

UC Davis

UC Davis Previously Published Works

Title

Evaluation of a semiochemical tool for management of southwestern pine beetle, *Dendroctonus barberi* (Coleoptera: Curculionidae), in West Texas

Permalink

<https://escholarship.org/uc/item/0hg6q15s>

Journal

Journal of Economic Entomology

ISSN

0022-0493

Authors

Gomez, Demian F
Audley, Jackson P
Fettig, Christopher J
[et al.](#)

Publication Date

2026-06-30

DOI

10.1093/jee/toag190

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

Forest Entomology

Evaluation of a semiochemical tool for management of southwestern pine beetle, *Dendroctonus barberi* (Coleoptera: Curculionidae), in West Texas

Demian F. Gomez^{1,*}, Jackson P. Audley^{2,3}, Christopher J. Fettig³, Jayme Trainer⁴,
Leif A. Mortenson⁵, Erin E. Davis⁶, Camille Wiseman⁷, and Agenor Mafra-Neto⁸

¹Forest Health Program, Texas A&M Forest Service, Austin, TX, USA

²Department of Plant Sciences, University of California, Davis, CA, USA

³Pacific Southwest Research Station, USDA Forest Service, Woodland, CA, USA

⁴Forest Systems, Texas A&M Forest Service, Alpine, TX, USA

⁵Pacific Southwest Research Station, USDA Forest Service, Placerville, CA, USA

⁶Forest Systems, Texas A&M Forest Service, Kerrville, TX, USA

⁷Field Operations, Texas A&M Forest Service, Austin, TX, USA

⁸ISCA Inc, Riverside, CA, USA

*Corresponding author. Texas A&M Forest Service, 6330 Hwy 290 East, Suite 115, Austin, TX 78723, USA (Email: demian.gomez@tfs.tamu.edu).

Subject Editor: Kevin Dodds

Southwestern pine beetle, *Dendroctonus barberi* Hopkins (Coleoptera: Curculionidae), is a pest of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. (Pinales: Pinaceae), in the southwestern United States and northern Mexico. *D. barberi* is closely related to the western pine beetle, *D. brevicomis* LeConte, but was reinstated as a distinct species in 2019. Verbenone Plus, a semiochemical blend of (–)-verbenone, acetophenone, (E)-2-hexen-1-ol, and (Z)-2-hexen-1-ol, was found to be inhibitory to *D. brevicomis* in 2009 and later reported to reduce mortality of *P. ponderosa* attributed to *D. brevicomis*. We evaluated the effects of Verbenone Plus on inhibition of *D. barberi* at the Davis Mountains Preserve, Texas, United States. A commercial formulation of (–)-verbenone (SPLAT Verb, EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States) was used in all experiments. SPLAT Verb is a flowable matrix containing 10.0% (–)-verbenone by weight. Acetophenone, (E)-2-hexen-1-ol, and (Z)-2-hexen-1-ol were loaded into pouches with (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol combined in a single pouch. Trapping assays were conducted from 16 to 23 June 2024 and from 2 to 9 October 2024 to evaluate responses of *D. barberi* to a low dose (3.5 g of (–)-verbenone/trap, VPL) and high dose (7.0 g of (–)-verbenone/trap, VPH) of Verbenone Plus in multiple-funnel traps baited with a *D. barberi* lure (Synergy Semiochemical Corp., Delta, BC, Canada). VPL and VPH inhibited attraction of total *D. barberi*, female *D. barberi*, and male *D. barberi* in both trapping assays. In the October assay, VPH captured fewer total *D. barberi* and female *D. barberi* than VPL, whereas no differences were observed between doses in the April assay. A zone-of-inhibition assay was conducted from 7 to 17 October 2025 to evaluate responses of *D. barberi* to multiple-funnel traps baited with a *D. barberi* lure at 5 distances (1.5, 3, 6, 9, and 12 m) from *P. ponderosa* treated with VPL and VPH. No significant differences in captures occurred among distances for VPL. For VPH, significant reductions in captures occurred at 1.5, 3, and 6 m compared to 12 m, with maximum inhibition (defined as the farthest distance at which the highest levels of inhibition occurred) observed up to 3 m. In a tree protection study, 5 plots containing 25 *P. ponderosa* were treated with VPH and 5 were left untreated in 2024 and 2025. Significantly less *P. ponderosa* mortality occurred on plots treated with VPH (27.4 ± 3.5%) than in the control (52.4 ± 3.9%) during the 2-year period. The implications of these and other results to management of *D. barberi* are discussed.

Keywords: antiaggregation pheromone, bark beetles, *Dendroctonus brevicomis*, inhibition, *Pinus ponderosa*, ponderosa pine, tree protection

Introduction

Southwestern pine beetle, *Dendroctonus barberi* Hopkins (Coleoptera: Curculionidae), is a pest of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. (Pinales: Pinaceae). Pinyon pine, *Pinus edulis* Engelm., and Douglas-fir, *Pseudotsuga menziesii*

(Mirbel) Franco (Pinales: Pinaceae), have also been recorded as hosts, but colonization of these tree species is rare. *D. barberi* and western pine beetle, *D. brevicomis* LeConte, were synonymous from 1963 to 2019 (Wood 1963) but were reinstated as distinct species in 2019 through a combination of evidence

Received: 19 April 2026. Revised: 2 June 2026. Accepted: 5 June 2026

© The Author(s) 2026. Published by Oxford University Press on behalf of Entomological Society of America. All rights reserved. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

2024 and from 2 to 9 October 2024 to evaluate responses of *D. barberi* to traps baited with the *D. barberi* lure (Table 1). Mean stocking ($\pm$ SEM) of live trees ≥ 12.7 cm dbh was 7.3 ± 0.7 m² of basal area per ha, of which 43.5% was gray oak, *Quercus grisea* Liebmman (Fagales: Fagaceae). The remainder was Mexican pinyon pine, *P. cembroides* Zuccarini (30.9%), alligator juniper, *Juniperus deppeana* von Steudel (Cupressales: Cupressaceae) (21.2%), and Emory oak, *Q. emoryi* Torrey (4.4%). Areas of *P. ponderosa* were avoided to reduce the chance of spillover whereby beetles are attracted to baited traps but attack adjacent host trees. Both assays were conducted in the same location and within ~ 200 m of an area containing *P. ponderosa*, some of which were recently colonized by *D. barberi*.

Fifteen traps were deployed in 3 transects of 5 traps and separated by ≥ 30 m to avoid interference among treatments in a completely randomized design. At each location, a 1-m long rebar was hammered into the ground. A 2.4-m long steel conduit pole was inserted over the rebar from which a trap was hung placing the bottom of the trap ~ 95 cm above the forest floor. Each trap was randomly assigned to 1 of 3 treatments ($n=5$): (1) *D. barberi* lure (control); (2) *D. barberi* lure + 35 g SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol (VPL); and (3) *D. barberi* lure + 70 g SPLAT Verb, acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol (VPH) (Table 1). Traps were randomly assigned to trapping locations and left in place for ~ 24 h after which captured insects were removed and the traps were rerandomized among locations for 7 d ($n=35$). The *D. barberi* lure, acetophenone pouch, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol pouch were suspended between the sixth and seventh funnels with twist ties. Dollops of SPLAT Verb were dispensed into 9-cm by 9-cm plastic weighing trays which were attached to the top edge of the sixth funnel with binder clips. Propylene glycol was used in each collection cup to kill arriving insects. All *D. barberi* were tallied, and the sex was determined by examining the seventh abdominal tergite (Lyon 1958).

Mean per trap, per day captures of total *D. barberi*, female *D. barberi*, and male *D. barberi* were compared by fitting generalized linear models with a negative binomial distribution and a log link (lme4 package). Treatment, day, trap location, and their interactions were considered in each model. Model selections were informed by Akaike information criterion (AIC) values and likelihood ratio tests (Zuur et al. 2009). Multiple means comparisons were made with post hoc pairwise, least squares means (emmeans package) tests with the Tukey's correction ($\alpha=0.05$).

Zone-of-Inhibition Assay

We conducted a zone-of-inhibition assay at the Davis Mountains Preserve (30.667°N, 104.145°W; 1,800 m elevation) from 7 to 17 October 2025 to evaluate responses of *D. barberi* to traps baited with a *D. barberi* lure at 5 distances (1.5, 3, 6, 9, and 12 m) from *P. ponderosa* treated with VPL and VPH. Prior to the assay on 5 March 2025, 6 *P. ponderosa* (mean $\pm$ SEM = 41.6 ± 6.2 cm dbh) were selected and confirmed to be uninfested by *D. barberi*. Each *P. ponderosa* was randomly assigned to 1 of 2 treatments ($n=3$): VPL or VPH. Arrays consisting of 25 trapping locations (stations) per tree were established on 5 March 2025 by hammering rebar into

the ground with 1 station at each of 5 distances (1.5, 3, 6, 9, and 12 m) from the tree on each of 5 bearings (0, 72, 144, 216, and 288°) from the tree. Traps were not deployed until the beginning of the assay. Mean stocking ($\pm$ SEM) of live trees ≥ 12.7 cm dbh was 4.8 ± 1.4 m² of basal area per ha, of which 81.0% was *P. ponderosa*. The remainder was *Q. emoryi* (9.3%), *J. deppeana* (5.8%), and *P. cembroides* (3.9%).

At the beginning of the assay on 7 October 2025, an acetophenone pouch and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol pouch were stapled to the N aspect of each tree at ~ 1.8 m in height. Dollops of SPLAT Verb (17.5 g) were dispensed on each tree at ~ 1.9 m in height on the N and S aspects (VPL) or N, S, E, W aspects (VPH). During the assay, each trapping array received 5 traps hung from 2.4-m long steel conduit poles that were placed over the rebar at the designated station for each day. A *D. barberi* lure was suspended between the sixth and seventh funnels with twist ties. Insecticide strips (Hot Shot No Pest Strips) were placed in each collection cup to kill arriving insects. Stations were randomized daily within each array such that there was a single trap per distance and bearing (per day) from 7 to 17 October 2025 ($n=30$). Traps were left in place for ~ 24 h after which captured insects were removed and the stations were rerandomized. All *D. barberi* were tallied.

Mean per trap, per day captures of *D. barberi* were compared by fitting a generalized linear mixed effects model with the nbinom1 family and a log link (glmmTMB package, Bolker 2015). Treatments were initially modeled together and then independently as treatment and treatment by distance interactions were significant. Treatment, distance, and bearing were considered as fixed effects, and collection day was considered a random effect in each model. Interactions between treatment and distance were also considered. Model fit and assumptions were assessed based on simulated residuals plots (DHARMA package). Following final model selection, Type II Wald chi-squared tests were used to determine significant variables within each model, followed by post hoc lsmeans comparisons to separate means ($\alpha=0.05$).

Tree Protection Study

We conducted a tree protection study at the Davis Mountains Preserve during 2024–2026 to determine the effectiveness of VPH for protecting *P. ponderosa* from mortality attributed to *D. barberi*. Only VPH (the high-dose formulation) was evaluated in the tree protection study, as resources were limited and maximizing replication was prioritized to establish a robust best-case protection scenario before assessing reduced doses in future studies. Ten plots containing 25 live *P. ponderosa* ≥ 20 cm dbh were established during 5–7 March 2024 and randomly assigned 1 of 2 treatments ($n=5$): control or VPH (Table 2). These *P. ponderosa* were confirmed uninfested, tagged and georeferenced, and the dbh was recorded. Plot locations were based on ground surveys, indicating that *D. barberi* infestations were active in surrounding areas. Given the low tree densities at the Davis Mountains Preserve, the area required to reach 25 *P. ponderosa* per plot varied considerably, ranging from 0.28 to 1.5 ha (Table 2). All live trees ≥ 12.7 cm dbh (regardless of species, including *P. ponderosa*) on each plot were identified to species and the dbh was recorded.

On treated plots, an acetophenone pouch and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol pouch were stapled to the N aspect of

Table 2. Experimental plots included in the tree protection study, Davis Mountains Preserve, Texas, 2024–2025

Plot	Treatment ^a	Coordinates (N, W)	Size (ha) ^b	Trees/ha ^c	BA (m ² /ha) ^c	Percent <i>P. ponderosa</i> ^d	Mean dbh, <i>P. ponderosa</i> ^c (cm)
1	Verbenone Plus	30.667°, 104.150°	0.45	58	10.4	100	44.4 ± 3.5
2	Control	30.663°, 104.155°	0.38	97	9.3	75.7	37.0 ± 2.2
3	Control	30.662°, 104.153°	0.45	156	9.7	44.3	34.1 ± 2.3
4	Verbenone Plus	30.663°, 104.156°	1.09	90	7.4	37.8	34.6 ± 2.9
5	Verbenone Plus	30.661°, 104.160°	0.45	81	7.5	83.3	33.1 ± 2.8
6	Verbenone Plus	30.660°, 104.162°	0.40	162	7.8	67.7	24.8 ± 1.5
7	Control	30.659°, 104.164°	0.28	178	9.4	79.6	25.6 ± 1.6
8	Control	30.662°, 104.159°	0.34	153	12.1	57.7	33.5 ± 2.4
9	Control	30.670°, 104.143°	1.5	44	3.6	54.6	28.0 ± 1.9
10	Verbenone Plus	30.695°, 104.155°	0.15	180	16.6	96.3	33.0 ± 2.1

^aVerbenone Plus = 70 g of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol (VPH) applied twice in 2024 and 2025. Plots were not baited due to concerns regarding levels of tree mortality at the Davis Mountains Preserve.

^bPlot size represents the smallest contiguous area containing 25 live *Pinus ponderosa* ≥20 cm diameter at breast height (dbh, 1.37 m in height).

^cLive trees ≥12.7 cm dbh at the beginning of the study (mean ± SEM for dbh).

^dBased on number of live trees ≥12.7 cm dbh at the beginning of the study. Others included *Quercus grisea* (70 trees), *Q. emoryi* (39), *P. cembroides* (33), *Juniperus deppeana* (21), *Juglans microcarpa* (14), *Q. gravesii* (8), *Arbutus xalapensis* (5), *Prunus serotina* (4), and *Q. hypoleucoides* (4). Total number was 525.



Fig. 1. Verbenone Plus (VPH) applied to *Pinus ponderosa* at the Davis Mountains Preserve, Texas, during the tree protection study. Visible in the small oval is 1 (of 4) 17.5-g dollop of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States) (top oval) and the acetophenone and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol pouches (bottom oval). Photo by Demian F. Gomez, Texas A&M Forest Service.

each tree at ~1.8 m in height. Four 17.5-g dollops of SPLAT Verb were dispensed at ~1.9 m in height on the N, S, E, W aspects (Fig. 1). Plots were not baited as supplemental goals of our work were to protect some *P. ponderosa* from *D. barberi* at the Davis Mountains Preserve and not to induce further tree mortality by baiting. VPH was applied twice each year during 5–7 March 2024, 4 June 2024, 5–6 March 2025, and 5–6 June 2025.

We conducted a census of plots for *D. barberi* attacks and other sources of tree mortality during 2–9 October 2024, 3–5 March 2025, 7–17 October 2025, and 24 March 2026. Tree

mortality was based on the presence of crown fade. Numbers of *P. ponderosa* ≥12.7 cm dbh colonized and killed by *D. barberi* were compared among treatment groups using logistic regressions with Bernoulli, tree-level responses (0 = not colonized/not killed, 1 = colonized/killed) with a binomial error distribution and a logit link using the glm() function (base package). Colonization and mortality were compared separately between treatments in 2024, 2025, and 2024–2025. For the total number of *P. ponderosa* ≥12.7 cm dbh killed by *D. barberi*, we included tree dbh as an explanatory variable and tested for an interaction between treatment and dbh.

Results

Flight Activity

A total of 8,873 *D. barberi* were captured. *D. barberi* were active during all months; however, only a few beetles were captured from late December to early March (Fig. 2). Peaks in flight activity occurred from June to August and from October to November.

Trapping Assays

A total of 82 *D. barberi* (48 females, 34 males) were captured from 16 to 23 April, and 1,265 *D. barberi* (811 females, 454 males) were captured from 2 to 9 October 2024. The final model for the April assay retained trapping location and treatment as significant explanatory variables for total *D. barberi*, female *D. barberi*, and male *D. barberi*. Although trapping location was significant, a lack of significant interaction between trapping location and treatment suggested that the location influence was spread similarly between treatments. VPL and VPH inhibited attraction of total *D. barberi* (both z ratios ≥ 4.27 , $P < 0.01$), female *D. barberi* (both z ratios ≥ 4.33 , $P < 0.01$), and male *D. barberi* (both z ratios ≥ 3.42 , $P < 0.01$) compared to the control during the April assay (Fig. 3). Mean trap captures did not differ between VPL and VPH for total *D. barberi* (z ratio = -0.51 , $P = 0.86$), female *D. barberi* (z ratio = 0.001 , $P = 1.0$), or male *D. barberi* (z ratio = 0.004 , $P = 1.0$) (Fig. 3).

Final model selection for the October assay only retained treatment as an explanatory variable. VPL and VPH inhibited attraction of total *D. barberi* (both z ratios ≥ 11.84 , $P < 0.01$), female *D. barberi* (both z ratios ≥ 10.65 , $P < 0.01$), and male *D. barberi* (both z ratios ≥ 9.74 , $P < 0.01$) compared to the control (Fig. 4). Higher levels of inhibition were observed for VPH than VPL for total *D. barberi* (z ratio = 4.21 , $P < 0.01$) and female *D. barberi* (z ratio = 3.83 , $P < 0.01$) during the October assay, but not for males (Fig. 4). Total captures were reduced by 97.3% and 98.7% in the April assay and 96.2% and 99.5% in the October assay by VPL and VPH, respectively.

Zone-of-Inhibition Assay

A total of 35,314 *D. barberi* were captured from 7 to 17 October 2025. Distance, trapping location, and bearing were retained as fixed effects in both the VPL and VPH models, and no interactions among these variables were significant in either model. Trapping location (ie the treated *P. ponderosa* and associated trapping array) was significant in both models ($\chi^2 = 11.52$, $P < 0.01$ for VPL; $\chi^2 = 50.0$, $P < 0.01$ for VPH), while bearing was not significant in either model. No significant differences were observed among distances for VPL (range = 110.5 ± 13.7 *D. barberi* per trap per day at 12 m to 176.2 ± 31.1 at 1.5 m; mean $\pm$ SEM). For VPH, significant reductions in captures occurred at 1.5 m (z ratio = 8.41 , $P < 0.01$), 3 m (z ratio = 6.80 , $P < 0.01$), and 6 m (z ratio = 3.73 , $P < 0.01$) compared to 12 m (Fig. 5). Maximum inhibition (defined as the farthest distance that the highest levels of inhibition occurred) was observed to 3 m (Fig. 5). All *P. ponderosa* treated with VPL and 1 *P. ponderosa* treated with VPH were attacked by *D. barberi* prior to the start of the assay on 7 October 2025. The dates of attack were undetermined but may have begun days earlier based on the presence of natural enemies of *D. barberi* on the tree bole.

Tree Protection Study

In 2024, no *P. ponderosa* were colonized or killed by *D. barberi* on plots treated with VPH, while 8 *P. ponderosa* were colonized and 6 were killed on control plots. No significant differences were observed between treatments in 2024 ($z = 0.01$, $P = 0.99$ for both colonized and killed) (Table 3). In 2025, during the second evaluation of the study, 46 *P. ponderosa* were colonized and 45 were killed by *D. barberi* on plots treated with VPH and 84 *P. ponderosa* were colonized and 80 were killed on control plots. Fewer *P. ponderosa* were colonized ($z = -4.53$, $P < 0.01$) and killed ($z = -4.22$, $P < 0.01$) by *D. barberi* on VPH than the control in 2025 (Table 3). Cumulatively

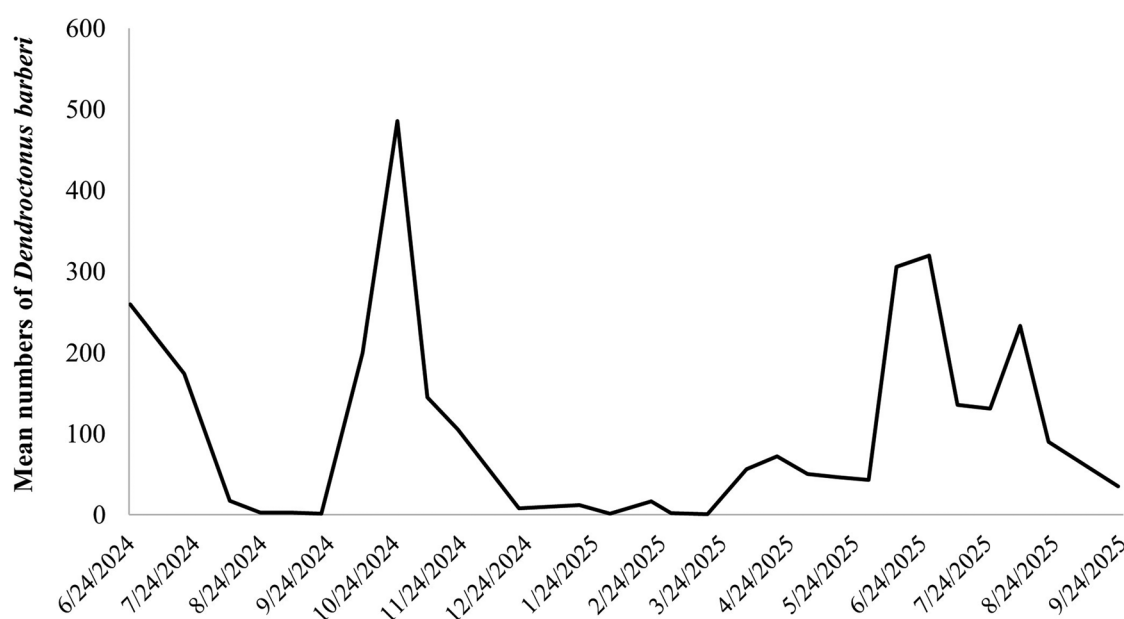


Fig. 2. Mean numbers of *Dendroctonus barberi* captured in 3 12-unit, multiple-funnel traps baited with a *D. barberi* lure (Product #3151, Synergy Semiochemical Corp., Delta, BC, Canada), Davis Mountains Preserve, Texas, 24 June 2024 to 3 October 2025.

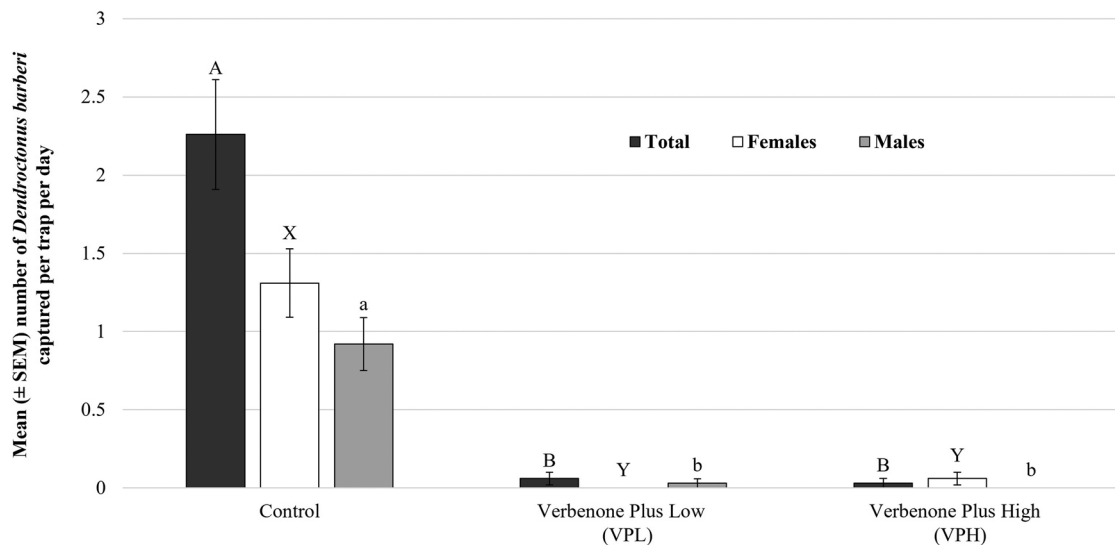


Fig. 3. Mean ($\pm$ SEM) numbers of total *Dendroctonus barberi*, female *D. barberi*, and male *D. barberi* captured per trap per day in 12-unit, multiple-funnel traps baited with a *D. barberi* lure (Product #3151, Synergy Semiochemical Corp., Delta, BC, Canada), Davis Mountains Preserve, Texas, 16 to 23 April 2024. Control = lure only; VPL = 35 g of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol; VPH = 70 g of SPLAT Verb, acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol. Different letters among bars of the same color indicate significantly different means ($\alpha = 0.05$) based on negative binomial generalized linear modeling and least squares means comparisons with a Tukey's correction.

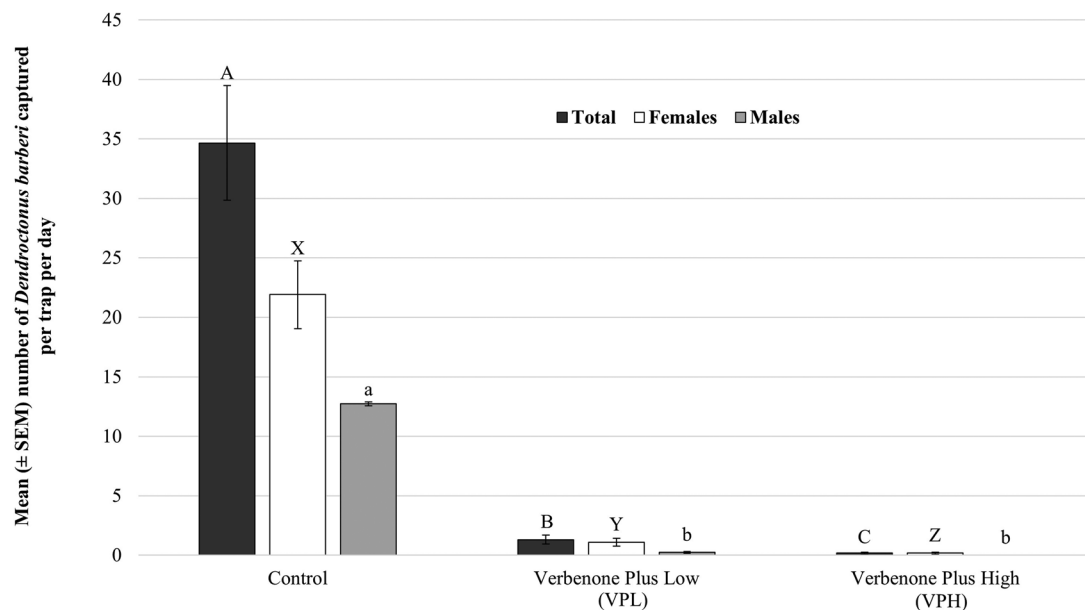


Fig. 4. Mean ($\pm$ SEM) numbers of total *Dendroctonus barberi*, female *D. barberi*, and male *D. barberi* captured per trap per day in 12-unit, multiple-funnel traps baited with a *D. barberi* lure (Product #3151, Synergy Semiochemical Corp., Delta, BC, Canada), Davis Mountains Preserve, Texas, 2 to 9 October 2024. Control = lure only; VPL = 35 g of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol; VPH = 70 g of SPLAT Verb, acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol. Different letters among bars of the same color indicate significantly different means ($\alpha = 0.05$) based on negative binomial generalized linear modeling and least squares means comparisons with a Tukey's correction.

(2024–2025), fewer *P. ponderosa* were colonized ($z = -4.86$, $P < 0.01$) and killed ($z = -4.99$, $P < 0.01$) by *D. barberi* on VPH than the control (Table 3). The final logistic regression for total mortality retained both treatment and dbh, both of which were significant. Larger dbh *P. ponderosa* were more likely to be killed by *D. barberi* ($z = 5.06$, $P < 0.01$) (Fig. 6). There was no interaction between treatment and dbh.

Discussion

Selection of Verbenone Plus was based on *D. barberi* being closely related to *D. brevicornis*, years of study of electroantennogram and behavioral responses of *D. brevicornis* to verbenone, nonhost volatiles, and Verbenone Plus (see Fetting et al. 2023 for review), and the immediate need to address *P. ponderosa* mortality attributed to *D. barberi* at the Davis

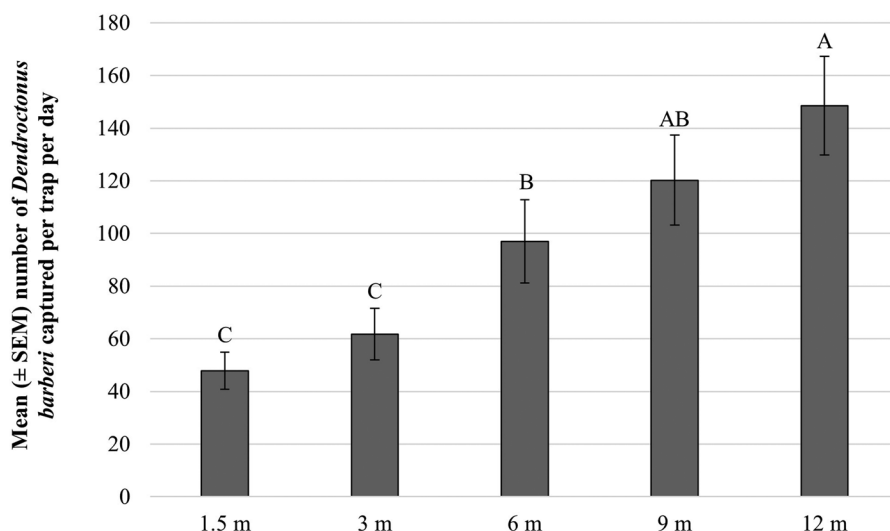


Fig. 5. Mean ($\pm$ SEM) numbers of *Dendroctonus barberi* captured in 12-unit, multiple-funnel traps baited with a *D. barberi* lure (Product #3151, Synergy Semiochemical Corp., Delta, BC, Canada) during the zone-of-inhibition assay, Davis Mountains Preserve, Texas, 7 to 17 October 2025. Trapping arrays consisted of 25 stations with stations at 1.5, 3, 6, 9, and 12 m along each of 5 bearings surrounding a *Pinus ponderosa* treated with 70 g of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol (VPH). Different letters among bars indicate significantly different means ($\alpha = 0.05$) based on negative binomial generalized linear modeling and least squares means comparisons with a Tukey's correction.

Table 3. Mean ($\pm$ SEM) percent of *Pinus ponderosa* colonized and killed by *Dendroctonus barberi* in the tree protection study, Davis Mountains Preserve, Texas, 2024–2025

Treatment ^a	2024 Colonized ^b	2024 Killed ^c	2025 Colonized ^b	2025 Killed ^c	2024–2025 Colonized ^b	2024–2025 Killed ^c
Control	4.9 $\pm$ 1.2% a	3.7 $\pm$ 1.5% a	53.2 $\pm$ 4.0% a	50.6 $\pm$ 4.0% a	54.9 $\pm$ 3.9% a	52.4 $\pm$ 3.9% a
Verbenone Plus	0.0 $\pm$ 0.0% a	0.0 $\pm$ 0.0% a	28.0 $\pm$ 3.5% b	27.4 $\pm$ 2.1% b	28.0 $\pm$ 3.5% B	27.4 $\pm$ 3.5% b

Different letters within a column indicate significant differences ($\alpha = 0.05$).

^aVerbenone Plus = 70 g of SPLAT Verb (10% (–)-verbenone by weight; EPA Reg. No. 80286-20, ISCA Inc., Riverside, California, United States), acetophenone, and (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol (VPH) applied twice in 2024 and 2025. Plots were not baited due to concerns regarding levels of tree mortality at the Davis Mountains Preserve.

^bPercent of *P. ponderosa* ≥ 12.7 cm dbh with evidence of *Dendroctonus barberi* colonization but no crown fade.

^cPercent of *P. ponderosa* ≥ 12.7 cm dbh with evidence of *Dendroctonus barberi* colonization and presence of crown fade.

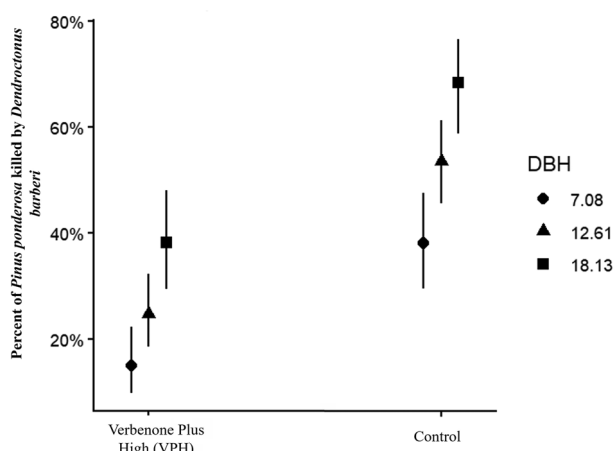


Fig. 6. Predicted mean ($\pm$ SEM) percent of *Pinus ponderosa* killed by *Dendroctonus barberi* by treatment (Verbenone Plus High [VPH], control) and diameter at breast height (dbh, 1.37 m in height) based on fitted logistic regression of the total numbers of *P. ponderosa* killed by *D. barberi* during the tree protection study at the Davis Mountains Preserve, Texas, 2024–2025. Results indicate that dbh is positively correlated with *P. ponderosa* mortality irrespective of treatment.

Mountains Preserve. We've demonstrated that VPL and VPH inhibit attraction of *D. barberi* to baited traps (Figs. 3–5), that maximum inhibition of VPH occurs to 3 m (Fig. 5), and that VPH protects *P. ponderosa* from mortality attributed to *D. barberi* (Table 3, Fig. 6). While comparisons with other published data are tenuous due to differences in formulations and releases of attractants and inhibitors (among other factors, see Dodds et al. 2024 for review), the levels of inhibition observed in our assays (range = 96.2 to 99.5%) are higher than reported for Verbenone Plus and *D. brevicomis*. For example, Fettig et al. (2012a) studied the responses of *D. brevicomis* to various combinations of (–)-verbenone and nonhost volatiles in baited traps in 8 assays over a 4-year period in *P. ponderosa* forests in California, United States. A total of 88,942 *D. brevicomis* were captured. Among inhibitors, Verbenone Plus had the strongest inhibitory effect (89.2%, Fettig et al. 2012a). A rule of thumb is that a > 90% reduction in attraction is desired before selecting an inhibitor for inclusion in tree protection studies (Audley et al. 2025). To that end, Fettig et al. (2005) reported low (4 mg/d) and high releases (50 mg/d) of (–)-verbenone inhibited attraction of *D. brevicomis* to baited traps by only 35.5 to 48.2%. It is therefore not surprising that verbenone alone is ineffective for protecting *P. ponderosa* from *D. brevicomis*.

Given the high levels of inhibition observed for VPL and VPH in our trapping assays, verbenone alone might be considered in future experiments. We did not evaluate verbenone alone given time and resource constraints and our goal of protecting some *P. ponderosa* at the Davis Mountains Preserve. Verbenone is produced by several pathways in bark beetle-host systems, including auto-oxidation of α -pinene via the intermediary compounds *cis*- and *trans*-verbenol (Hunt et al. 1989), by beetles themselves (Byers et al. 1984), and by degradation of host materials by microorganisms often associated with bark beetles (Leufvén et al. 1984, Hunt and Borden 1990, Lindgren et al. 1996). Verbenone has been evaluated for mitigating conifer mortality due to bark beetles in North America, Europe, and Asia (Frühbrodt et al. 2024). Several formulations of verbenone are registered by regulatory agencies for tree protection in the United States and Canada. Combining verbenone with nonhost volatiles, such as acetophenone and (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, often yields increased levels of inhibition compared to verbenone alone (Zhang and Schlyter 2004, Huber et al. 2021).

Maximum inhibition of *D. barberi* to VPH was constant to 3 m, with a statistically significant reduction in inhibition occurring between 3 m and 6 m (Fig. 5). These data are similar to those reported for verbenone and other bark beetle species. For example, the maximum range of inhibition provided by (–)-verbenone was statistically constant to 2 m for *D. brevicomis* in *P. ponderosa* forests in California (Fettig et al. 2009a), ≤ 4 m for *D. ponderosae* in *P. contorta* forests in British Columbia, Canada (Miller 2002) and Utah (Fettig et al. 2015), and 6 m for European spruce beetle, *I. typographus* (L.), in Norway spruce, *Picea abies* (L.) H. Karst (Pinales: Pinaceae), forests in Germany (Löcken et al. 2024). A conservative estimate of the maximum zone of inhibition provided by VPH for *D. barberi* is $\sim 30 \text{ m}^2$ (based on radius = 3 m), suggesting that achieving area-wide protection across a 0.41-ha plot would require approximately 140 release points. Assuming a radius of 4.5 m (ie the midpoint between 3 and 6 m, Fig. 5), ~ 64 release points would be required per 0.41 ha. Alternatively, in areas of low *P. ponderosa* density, treating individual *P. ponderosa* may be most appropriate. All *P. ponderosa* treated with VPL and 1 treated with VPH were attacked by *D. barberi* prior to the start of the zone-of-inhibition assay on 7 October 2025, which likely had confounding effects. For example, levels of attraction to traps nearest *P. ponderosa* colonized by *D. barberi* (1.5 m) were likely higher due to higher releases of host volatiles (due to wounding of the tree from the *D. barberi* attacks) and perhaps aggregation pheromone components by *D. barberi*, depending on the timing of attacks. The zone-of-inhibition assay was conducted during October 2025, which coincided with a peak in *D. barberi* flight activity at the Davis Mountains Preserve (Fig. 2). While a fall flight peak is consistent with observations for related bark beetle species in some *P. ponderosa* forests (Fettig et al. 2004, Williams et al. 2008), flight periodicity and bark beetle density can vary seasonally in response to temperature, wind, and stand structure, all of which influence pheromone dispersal and bark beetle behavioral responses. Accordingly, the zone of inhibition results presented here represent an important first characterization of the zone of inhibition provided by VPH for *D. barberi*. Future work across seasons and stand conditions will further inform area-wide tree protection guidelines.

During the tree protection study, *P. ponderosa* mortality was limited in 2024 but increased substantially in 2025 (Table 3).

The high level of mortality observed in 2025 was unexpected, given that plots were not baited. Baiting is common to enhance attraction of bark beetles to experimental plots in order to challenge the treatments being evaluated (Fettig et al. 2023). Relatedly, we were concerned that without baiting, few *P. ponderosa* would be colonized and killed by *D. barberi*, limiting our ability to draw inference from the tree protection study. This was not the case. While VPH was effective for reducing *P. ponderosa* mortality (Table 3), we were surprised by the levels of mortality observed on some plots. For example, while 2 of 5 plots (Plots 5 and 10) treated with VPH experienced no mortality, 1 plot (Plot 1) lost 96.1% of *P. ponderosa* ($\geq 12.7 \text{ cm dbh}$). Plot 1 had the largest dbh *P. ponderosa* (Table 2). Larger dbh *P. ponderosa* were more likely to be killed by *D. barberi* in our study (Fig. 6), which agrees with the beetle's preference for colonizing *P. ponderosa* $> 30.5 \text{ cm dbh}$ (Massey 1961).

Given that *D. barberi* flight occurred year-round with a peak in the fall (Fig. 2), it may be advisable to include a third VPH application in late summer to early fall to ensure tree protection through the full duration of flight activity. Under laboratory conditions, the release of acetophenone from some pouches ceased after 67 d at 20 °C (C.J.F., unpublished data), which suggests that acetophenone pouches in the field ceased releasing by about mid-August. For comparison, the daily mean temperature for September 2025 at McDonald Observatory ($\sim 12 \text{ km E}$) was 18.9 °C. SPLAT Verb and the (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol pouch release for longer periods than the acetophenone pouch. Given the supplemental goal of protecting *P. ponderosa* from *D. barberi* at the Davis Mountains Preserve, we plan to retreat the surviving *P. ponderosa* on each VPH plot in late March 2026, mid-June 2026, and late August 2026.

Verbenone Plus has also been evaluated for protecting stands of whitebark pine, *P. albicaulis* Engelm., a threatened tree species in the United States and Canada, from mortality attributed to *D. ponderosae* in California (Fettig et al. 2012c). Significantly fewer *P. albicaulis* were killed by *D. ponderosae* on Verbenone Plus-treated plots compared to the untreated control. Fettig and Munson (2020) evaluated the efficacy of verbenone alone and Verbenone Plus for protecting individual lodgepole pine, *Pinus contorta* Dougl. ex Loud., and stands of *P. contorta* from mortality attributed to *D. ponderosae* in Utah. Both verbenone and Verbenone Plus were effective, but no difference was observed between treatments. Furthermore, verbenone alone and Verbenone Plus provided similar levels of inhibition for pine engraver, *I. pini* (Say), in baited traps in *P. ponderosa* forests in Arizona (Gaylord et al. 2023). The inhibitory effect of verbenone alone on *D. ponderosae* is well studied (Progar et al. 2014) and is higher than the inhibitory effect of verbenone alone on *D. brevicomis* (Fettig et al. 2005), which likely explains why the addition of nonhost volatiles to verbenone does not confer additional tree protection from *D. ponderosae* like it does from *D. brevicomis*. For example, Borden et al. (2004) reported that low releases of (–)-verbenone (1.8 mg/d) inhibited attraction of *D. ponderosae* to baited traps by $> 97\%$ in *P. contorta* forests in British Columbia. Of note, unlike *D. ponderosae* studies in *P. albicaulis*, *P. contorta*, and sugar pine, *P. lambertiana* Dougl., verbenone alone is not effective for protecting *P. ponderosa* from *D. ponderosae* (Negrón et al. 2006, Fettig et al. 2016). An outbreak of *D. ponderosae* is ongoing in *P. ponderosa* forests in Colorado, and a task force has been established to

address the outbreak (State of Colorado 2025). To our knowledge, Verbenone Plus has not been evaluated for protecting *P. ponderosa* from *D. ponderosae* but warrants consideration.

Verbenone Plus has yet to be commercialized due, in part, to inhibitors requiring registration with the US Environmental Protection Agency and the Health Canada Pest Management Regulatory Agency. Furthermore, Verbenone Plus addresses the needs of a relatively small market. Efforts to develop Verbenone Plus as a more generalized bark beetle inhibitor have been met with limited success (eg Fettig and Munson 2020, Gaylord et al. 2023). Our efforts extend results for Verbenone Plus from *D. brevicomis* to *D. barberi* (Figs. 3–5, Table 3). Continued research and commercialization of Verbenone Plus would give natural resource managers a much needed tool to limit *P. ponderosa* losses to bark beetles.

Acknowledgements

We thank R. Edmonson, K. Flocke, L. Haldeman, E. Law, M. Mahurin, L. McMillan, E. Nyawo, K. Peterson, and C. Ybarra (Texas A&M Forest Service) and A.S. Munson (Forest Health Protection, USDA Forest Service, retired) for technical support. We extend a special thanks to our long-standing partners G. Crow, K. French, and C. Reemts (The Nature Conservancy) for logistic support and access to the study site. We thank B. Sullivan (Southern Research Station, USDA Forest Service) for his thoughtful discussions on the chemical ecology of *D. barberi* and 2 anonymous reviewers whose critiques improved earlier versions of this manuscript.

Author Contributions

Demian F. Gomez (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Jackson P. Audley (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Christopher J. Fettig (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Jayme Trainer (Data curation [equal], Investigation [equal], Writing—review & editing [equal]), Leif A. Mortenson (Data curation [equal], Investigation [equal], Writing—review & editing [equal]), Erin E. Davis (Data curation [equal], Investigation [equal], Writing—review & editing [equal]), Camille Wiseman (Data curation [equal], Investigation [equal], Writing—review & editing [equal]), and Agenor Mafrá-Neto (Funding acquisition [equal], Project administration [equal], Resources [equal], Writing—review & editing [equal])

Funding

Funding for this project was provided, in part, by a Collection Agreement between ISCA Inc. and the USDA Forest Service (25-CO-11272122-014 to C.J.F.) with in-kind contributions from ISCA Inc. and The Nature Conservancy. This article was written and prepared by US Government employees on official time, and it is, therefore, in the public domain and not subject to copyright. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

Conflicts of Interest

None declared.

References

- Audley JP, Fettig CJ, Moan JE, et al. 2025. “No vacancy”: masking spruce trees from spruce beetles with semiochemicals on the Kenai Peninsula. *Alaska Entomol. Soc. Newsletter* 17:16–23. <http://www.akentsoc.org/newsletter.php>
- Bolker BM. 2015. Linear and generalized linear mixed models. In: Fox GA, Negrete-Yankelevich S, Sosa VJ, editors. *Ecological statistics: contemporary theory and application*, Chapter 13. Oxford University Press. p. 309–333. <https://doi.org/10.1093/acprof:oso/9780199672547.001.0001>
- Borden JH, Pureswaran DS, Poirier LM. 2004. Evaluation of two repellent semiochemicals for disruption of attack by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *J. Entomol. Soc. B. C.* 101:117–123.
- Byers JA, Wood DL, Craig J, et al. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. *J. Chem. Ecol.* 10:861–877. <https://doi.org/10.1007/BF00987969>
- Dodds KJ, Sweeney J, Francese JA, et al. 2024. Factors affecting catches of bark beetles and woodboring beetles in traps. *J. Pest. Sci.* 97:1767–1793. <https://doi.org/10.1007/s10340-024-01774-1>
- Fettig CJ, Audley JP, Homicz CS, et al. 2023. Applied chemical ecology of the western pine beetle, an important pest of ponderosa pine. *Forests* 14:757. <https://doi.org/10.3390/f14040757>
- Fettig CJ, Bulaon BM, Dabney CP, et al. 2012c. Verbenone Plus reduces levels of tree mortality attributed to mountain pine beetle infestations in whitebark pine, a tree species of concern. *J. Biofert. Biopest.* 3:1–5. <https://doi.org/10.4172/2155-6202.1000123>
- Fettig CJ, McKelvey SR, Borys RR, et al. 2009a. Efficacy of verbenone for protecting ponderosa pine stands from western pine beetle (Coleoptera: Curculionidae, Scolytinae) attack in California. *J. Econ. Entomol.* 102:1846–1858. <https://doi.org/10.1603/029.102.0515>
- Fettig CJ, McKelvey SR, Dabney CP, et al. 2009b. Response of western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Curculionidae), to different release rates of nonhost angiosperm volatiles and verbenone. *J. Appl. Ent.* 133:143–154. <https://doi.org/10.1111/j.1439-0418.2008.01317.x>
- Fettig CJ, McKelvey SR, Dabney CP, et al. 2012a. Responses of *Dendroctonus brevicomis* (Coleoptera: Curculionidae) in behavioral assays: implications to development of a semiochemical-based tool for tree protection. *J. Econ. Entomol.* 105:149–160. <https://doi.org/10.1603/EC11121>
- Fettig CJ, McKelvey SR, Dabney CP, et al. 2012b. Efficacy of “Verbenone Plus” for protecting ponderosa pine trees and stands from *Dendroctonus brevicomis* (Coleoptera: Curculionidae) attack in British Columbia and California. *J. Econ. Entomol.* 105:668–1680. <https://doi.org/10.1603/EC12184>

- Fettig CJ, McKelvey SR, Huber DPW. 2005. Nonhost angiosperm volatiles and verbenone disrupt response of western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to attractant-baited traps. *J. Econ. Entomol.* 98:2041–2048. <https://doi.org/10.1093/jee/98.6.2041>
- Fettig CJ, Munson AS. 2020. Efficacy of verbenone and a blend of verbenone and nonhost volatiles for protecting lodgepole pine from mountain pine beetle (Coleoptera: Curculionidae). *Agric. For. Entomol.* 22:373–378. <https://doi.org/10.1111/afe.12392>
- Fettig CJ, Munson AS, Reinke M, et al. 2015. A novel semiochemical tool for protecting lodgepole pine from mortality attributed to mountain pine beetle (Coleoptera: Curculionidae). *J. Econ. Entomol.* 108:173–182. <https://doi.org/10.1093/jee/tou038>
- Fettig CJ, Shea PJ, Borys RR. 2004. Seasonal flight patterns of four bark beetle species (Coleoptera: Scolytidae) along a latitudinal gradient in California. *Pan-Pac. Entomol.* 80:4–17.
- Fettig CJ, Steed BE, Bulaon BM, et al. 2016. The efficacy of SPLAT® Verb for protecting individual *Pinus contorta*, *Pinus ponderosa*, and *Pinus lambertiana* from colonization by *Dendroctonus ponderosae*. *J. Entomol. Soc. B. C.* 113:11–20.
- Fettig CJ, Steed BE, Munson AS, et al. 2020. Evaluating doses of SPLAT® Verb to protect lodgepole pine trees and stands from mountain pine beetle. *Crop Prot.* 136:105228. <https://doi.org/10.1016/j.cropro.2020.105228>
- Frühbrodt T, Schebeck M, Andersson MN, et al. 2024. Verbenone - the universal bark beetle repellent? Its origin, effects, and ecological roles. *J. Pest. Sci.* 97:35–71. <https://doi.org/10.1007/s10340-023-01635-3>
- Gaylord MA, Audley JP, McMillin JD, et al. 2023. Acetophenone and green leaf volatiles do not enhance the efficacy of verbenone for inhibiting attraction of *Ips pini* (Coleoptera: Curculionidae) to pheromone-baited traps in northern Arizona. *J. Econ. Entomol.* 116:32–26. <https://doi.org/10.1093/jee/toad016>
- Gillette NE, Stein JD, Owen DR, et al. 2006. Verbenone-releasing flakes protect individual *Pinus contorta* trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). *Agric. For. Entomol.* 8:243–251. <https://doi.org/10.1111/j.1461-9563.2006.00303.x>
- Gomez DF, Audley JP, Fettig CJ. 2025. Southwestern pine beetle. *Forest Insect and Disease Leaflet FIDL-192*. U.S. Department of Agriculture, Forest Service. 12 p. <https://www.fs.usda.gov/foresthealth/docs/fidls/FIDL-192-SouthwesternPineBeetle.pdf>
- Hopkins AD. 1909. Contributions toward a monograph of scolytid beetles. I. The genus *Dendroctonus*. *U.S. Department of Agriculture, Bureau of Entomology, Technical Service Bulletin* 17.
- Huber DPW, Fettig CJ, Borden JH. 2021. Disruption of coniferophagous bark beetle (Coleoptera: Curculionidae: Scolytinae) mass attack using angiosperm nonhost volatiles: from concept to operational use. *Can. Entomol.* 153:19–35. <https://doi.org/10.4039/tce.2020.63>
- Hunt DWA, Borden JH. 1990. Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 16:1385–1397. <https://doi.org/10.1007/BF01021034>
- Hunt DWA, Borden JH, Lindgren BS, et al. 1989. The role of autoxidation of α -pinene in the production of pheromones of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. J. For. Res.* 19:1275–1282. <https://doi.org/10.1139/x89-194>
- Leufvén AG, Bergström G, Falsen E. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *J. Chem. Ecol.* 10:1349–1361. <https://doi.org/10.1007/BF00988116>
- Lindgren BS. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *Can. Entomol.* 115:299–302. <https://doi.org/10.4039/Ent115299-3>
- Lindgren BS, Nordlander G, Birgersson G. 1996. Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). *J. Appl. Ent.* 120:397–403. <https://doi.org/10.1111/j.1439-0418.1996.tb01627.x>
- Löcken H, Frühbrodt T, Du B, et al. 2024. Potential applicability of SPLAT® Verb for management of European spruce bark beetle, *Ips typographus* (L.). *J. Appl. Ent.* 148:1157–1171. <https://doi.org/10.1111/jen.13336>
- Lyon RL. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. *Can. Entomol.* 90:582–584. <https://doi.org/10.4039/ent90582-10>
- Massey CL. 1961. Biology of the southwestern pine beetle, *Dendroctonus barberi*. *Ann. Entomol. Soc. Am.* 54:354–359. <https://doi.org/10.1093/aesa/54.3.354>
- Miller DR. 2002. Short-range horizontal disruption by verbenone in attraction of mountain pine beetle (Coleoptera: Scolytidae) to pheromone-baited funnel traps in stands of lodgepole pine. *J. Entomol. Soc. B. C.* 99:103–105.
- Negrón JF, Allen K, McMillin J, et al. 2006. Testing verbenone for reducing mountain pine beetle attacks in ponderosa pine in the Black Hills, South Dakota. *Res. Note RMRS-RN-31*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 7 p. <https://doi.org/10.2737/RMRS-RN-31>
- Progar RA, Gillette N, Fettig CJ, et al. 2014. Applied chemical ecology of the mountain pine beetle. *For. Sci.* 60:414–433. <https://doi.org/10.5849/forsci.13-010>
- Pureswaran DS, Hofstetter RW, Sullivan BT, et al. 2016. Western pine beetle populations in Arizona and California differ in the composition of their aggregation pheromones. *J. Chem. Ecol.* 42:404–413. <https://doi.org/10.1007/s10886-016-0696-9>
- R Core Team. 2020. R: A language and environment for statistical computing. R Core Team. <http://R-project.org/>
- State of Colorado. 2025. Executive Order B 2025 001 - Protecting Front Range communities and forests through creation of the Ponderosa Mountain Pine Beetle Task Force. <https://drive.google.com/file/d/1TY0Ryt8R-wrhequ-Ad7IEWf7Y87V8DM7/view>
- Sullivan BT. 2024. Composition of attractant semiochemicals of North American species of *Dendroctonus* bark beetles: a review. *Forests* 15:642. <https://doi.org/10.3390/f15040642>
- Sullivan BT, Grady AM, Hofstetter RW, et al. 2021. Evidence for semiochemical divergence between sibling bark beetle species: *Dendroctonus brevicomis* and *Dendroctonus barberi*. *J. Chem. Ecol.* 47:10–27. <https://doi.org/10.1007/s10886-020-01233-y>
- Texas A&M Forest Service. 2025. Operation Ponderosa. <https://tfsweb.tamu.edu/forest-land/texas-forests/forest-restoration-projects/operation-ponderosa/>
- The Nature Conservancy. 2025. Places we protect: The Davis Mountains Preserve, Texas. https://www.nature.org/en-us/get-involved/how-to-help/places-we-protect/davis-mountains-preserve/?en_txn1=bl.ch_tx.eg.x.g
- Valerio-Mendoza O, Armendáriz-Toledano F, Cuéllar-Rodríguez G, et al. 2017. The current status of the distribution range of the western pine beetle, *Dendroctonus brevicomis* (Curculionidae: Scolytinae) in northern Mexico. *J. Insect Sci.* 17:92. <https://doi.org/10.1093/jisesa/ix070>
- Valerio-Mendoza O, García-Román J, Becerril M, et al. 2019. Cryptic species discrimination in western pine beetle, *Dendroctonus brevicomis* LeConte (Curculionidae: Scolytinae), based on morphological characters and geometric morphometrics. *Insects* 10:377. <https://doi.org/10.3390/insects10110377>
- Vickers LA, Houser J, Rooni J, 2018. Restoring ponderosa pine in the Davis Mountains of West Texas: impacts of planting practices on seedling survival. In: Kirschman JE, compiler. *Proceedings of the 19th Biennial Southern Silvicultural Research Conference. Gen. Tech Rep. SRS-GTR-234*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. p. 82–88. https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs234/gtr_srs234-13.pdf
- Vickers LA, Houser J, Rooni J, et al. 2019. Some lessons learned on early survival and growth of containerized, locally-sourced ponderosa pine seedlings in the Davis Mountains of Western Texas, US. *Forests* 10:267. <https://doi.org/10.3390/f10030267>
- Williams KK, McMillin JD, DeGomez TE, et al. 2008. Influence of elevation on bark beetle (Coleoptera: Curculionidae, Scolytinae)

- community structure and flight periodicity in ponderosa pine forests of Arizona. *Environ. Entomol.* 37:94–109. [https://doi.org/10.1603/0046-225X\(2008\)37\[94:IOEOBB\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2008)37[94:IOEOBB]2.0.CO;2)
- Wood SL. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). *Great Basin Nat.* 23:1–117. <http://www.jstor.org/stable/41711083>
- Zhang QH, Schlyter F. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agric. For. Entomol.* 6:1–19. <https://doi.org/10.1111/j.1461-9555.2004.00202.x>
- Zuur A, Leno E, Walker N, et al. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag. <https://doi.org/10.1007/978-0-387-87458-6>