to *D. ponderosae* in *P. contorta* (e.g. Amman *et al.*, 1989; Lindgren *et al.*, 1989; Gibson *et al.*, 1991; Safranyik *et al.*, 1992) some later studies reported inconsistent or ambiguous results, especially when *D. ponderosae* populations were at outbreak levels (Progar, 2003, 2005; Progar *et al.*, 2013). Negative results have been linked to several factors, including differences in stand structure, photoisomerization of verbenone to chrysanthenone (Kostyk *et al.*, 1993), rapid dispersal of verbenone, inconsistent or inadequate release, and/or limitations in the range of inhibition of verbenone (Progar *et al.*, 2014). More recently, it has been argued that a lack of efficacy may be due to the complexity of host finding and selection processes, which involves other visual and olfactory signals produced by hosts, nonhosts, and competing insect species that are often ignored. That is, a diverse array of chemical cues and signals may disrupt host finding and/or selection more than a single semiochemical or mixtures of semiochemicals that mimic one type of signal (e.g. antiaggregation pheromones) (Borden, 1997). As such, nonhost volatiles have been the focus of more recent studies that demonstrated these compounds are capable of reducing aggregation in several *Dendroctonus* spp. (Zhang & Schlyter, 2004; Erbilgin *et al.*, 2007, 2008; Seybold *et al.*, 2018).

Verbenone Plus is a four-component blend of semiochemicals [(−)-verbenone, acetophenone, and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] that was originally developed to inhibit aggregation of western pine beetle *D. brevicomis* LeConte (Fettig *et al.*, 2012a). The objective of our research was to compare the efficacy of verbenone and Verbenone Plus for protecting individual *P. contorta* and small stands of *P. contorta* from mortality attributed to *D. ponderosae*.

Materials and methods

Individual tree study

This study was conducted on the Evanston and Mountain View Ranger Districts, Uinta-Wasatch-Cache National Forest, Utah, U.S.A. (40.92° N, 110.39° W; ~2700 m elevation) during 2008–2009. The experimental design was a randomized complete block design (RCBD) with three treatments and 25 replicates (blocks)/treatment. Replicates were separated by >50 m. Treatments included: (i) untreated, baited control (MPB) [*trans*-verbenol (1.2 mg/d), and *exo*-brevicomin (0.3 mg/d); Contech Inc., Delta, BC, Canada] [mean diameter at 1.37 m in height (dbh) ± SEM = 25.3 ± 0.9 cm), (ii) (−)-verbenone + MPB (mean dbh ± SEM = 25.6 ± 0.9 cm], and (iii) Verbenone Plus + MPB (mean dbh ± SEM = 25.2 ± 0.8 cm) (Table 1). There was no significant difference in tree dbh among treatments ($F_{2,\,48} = 0.08$; $P = 0.93$). Mean basal area (cross-sectional area of trees at 1.37 m in height, ± SEM) was 32.2 ± 2.9 m^2/ha, of which 98% was *P. contorta* with the remainder quaking aspen *Populus tremuloides* Michx. *Dendroctonus ponderosae* killed 42% of *P. contorta* in the area in 2006 and 2007 (C.J. Fettig, unpublished data).

Semiochemical repellents were stapled to the tree bole at ~2 m in height on the north (verbenone pouch), east (acetophenone bottle, with wire attached), and west [(*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol pouch] aspects. Baits were stapled to the tree bole at ~2.5 m in height on the north aspect 10–12 June 2008 (i.e. prior to initiation of *D. ponderosae* flight activity), and removed after 28 days (i.e. following peak *D. ponderosae* flight). The position of semiochemicals on the tree bole was standardized as aspect influences bark temperature (Schmid *et al.*, 1992), and temperature influences the release rates of semiochemicals and *D. ponderosae* behaviour (Bartos & Amman, 1989). We counted the number of *D. ponderosae* attacks (i.e. pitch tubes or points of attack containing boring dust and/or frass) in 400-cm^2 (20 × 20 cm) sample windows at ~1.5 and ~4 m in height at the north and south aspects. Sampling was conducted at 42 days and 84 days. These data are useful in assessing repellency below critical attack density thresholds necessary to cause tree mortality. A two-way analysis of variance (treatment and block) was performed on the density of *D. ponderosae* attacks using $\alpha = 0.05$ (SigmaStat Version 12.0, Systat Software Inc., San Jose, CA, U.S.A.). Mortality was based on the presence of crown fade on 14–15 July 2009. This period of time (~13 months) is sufficient for crowns to fade following mass attack the previous year. Data on proportions of experimental trees that died from *D. ponderosae* attack were analysed by chi-square tests for comparisons between multiple proportions (Jones, 1984; Huber & Borden, 2001).

Small stand study

This study was conducted on the Montpelier Ranger District, Caribou-Targhee National Forest, Idaho, U.S.A. (plot 1 = 42.40° N, 111.56° W, ~2240 m) during 2011–2013. The experimental design was completely randomized with three treatments and five replicates (0.41-ha square plots) per treatment. Replicates were separated by >150 m. Treatments included: (i) untreated, baited control (MPB) [*trans*-verbenol (1.2 mg/d), and *exo*-brevicomin (0.3 mg/d); Contech Inc.], (ii) (−)-verbenone + MPB, and (iii) Verbenone Plus + MPB (Table 1). Mean basal area (±SEM) was 33.0 ± 1.6 m^2/ha, of which 87% was *P. contorta* with the remainder subalpine fir *Abies lasiocarpa* (Hooker) Nuttall, Engelmann

Table 1 Descriptions of semiochemical repellents used in tree protection studies

Semiochemical	Source	Purity (%)	Release device	Release rate (mg/d)
Verbenone				
Verbenone [77%-(−)]	Phero Tech	97	7-g Phero Tech pouch	50.0 (20 °C)
Verbenone Plus:				
Verbenone [77%-(−)]	Phero Tech	97	7-g Phero Tech pouch	50.0 (20 °C)
Acetophenone	Sigma-Aldrich	99	Phero Tech 15 mL polyethylene bottle	18.0 (20 °C)
(*E*)-2-Hexen-1-ol (*Z*)-2-Hexen-1-ol	Bedoukian	97	Phero tech pouch (1:1 blend)	50.0 (20 °C)

Phero Tech = Phero Tech Inc., Delta, BC, Canada (which became Contech Inc., Delta, BC, Canada); Sigma-Aldrich = Sigma-Aldrich Canada Ltd., Oakville, ON, Canada; Bedoukian = Bedoukian Research Inc., Danbury, CT, U.S.A.

spruce *Picea engelmannii* Parry ex Engelm., Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco, *Po. tremuloides*, and white fir *A. concolor* (Gord. and Glend.) Lindl. ex Hildebr (1 tree). *Dendroctonus ponderosae* killed 9% of *P. contorta* within these plots in 2010.

Treatments were applied 11–13 July 2011 and reapplied 19–21 June 2012 following the same methods. Semiochemical repellents were stapled to tree boles at ~2 m in height (with placement as described above) along a ~ 9.1 by 9.1-m grid ($N = 50$ units/plot). Repellents were applied to achieve as uniform coverage as possible accounting for the natural distribution of vertical substrates (tree boles, regardless of tree species or tree size) to which repellents were attached. A 1.7-m tall wooden stake was driven into the ground at a grid point if no tree was within ~4 m of the grid point, and semiochemical repellents were stapled to the top of the stake. One bait was stapled to the tree nearest to the centre of each plot (regardless of tree species or tree size) at ~2 m in height on the north aspect 11–13 July 2011 and 19–21 June 2012. All semiochemicals (repellents and baits) deployed in 2011 were removed 19–21 June 2012, and those deployed in 2012 were removed 24–25 July 2013.

Prior to treatment in 2011, stand structure and composition were determined by the census of live trees (≥12.7 cm dbh) on each experimental plot 12–14 July 2011. At the same time, all trees infested by *D. ponderosae* were identified, tagged, and excluded from statistical analyses (i.e. these trees were colonized and/or killed prior to the implementation of treatments in 2011). A census was conducted of each plot for trees colonized and killed by bark beetles on 11 October 2012 and 30–31 October 2012 (due to weather and limitations concerning accessibility to some plots) and 24–25 July 2013. Tree mortality was based on the presence of crown fade on these dates. A one-way analysis of variance (treatment) was performed on the proportion of trees killed by *D. ponderosae* using $\alpha = 0.05$ (SigmaStat Version 12.0).

Results

Individual tree study

The density of *D. ponderosae* attacks was significantly higher for MPB than verbenone + MPB or Verbenone Plus + MPB (Fig. 1) at 42 days ($F_{2, 48} = 32.2$, $P < 0.001$) and 84 days ($F_{2, 48} = 31.6$, $P < 0.001$). The application of both verbenone and Verbenone Plus to attractant-baited *P. contorta* significantly reduced levels of tree mortality compared to MPB ($P < 0.05$, all comparisons).

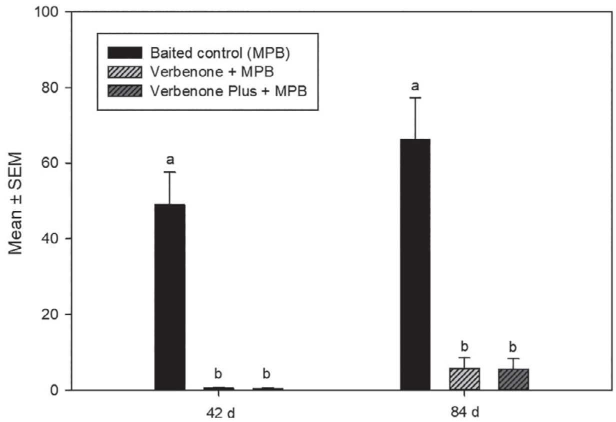

Figure 1 Mean number (+SEM) of *Dendroctonus ponderosae* attacks/m^2 occurring on attractant-baited *Pinus contorta* untreated and treated with verbenone and Verbenone Plus [(−)-verbenone, acetophenone, and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] at 42 days and 84 days after treatment, Uinta-Wasatch-Cache National Forest, Utah, U.S.A., 2008. Means followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$).

No significant differences were observed between verbenone + MPB and Verbenone Plus + MPB (Figs. 1 and 2). Overall, the density of *D. ponderosae* attacks was significantly higher on trees that died (mean ± SEM = 71.7 ± 9.2 attacks/m^2) than those that survived (3.9 ± 1.1 attacks/m^2) ($H = 55.5$, $df = 1$, $P < 0.001$).

Small stand study

In total, 193 *P. contorta* were attacked by *D. ponderosae*, 139 at densities sufficient to cause tree mortality. A significant treatment effect was observed ($F_{2, 12} = 5.3$, $P = 0.023$). Fewer *P. contorta* were killed by *D. ponderosae* on plots treated with verbenone and Verbenone Plus compared to the untreated control over the two-year period (Fig. 3). No significant difference was observed between verbenone and Verbenone Plus.

Discussion

Recruitment of a critical minimum number of beetles to the target tree is required to overwhelm tree defences, which varies with changes in host vigour (Fettig *et al.*, 2007). Based on research in northeastern Oregon, U.S.A., Raffa & Berryman (1983) reported

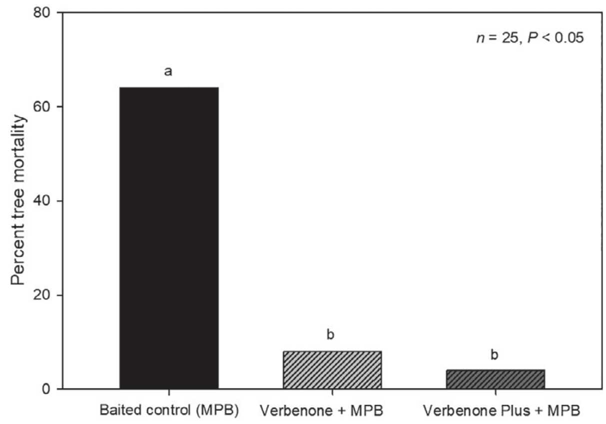

Figure 2 Percentage of attractant-baited *Pinus contorta* untreated and treated with verbenone and Verbenone Plus [(–)-verbenone, acetophenone, and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] that died due to colonization by *Dendroctionus ponderosae* in 2008, Uinta-Wasatch-Cache National Forest, Utah, U.S.A. Tree mortality was based on the presence of crown fade in July 2009. Columns followed by the same letter are not significantly different (chi-square tests for comparisons between multiple proportions; $P > 0.05$).

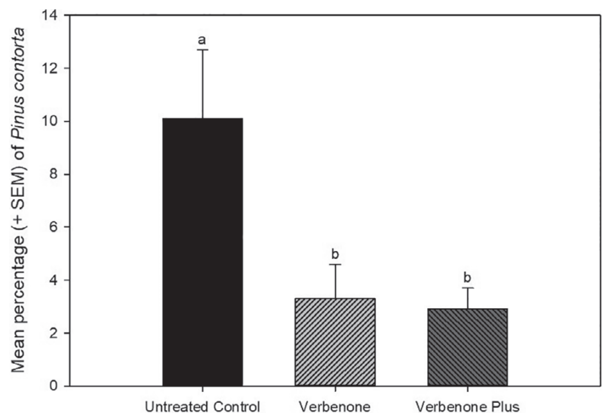

Figure 3 Cumulative mean percentage (+SEM) of *Pinus contorta* killed by *Dendroctonus ponderosae* on 0.41-ha square plots untreated and treated with verbenone and Verbenone Plus [(–)-verbenone, acetophenone, and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol] over a two-year period, Caribou–Targhee National Forest, Idaho, U.S.A. Semiochemical repellents were applied in July 2011 and June 2012. Tree mortality was based on the presence of crown fade in October 2012 (for trees colonized in 2011) and July 2013 (for trees colonized in 2011 that survived and those colonized in 2012). Means (+SEM) followed by the same letter are not significantly different (Tukey's HSD; $P > 0.05$).

that ~40 *D. ponderosae* attacks/m^2 are required to overwhelm the defensive capacity of *P. contorta* and to induce tree mortality, which largely agrees with our data. In the individual tree study, only one (of 72) tree with >40 attacks/m^2 (value = 50 attacks/m^2) survived. However, 6 of the 28 trees that died had <40 attacks/m^2. Attack densities ranged from 0 (59 trees, including three that died but with evidence of *D. ponderosae* colonization outside our sampling windows) to 219 attacks/m^2 (one tree). Reproduction and brood survival is maximized at ~62 attacks/m^2 (Raffa & Berryman, 1983). Successful reproduction of *D. ponderosae* is contingent upon the death of all or part of the host (i.e. a strip attack).

Several years of research resulted in the development of Verbenone Plus for protecting ponderosa pine *P. ponderosa* Dougl. ex Laws. from mortality attributed to *D. brevicomis* (e.g. Fettig *et al.*, 2009a, 2012a, 2012b). *Pinus ponderosa* is the only host of *D. brevicomis* throughout Canada and most of the western U.S.A. (Fettig, 2016). To date, Verbenone Plus remains the only effective semiochemical repellent for *D. brevicomis* (Seybold *et al.*, 2018), although an eight-component blend of semiochemicals showed efficacy in an early study (Fettig *et al.*, 2008). Despite this, Verbenone Plus has yet to be registered or commercialized for tree protection. In California, U.S.A., Fettig *et al.* (2012c) evaluated Verbenone Plus for protecting stands of whitebark pine *P. albicaulis* Engelm., a tree species of concern being considered for listing as a threatened and endangered species in the U.S.A. by the U.S. Fish and Wildlife Service, from *D. ponderosae*. Significantly fewer *P. albicaulis* were killed by *D. ponderosae* on plots treated with Verbenone Plus compared to the untreated control. A 78% reduction in tree mortality was observed. Whereas verbenone alone was not evaluated in their study, previous attempts by forest health specialists to protect nearby trees with verbenone failed (Fettig *et al.*, 2012c). Our research demonstrates that verbenone and Verbenone Plus did not significantly differ in attack rates and host mortality at the tree or small stand level (Figs. 2 and 3). As such, we recommend the use of verbenone alone for *D. ponderosae* in *P. contorta*. However, given trends observed in our data (i.e. numerically lower levels of colonization and tree mortality, and less variability, with Verbenone Plus compared to verbenone) further study under higher levels of beetle pressure (e.g. when ≥20% of *P. contorta* are killed in a single year in untreated areas as observed in the individual tree study) should be considered for small stand protection.

An obstacle to the broader use of semiochemical repellents for the management of bark beetles is the relatively high cost and specificity of the semiochemicals involved. This is a common challenge for minor use crops. Although populations of *D. ponderosae* have declined in recent years, *D. ponderosae* is still recognized as the most damaging forest insect in the U.S.A. with a projected loss of ~65.8 million m^2 of the basal area between 2013 and 2027 (Krist *et al.*, 2014). At the same time, *D. brevicomis* is recognized as the eighth-most damaging forest insect in the U.S.A. with a projected loss of ~15.4 million m^2 of the basal area between 2013 and 2027 (Krist *et al.*, 2014). In response to a severe drought in California in 2012–2015, levels of tree mortality attributed to *D. brevicomis* peaked nationally (U.S.A.) in 2016 when 892 041 ha were impacted that year. Tree mortality exceeded 90% in some areas (Fettig *et al.*, 2019) prompting a declaration of a state of emergency over concerns regarding public health and safety. Stakeholders have lamented over the lack of tools available for tree protection during the *D. brevicomis* outbreak in California (Axelson *et al.*, 2019). To that end, with climate change levels of tree mortality attributed to *D. brevicomis* are projected to increase in areas where suitable hosts occur (Bentz *et al.*, 2010), due largely to increases in the frequency and severity of droughts which are important inciting factors (Kolb *et al.*, 2016).

Occasionally, *D. ponderosae* and *D. brevicomis* colonize the same *P. ponderosa*, and some failures of verbenone to protect *P. ponderosa* from mortality attributed to *D. ponderosae* likely result from colonization by *D. brevicomis*. For example, the failure of verbenone to protect *P. ponderosa* from mortality attributed to *D. ponderosae* in a study in Montana, U.S.A. were linked, in part, to most dead trees (89%) being colonized by *D. brevicomis*, emarginated ips *Ips emarginatus* (LeConte) and/or pine engraver *I. pini* Say in addition to *D. ponderosae* (Fettig *et al.*, 2016). Like *D. brevicomis* (Fettig *et al.*, 2009b), North American *Ips* spp. are generally not inhibited by verbenone alone at levels sufficient to impart tree protection (Devlin & Borden, 1994). In this regard, a more generic semiochemical repellent with efficacy across multiple bark beetle species and hosts, such as Verbenone Plus, would be desirable assuming the additional components are not cost-prohibitive or limit registration. Acetophenone has been demonstrated to reduce aggregation in several notable bark beetles indigenous to the U.S.A., including *D. brevicomis*, Douglas-fir beetle *D. pseudotsugae* Hopkins, and southern pine beetle *D. frontalis* Zimmerman (Pureswaran & Borden, 2004; Sullivan, 2005; Erbilgin *et al.*, 2007; Sullivan *et al.*, 2007). Relatedly, ongoing studies in Wyoming, U.S.A. indicate that combining acetophenone and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol with MCH, the antiaggregation pheromone of spruce beetle, *D. rufipennis* (Kirby), results in high levels of protection of *Pi. engelmannii* (C.J.Fettig *et al.*, unpublished data). Of note, acetophenone is substantially cheaper than verbenone (∼13% of the cost); can be released at lower rates than verbenone (e.g. 20 vs. 50 mg/d @ 20 °C in our study); and is approved by the U.S. Food and Drug Administration as a synthetic flavouring substance and adjuvant in food, non-alcoholic beverages, soaps, and lotions. Additional research on Verbenone Plus should concentrate on determining optimal doses for protecting *P. contorta*, and expanding Verbenone Plus into other bark beetle-host systems.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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