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Developing semiochemical repellents for protecting *Picea* from *Dendroctonus rufipennis* (Coleoptera: Curculionidae) in Alaska and Utah, USA

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Spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), is the most destructive pest of mature spruce (*Picea*) in western North America. Recent outbreaks in Alaska and other western US states highlight the need for tools to protect *Picea* from *D. rufipennis*. The primary antiaggregation pheromone of *D. rufipennis* (3-methylcyclohex-2-en-1-one, MCH) and various combinations of potential repellents (1-octen-3-ol, *exo*-brevicomin, *endo*-brevicomin, ipsdienol, ipsenol, limonene, and verbenone) were tested for their ability to disrupt the response of *D. rufipennis* to attractant-baited multiple-funnel traps. Two assays were conducted on the Kenai Peninsula, Alaska, in June and July 2021. All treatments significantly reduced the mean number of *D. rufipennis* caught compared to the baited control. No other significant differences were observed among treatments. Informed by these and other data, tree protection studies were established in Lutz spruce, *Picea* × *lutzii*, on the Kenai Peninsula in 2022 and in Engelmann spruce, *Pi. engelmannii*, in the Uinta Mountains, Utah, in 2021. All experimental trees were baited with frontalin. Repellent treatments included MCH (SPLAT MCH, ISCA Inc., Riverside, CA, USA) and at least 1 additional repellent combination. In Alaska, all treatments significantly reduced colonization (strip attacks + mass attacks) and mortality of individually treated *Pi.* × *lutzii* and all *Picea* within 11.3-m radius of each treated *Pi.* × *lutzii* compared to the control. In Utah, all treatments except for SPLAT MCH + octenol significantly reduced colonization compared to the control. Only SPLAT MCH + *Acer* kairomone blend (AKB) and SPLAT MCH + octenol reduced *Pi. engelmannii* mortality compared to the control. SPLAT MCH + AKB and SPLAT MCH + acetophenone and green leaf volatiles (PLUS) were the most effective across both studies. The implications of these and other results to the development of an effective semiochemical repellent for *D. rufipennis* are discussed.

Key words: 3-methylcyclohex-2-en-1-one, *Picea engelmannii*, *Picea* × *lutzii*, spruce beetle, tree protection

Introduction

Spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), is an irruptive species of bark beetle endemic to North America (Furness and Carolin 1977, Bleiker and Safranyik 2021). *Dendroctonus rufipennis* exists across much of the continent, adhering to the ranges of host spruce trees, *Picea* spp. All species of *Picea*, and known hybrids, native to North America are potential hosts; however, *D. rufipennis* displays regional preferences. For example, white spruce, *Picea glauca* (Moench) Voss, Sitka spruce, *Pi. sitchensis* (Bong.) Carr., and their hybrid Lutz spruce, *Pi.* × *lutzii* Little, are common hosts in Alaska (Werner et al. 1977), yet outbreaks occur most commonly in *Pi.* × *lutzii* (Holsten and Werner

1990). In the Rockies, *D. rufipennis* commonly attacks Engelmann spruce, *Pi. engelmannii* Parry ex. Engelm., but seldomly blue spruce, *Pi. pungens* Engelm. (Ott et al. 2021). Across the range, *D. rufipennis* prefers recently downed (e.g., windthrow) or acutely stressed, large-diameter, mature *Picea* (Jenkins et al. 2014, Bleiker and Safranyik 2021). Under the right conditions, populations can quickly erupt to outbreak levels and cause significant, landscape-level tree mortality, making *D. rufipennis* among the most significant forest insect pests in North America (Jenkins et al. 2014).

In recent decades, *D. rufipennis* outbreaks in western North America have occurred more frequently and have impacted larger areas than reported historically (Jenkins et al. 2014, Fettig et al. 2022) due, in part, to climate change (Domke et al. 2023). Climate change will likely exacerbate future *D. rufipennis* outbreaks as summer temperatures (Bentz et al. 2010) and droughts (Hart et al. 2014) increase. In fact, several western US states are experiencing significant outbreaks. In Southcentral Alaska,>750,000 ha have been impacted by *D. rufipennis* since 2016 (USDA Forest Service 2022). The Uinta Mountains in Utah continue to experience irruptive *D. rufipennis* populations (Utah Department of Natural Resources 2023). Colorado is also experiencing notable outbreaks, with ~21,600 ha impacted in 2021 alone (Colorado State Forest Service 2022).

Like many bark beetle species, *D. rufipennis* host searching and aggregation behaviors are primarily semiochemically driven (Jenkins et al. 2014, Keeling et al. 2021). Semiochemical interruption is a management strategy that targets and influences host colonization and aggregation behaviors in bark beetle systems (Silverstein 1981, Borden 1997, Progar et al. 2014, Seybold et al. 2018, Huber et al. 2021, Ross 2021). Most of the previous work investigating semiochemical interruption of *D. rufipennis* has focused solely on the primary antiaggregation pheromone 3-methycyclohex-2-en-1-one (MCH, Rudinsky et al. 1974) and has yielded mixed results (Seybold et al. 2018). In Wyoming, Audley et al. (2021) evaluated the efficacy of MCH for protecting *Pi engelmannii* from *D. rufipennis* in a proprietary release technology (SPLAT, 10.0% MCH by weight; ISCA Inc., Riverside, CA) alone and with 2 semiochemical combinations, *Acer* kairomone blend (AKB; linalool [47.5%], β-caryophyllene [42%], and (*Z*)-3-hexanol [10.5%] based on the work of Hansen et al., 2019, for *D. rufipennis*) or "Plus" (PLUS; acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol based on the work of Fettig et al., 2012, for western pine beetle, *D. brevicomis* LeConte). All repellent-treated trees had 35 or 70 g of SPLAT MCH applied. Four additional repellent treatments combined AKB or PLUS with each dose of SPLAT MCH. All repellents except the 2 doses of SPLAT MCH alone significantly reduced colonization of individually treated *Pi. engelmannii* compared to the baited control. All repellents significantly reduced the mortality of individually treated *Pi. engelmannii*, and colonization and mortality of neighboring *Pi. Engelmannii* compared to the baited control (Audley et al. 2021).

Despite these promising results, a similar study from 2019 was conducted in Denali State Park, Alaska, in *Pi. glauca* found that these repellents were ineffective (i.e., nearly 100% of repellent-treated trees were mass attacked; J.E.M. and C.J.F., unpublished data). Genetic work by Maroja et al. (2007) revealed 2 sympatric northern haplotypes of *D. rufipennis* (Alaska to Newfoundland), with a third geographically isolated haplotype in the Rocky Mountains (British Colombia to Arizona). This divergence may influence relevant semiochemistry among haplotypes (e.g., Pureswaran et al. 2016), perhaps influencing the efficacy of semiochemical repellents and requiring the development of different repellents for different regions (haplotypes).

The studies below represent continued efforts toward developing an effective semiochemical repellent for protecting *Picea* trees from *D. rufipennis*. To address the tree protection failure in Alaska in 2019, we implemented 2 trapping assays in Alaska to screen additional potential repellents for this northern haplotype. These and other data informed the design and implementation of tree protection studies in Alaska for the northern haplotype and in Utah for the Rocky Mountain haplotype. The overall objective was to identify a single repellent treatment that imparts high levels of inhibition sufficient to impart tree protection in both haplotypes.

Materials and Methods

Trapping Assays

Two separate trapping assays were conducted on a site between the Kenai River and Funny River Road near Soldotna, Alaska (60.484°N, 150.873°W, elev. 43 m). The first assay was in June 2021, coinciding with the primary peak *D. rufipennis* flight period, and the second was in July 2021, coinciding with a secondary flight period (Holsten and Hard 2001). An array of 21, 12-unit, multiple-funnel traps was established to test semiochemical combinations in a completely randomized design. Trap locations were spaced 30 m apart, and traps were randomly assigned to a location using a completely randomized design. All semiochemicals were hung from each trap on the brackets between the 6th and 7th funnels, and insecticide strips (Hot Shot No Pest Strips, 18.6% 2,2-dichlorovinyl dimethyl phosphate, Spectrum Brands Inc., Middleton, WI) were placed at the bottom of each collection cup. Traps were hung from ~3 m, metal conduit poles that were placed over rebar to facilitate efficient movements of traps during daily randomizations. Ten 0.041-ha circular plots (11.3-m radius) were created at randomly selected trapping locations (1 plot/station). Within each circular plot, all trees ≥12.7 cm dbh were identified and tallied to estimate stand characteristics and recent levels of tree mortality attributed to *D. rufipennis*.

Following the failure of the 2019 tree protection study in Alaska, 1-octen-3-ol (octenol), *exo*-brevicomin, *endo*-brevicomin, ipsdienol, ipsenol, limonene, and verbenone were evaluated as potential repellents. Pureswaran and Borden (2004) demonstrated reductions in *D. rufipennis* trap captures with octenol. *exo*-Brevicomin and *endo*-brevicomin are aggregation pheromones of *Dryocoetes affaber (Mannerhiem)* (Comacho et al. 1994), and ipsdienol and ipsenol are aggregation pheromones of *Ips perturbatus (Eichhoff)* (Holsten et al. 2000), among other bark beetles (Coleoptera: Curculionidae). Both *Dr. affaber* and *I. perturbatus* are sympatric competitors with *D. rufipennis* in Alaska. *exo*-Brevicomin, *endo*-brevicomin, and ipsdienol significantly reduced the number of *D. rufipennis* caught in multiple-funnel traps and *D. rufipennis* attack densities on felled *Pi.* × *lutzii* in Alaska (Werner and Holsten 2002). *exo*-Brevicomin, *endo*-brevicomin, ipsdienol, and ipsenol are all commercially available as trapping lures and were combined as a "Competitors Combo." Limonene and verbenone were selected based on antennal activity and repellent effects observed in several assays of closely related bark beetle species in North America (Pureswaran et al. 2000, Shepherd and Sullivan 2013).

During the June trapping assay, treatments included (i) *D. rufipennis* lure (SBL), (ii) SBL + SPLAT MCH (7.0 g MCH), (iii) SBL + SPLAT MCH + PLUS, (iv) SBL + SPLAT MCH + AKB; (v) SBL + SPLAT MCH + octenol, (vi) SBL + SPLAT MCH + Competitors Combo, and (vii) SBL + SPLAT MCH + limonene + verbenone (release rates and component sources can be found in Table 1). Each treatment was replicated 3 times. Trap catches were collected daily

and rerandomized 6 times (i.e., immediately following collection) for a total of 18 reps/treatment. Trapping was conducted on 3–9 June 2021.

Based on the results of the June assay (below), we augmented treatments in the July assay by dropping the Competitors Combo. As we sought to further improve trap catch reductions, we added octenol to all repellent treatments (including 2x octenol) as SBL + SPLAT MCH + octenol caught the fewest *D. rufipennis* during the June assay (although SBL + SPLAT MCH + octenol was not statistically different from other treatments except SBL, Fig. 1). The reasoning for a second trapping assay was 2-fold. First, we wanted to ensure we captured data from the second peak flight activity period of *D. rufipennis*, which occurred over several years (Holsten and Hard 2001). Second, we did not achieve any statistical separation among repellent treatments in the June assay and hypothesized the addition of octenol to previous combinations would further reduce trap catch reductions (Fig. 1). Treatments included (i) SBL, (ii) SBL + SPLAT MCH, (iii) SBL + SPLAT MCH + octenol, (iv) SBL + SPLAT MCH + PLUS + octenol, (v) SBL + SPLAT MCH + AKB + octenol, (vi) SBL + SPLAT MCH + 2x octenol,

Table 1. Semiochemicals applied in trapping assays and tree protection studies in Alaska and Utah

Treatment components	Semiochemicals	Release rates	Sources
Spruce beetle lure (SBL)	Frontalin	1.25 mg/day at 20 °C[a]	Synergy
	MCOL	3–5 mg/day at 25 °C[a]	Synergy
	Spruce terpenes	270 mg/day at 23.5 °C[a]	Synergy
Spruce beetle tree bait (SBB)	Frontalin	1.25 mg/day at 20 °C[a]	Synergy
SPLAT MCH (7 g a.i.)	3-Methylcyclohex-2-en-1-one	294 mg/day at 26 °C[b]	ISCA[c]
AKB	Linalool + β-caryophyllene + (*E*)-3-hexen-1-ol	60 mg/day at 23 °C[d]	ISCA
Acetopheonone	Acetophenone	103 mg/day at 20 °C[d]	ISCA
GLVs	(*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol	20 mg/day at 20 °C[d]	ISCA
Octenol	1-octen-3-ol	58 mg/day at 20 °C[d]	ISCA
Competitors combo	*exo*-Brevicomin + *endo*-brevicomin	5–10 mg/day at 30 °C[a]	Synergy
	Ipsenol + ipsdienol	0.6–0.8 mg/day at 25 °C[a]	Synergy
Limonene	*R*-(+)-limonene[e]	700 mg/day at 30 °C[f]	Sigma-Aldrich
Verbenone	*S*-(−)-verbenone	19 mg/day at 20 °C[d]	ISCA

[a]Release rate reported by Synergy Semiochemical Corp., Delta, BC, Canada.
[b]Foote et al. (2020).
[c]ISCA Inc., Riverside, CA, USA.
[d]Release rate determined gravimetrically in a fume hood in the laboratory.
[e]Product 183164 Sigma-Aldrich Inc., St. Louis, MO, USA.
[f]Fifteen-millileter limonene in 15-ml screw-cap polyethylene bottle, Audley et al. (2020).

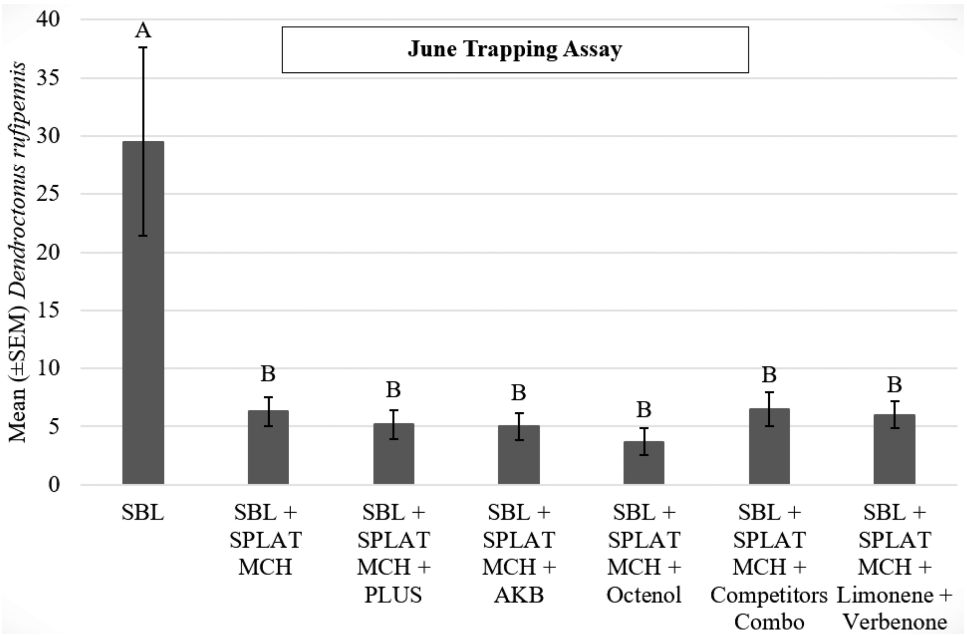

Fig. 1. Mean (± SEM) number of *Dendroctonus rufipennis* caught/day in 12-unit, multiple-funnel traps baited with an enhanced trapping lure (SBL = frontalin + MCOL + spruce terpenes; Product #3123, Synergy Semiochemical Corp., Delta, BC, Canada). Traps were deployed along the Kenai River near Soldotna, Alaska, 3–9 June 2021. Different letters indicate significantly different means ($\alpha = 0.05$) based on negative binomial generalized linear modeling and least squares means comparisons with a Bonferroni correction. SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; competitors combo = *exo*-brevicomin + *endo*-brevicomin + ipsdienol + ipsenol.

and (vii) SBL + SPLAT MCH + limonene + verbenone + octenol (Table 1). Each treatment was replicated 3 times. Trap catches were collected daily and rerandomized 5 times (i.e., immediately following collection) for a total of 15 reps/treatment. Trapping was conducted on 7–18 July 2021; however, cool temperatures (max. daily <14.5 °C; Holsten and Hard 2001) and rain precluded enough beetle catch (0–7 *D. rufipennis*/day) from 7 to 13 July. Only data collected from 14 to 18 July were used in our analyses.

Analyses were conducted using R Statistical Software (version 3.6.3) via RStudio (Version 1.2.5033, R Core Team 2020). Data were analyzed using generalized linear modeling with a negative binomial distribution with a log link (*lme4* package). Trap position and trap day were considered as covariates in the models. Post hoc least squares means with a Bonferroni correction were used to determine differences among treatments (*emmeans* package).

Tree Protection Studies

For our tree protection studies, we selected uncolonized *Picea* of a minimum diameter at breast height (dbh) of 20.3 cm for *Pi.* × *lutzii* in Alaska and 25.4 cm for *Pi. engelmannii* in Utah. The lower bole (~3 m) of each *Picea* was visually inspected for signs of attack by *D. rufipennis* and other bark beetles (i.e., pitch tubes and/or boring dust). If no evidence of attacks was found, each *Picea* was randomly assigned to a treatment group. All repellent-treated trees and control were baited with frontalin on the north face of the bole (Table 1). SPLAT MCH was applied as four 17.5-g dollops, 1 at each cardinal direction around the bole. All additional repellent compounds were stapled to the north face of the bole. All compounds were placed at ~2 m high on each tree. Treated trees were ≥30 m apart to reduce interference among semiochemicals. A 0.041-ha circular plot (11.3-m radius from the pith of the central, treated tree) was established following protocols by Foote et al. (2020). Every live tree (≥10.2 cm dbh in Alaska and ≥12.7 cm dbh in Utah) within the circular plot was measured and visually inspected for signs of *D. rufipennis* attack. Uncolonized trees had no evidence of *D. rufipennis* attacks; pitch-outs were trees that had 1 or more white pitch tubes (i.e., no boring dust and likely an unsuccessful attack); strip-attacked trees had evidence of successful attacks that encompassed <90% of the circumference of the bole; and mass-attacked trees had successful attacks on ≥90% of the circumference of the bole. Evidence of attacks included reddish pitch tubes (i.e., pitch tubes with frass) and/or frass at the base of the bole. Selected study sites had epidemic populations of *D. rufipennis* based on at least 2 clumps of 5 or more infested trees every 2 ha (Bentz and Munson 2000, Hansen et al. 2006).

Alaska.

This study was conducted southwest of Tern Lake in the Chugach National Forest, Alaska (60.527°N, 149.567°W –60.521°N, 149.601°W, elev. 175–258 m). 100 *Pi.* × *lutzii* ≥20.3 cm dbh were selected and randomly assigned to 1 of 5 treatments: (i) *D. rufipennis* bait (SBB), (ii) SBB + SPLAT MCH (7.0 g MCH.) + PLUS, (iii) SBB + SPLAT MCH + AKB, (iv) SBB + SPLAT MCH + octenol, and (v) SBB + SPLAT MCH + octenol + PLUS + AKB (All) (Table 1). Each treatment was replicated 20 times. Treatments were deployed on 20–21 May 2022 and assessments of *D. rufipennis* colonization were conducted on 16–18 August 2022 at which time all semiochemicals were removed. Final assessments of tree mortality assessment (based on crown fade) were made on 17–18 August 2023.

Utah.

This study was conducted near Hacking Lake in the Ashley National Forest, Utah (40.77°N, 109.80–109.81°W, elev. 3211–3257 m). One hundred and fifteen *Pi. engelmannii* of ≥25.4-cm dbh were selected and randomly assigned to 1 of 5 treatments: (i) *D. rufipennis* bait (SBB), (ii) SBB + SPLAT MCH (7.0 g MCH) + octenol, (iii) SBB + SPLAT MCH + PLUS, (iv) SBB + SPLAT MCH + AKB, and (v) SBB + SPLAT MCH + GLVs (Table 1). Each treatment was replicated 23 times. Treatments were deployed on 16–17 June 2021.

Due to some *Picea* being actively colonized by *D. rufipennis* during the installation of this study, 0.041-ha circular plots were only established around some experimental trees. A circular plot was established if at least 2 of the nearest 3 *Pi. engelmannii* were uncolonized by *D. rufipennis*. Only 47 (of 115) trees met this criterion. Following the initial assessment of *D. rufipennis* colonization on 28–29 September 2021 (at which time all semiochemicals were removed), we observed a few mass-attacked control trees and a decline in *Pi. engelmannii* mortality attributed to *D. rufipennis* across the study area. As such, we decided to retreat all *Pi. engelmannii* assigned to repellent treatments on 1–2 June 2022 in hopes that additional attacks on control trees would continue in 2022. Baits were not applied in 2022 under the assumption that trees would be sufficiently challenged by *D. rufipennis* without baiting. Reassessment of treated trees and plot trees was made on 27–28 August 2022, and a final assessment of mortality (based on crown fade) was made on 29–30 July 2023.

Statistical analyses.

Analyses were conducted using R Statistical Software (version 3.6.3) via RStudio (Version 1.2.5033, R Core Team 2020) on proportions of *Picea*, with data presented as percentages for reader clarity. The efficacy of repellents was determined by comparing *Picea* colonization (strip attacks + mass attacks) and mortality to the baited controls. Pairwise, 2-sample tests for equality of proportions (prop.test, base package) were used for comparisons among experimental trees. For the Utah study, we compared colonization activity among treatments for the first year and changed from year 1 to year 2 within and among treatments in the second year. Mean proportions of *Picea* on the plots were compared among treatments using a generalized linear model with a quasibinomial distribution with a log link (*lme4* package). Treatment, mean dbh, and mean percent *Picea* were considered as factors in each model. The final model selection was informed based on likelihood ratio tests (Zuur et al. 2009). Following model fit, differences among means were determined by least squares means (lsmeans) tests with a Tukey adjustment (emmeans package). Additional comparisons within the data were made using the nonparametric Kruskal–Wallis test (kruskal.test) and multiple means comparison (dunn.test) with a Bonferroni correction (stats package).

Results and Discussion

Trapping Assays

In 2019, live tree composition at our trapping site in Alaska (based on the number of trees and snags measured in 2021) was 71.2 ± 7.9% *Pi.* × *lutzii*, 22.3 ± 6.1% black spruce, *Pi. mariana* (Mill.) Britton, Sterns & Poggenb., and 6.2 ± 3.2% quaking aspen, *Populus tremuloides* Michx. In 2021, live tree composition was 54.3 ± 9.2% *Pi.* × *lutzii*, 28.5 ± 7.9% *Pi. mariana*, and 15.9 ± 6.9% *P. tremuloides* (all values, means ± SEMs). *Dendroctonus rufipennis* activity reduced the number of trees/ha by 71% (from 1529.7 ± 180.3 to 440 ± 116) and basal area by 82% (from 29.7 ± 1.2 to 5.4 ± 1.5 m^2/ha) between 2019 and 2021. About 83.8% of *Pi.* × *lutzii* were killed or mass attacked by *D. rufipennis* by 2021, suggesting significant *D. rufipennis* populations were present in the study area.

A total of 1,119 *D. rufipennis* (452 males, 667 females) were caught during the June assay. Adult beetles were sexed based on the appearance of the seventh abdominal tergite per Lyon (1958). The number of *D. rufipennis* caught per day varied widely, ranging from 6 to 420. All treatments significantly reduced the mean number of *D. rufipennis* caught compared to SBL (Fig. 1). No significant differences were observed among repellents; however, SBL + SPLAT MCH + octenol caught the fewest *D. rufipennis* and reduced trap catches by 87.5% compared to SBL. During the July assay, a total of 188 (57 males, 131 females) *D. rufipennis* were caught, ranging from 26 to 53 individuals per day. Once again, all repellent treatments significantly reduced trap catches compared to SBL; yet no differences were observed among repellent treatments (Fig. 2). All repellent treatments reduced the mean number of *D. rufipennis* caught by ≥94% compared to SBL.

The lack of statistical separation among repellent treatments may be a function of the relatively low numbers of *D. rufipennis* caught, especially during the July assay. Increasing the length of each assay may have yielded greater numbers of *D. rufipennis* and revealed variability among treatments. Based on the results of both trapping assays, we only included 1 additional repellent, octenol, in the tree protection studies as all other compounds/combinations performed similarly to octenol but included multiple compounds (Table 1; Figs. 1 and 2) conferring additional costs. The Competitors Combo, limonene, and verbenone may warrant additional investigation in future tree protection studies.

Tree Protection Studies

Alaska.

Live tree composition (based on the numbers of trees) was 29.7 ± 2.1% *Pi.* × *lutzii*, 0.01 ± 0.2% *Pi. mariana*, 39.0 ± 3.5% mountain hemlock, *Tsuga mertensiana* (Bong.) Carr., 23.1 ± 2.3% *Betula* spp., 3.9 ± % *Salix* spp., and 3.1 ± 1.0% *Populus* spp. with 888.1 ± 43.6 trees/ha and 38.0 ± 2.32 m²/ha of basal area. About 15.6% of *Picea* were colonized by *D. rufipennis* at the beginning of the study. Average dbh of treated *Pi.* × *lutzii* was 29.0 ± 0.8 cm and ranged from 20.3 to 59.2 cm. Average dbh differed slightly among treatments ($\chi^2 = 12.3$, df = 4, $P = 0.02$); however, a Dunn's test indicated no differences existed among any paired treatment groups. Additionally, we checked for similar numbers of trees on the plots surrounding our treatment trees, as tree density can impact bark beetle responses to semiochemicals. While the average number of trees per plot differed among treatments ($\chi^2 = 13.6$, df = 4, $P = 0.01$), a Dunn's test indicated only SBB + SPLAT MCH + All and SBB + SPLAT MCH + AKB were significantly different. This suggests that variation in tree densities had minimal, if any, effect on our results.

All repellent treatments significantly reduced *D. rufipennis* colonization (strip attacks + mass attacks; all $\chi^2 \geq 7.7$, df = 1, $P \leq 0.01$; Fig. 3) and mortality (all $\chi^2 \geq 14.7$, df = 1, $P \leq 0.01$; Fig. 4) of individually treated *Pi.* × *lutzii* compared to SBB. No other significant differences were observed among treatments. This result is similar to that of Audley et al. (2021) in Wyoming, where SPLAT MCH alone (of note, SPLAT MCH was not evaluated alone in the tree protection studies herein) applied at 35 g (3.5 g MCH) or 70 g (7.0 g MCH) was not sufficient to reduce *D. rufipennis* colonization of individually treated trees, but the addition of PLUS, AKB, and in this case octenol and all combinations was sufficient (Fig. 3). Among repellent treatments, the number of treated *Pi* × *lutzii* killed by *D. rufipennis* in our study ranged from 0 (SPLAT MCH + PLUS) to 2 (SPLAT MCH + octenol), while 15 SBB trees died (Fig. 4).

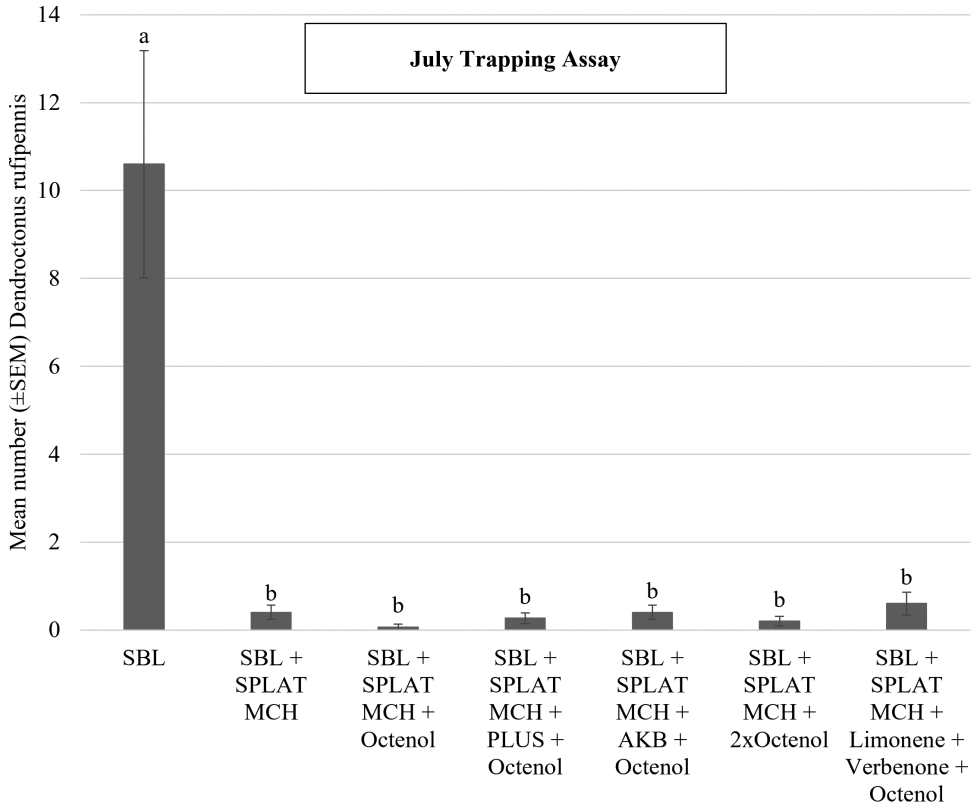

Fig. 2. Mean (± SEM) number of *Dendroctonus rufipennis* caught/day in 12-unit, multiple-funnel traps baited with the enhanced trapping lure (SBL = frontalin + MCOL + spruce terpenes; Product #3123, Synergy Semiochemical Corp., Delta, BC, Canada). Traps were deployed along the Kenai River near Soldotna, Alaska, 7–18 July 2021; however, only data from 13 to 18 July were used in these analyses. SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol. Different letters indicate significantly different means ($\alpha = 0.05$) based on negative binomial generalized linear modeling and least squares means comparisons with a Bonferroni correction.

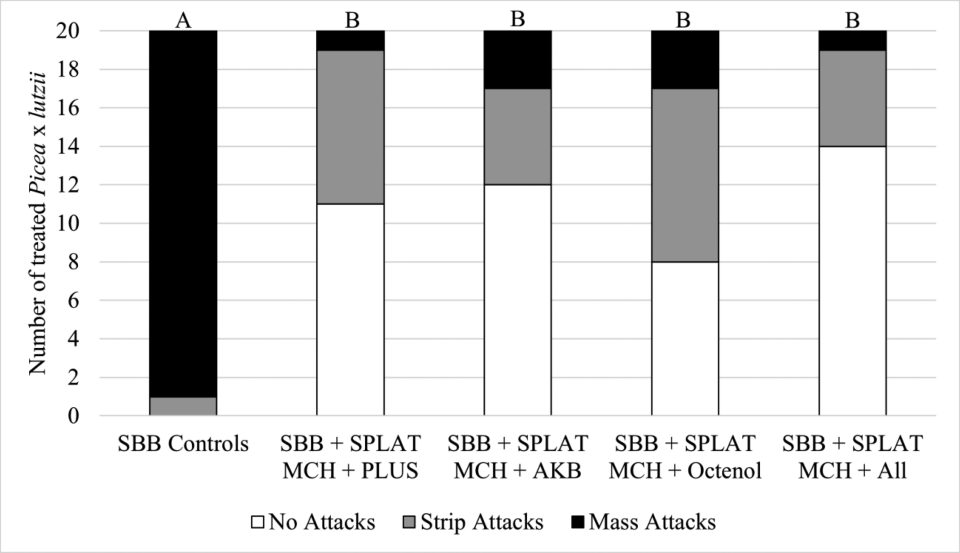

Fig. 3. Number of *Picea* × *lutzii* colonized by *Dendroctonus rufipennis* by colonization density category near Tern Lake on the Chugach National Forest, Alaska, 2022. No attacks indicate trees with no evidence of *D. rufipennis* attacks; pitch outs had 1 or more white pitch tubes (i.e., no boring dust and likely an unsuccessful attack); strip-attacked trees had evidence of successful attacks that encompassed <90% of the circumference of the bole; and mass-attacked trees had successful attacks on ≥90% of the circumference of the bole. Different letters indicate significant differences based on pairwise equality of proportions tests ($\alpha = 0.05$). All *Pi.* × *lutzii* were baited with frontalin (SBB). SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; All = octenol + PLUS + AKB.

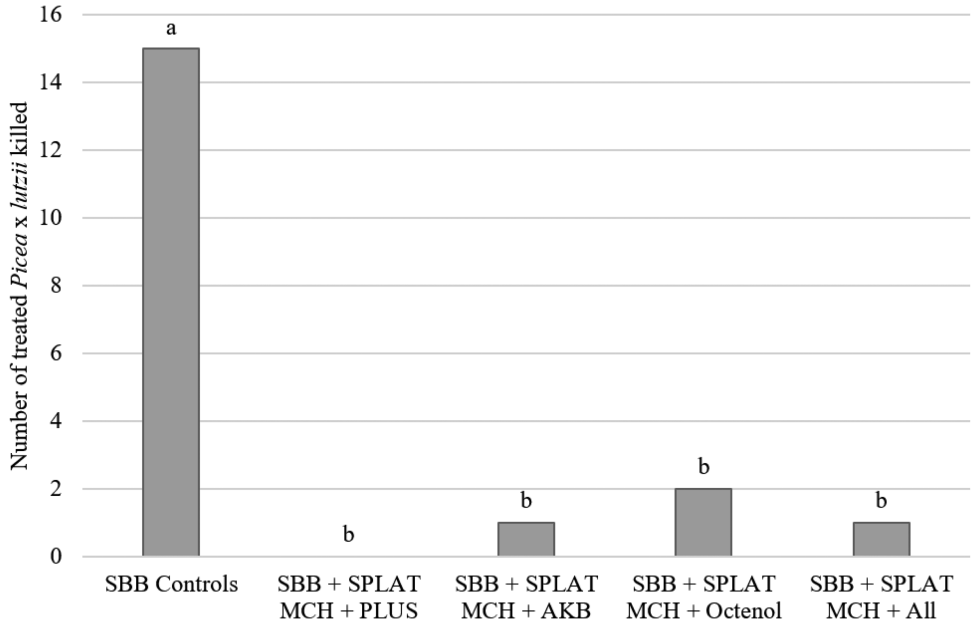

Fig. 4. Number of *Picea* × *lutzii* killed by *Dendroctonus rufipennis* near Tern Lake on the Chugach National Forest, Alaska, 2023. Mortality is based on the presence of crown fade following baiting with frontalin (SBB) in 2022. Different letters indicate significant differences based on pairwise equality of proportions tests ($\alpha = 0.05$). SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; All = octenol + PLUS + AKB.

Similarly, fewer *Picea* (*Pi.* × *lutzii* + *Pi. mariana*) were colonized (all z ratios ≥ 4.5, $P \leq 0.01$; Fig. 5) and killed by *D. rufipennis* (all z ratios ≥ 2.8, $P \leq 0.02$; Fig. 6) within 11.3 m of each individually treated *Pi.* × *lutzii* compared to SBB. Again, no other significant differences were observed among treatments. Less than 20% of *Picea* were colonized by *D. rufipennis* among repellent treatments compared to nearly 50% in SBB (Fig. 5). An average of ~25% of *Picea* on SBB plots were killed, while mortality among repellent treatments was <5% (Fig. 6). These results are similar to those in Wyoming where repellent treatments limited the average number of *Pi. engelmannii* colonized to ~20% and *Pi. engelmannii* mortality to ~5% (Audley et al. 2021). Interestingly, we observed similar repellency with the addition of AKB to SPLAT MCH in Alaska, as reported by Audley et al. (2021) in Wyoming. Hansen et al. (2019) reported MCH + AKB was ineffective for protecting individual *Pi.* × *lutzii*. In their study, MCH was released in a 1-g bubble capsule, eluting ~12 mg/day of MCH.

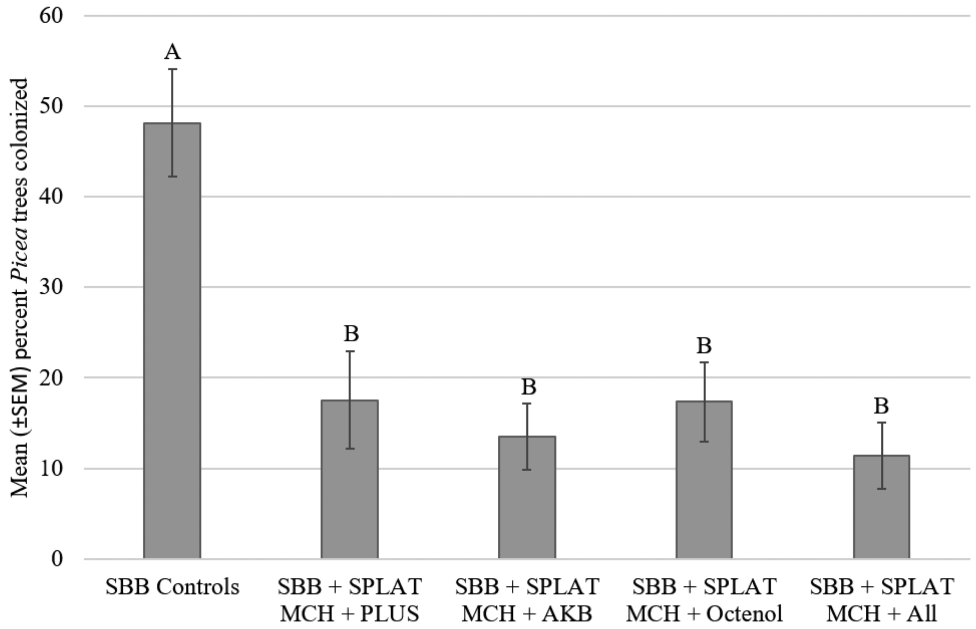

Fig. 5. Mean percent (± SEM) of *Picea* within 11.3 m of individually treated *Picea* × *lutzii* colonized (strip + mass attacks) by *Dendroctonus rufipennis* near Tern Lake on the Chugach National Forest, Alaska, 2022. Different letters indicate significantly different means based on pairwise, lsmeans tests ($\alpha = 0.05$). SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; All = octenol + PLUS + AKB.

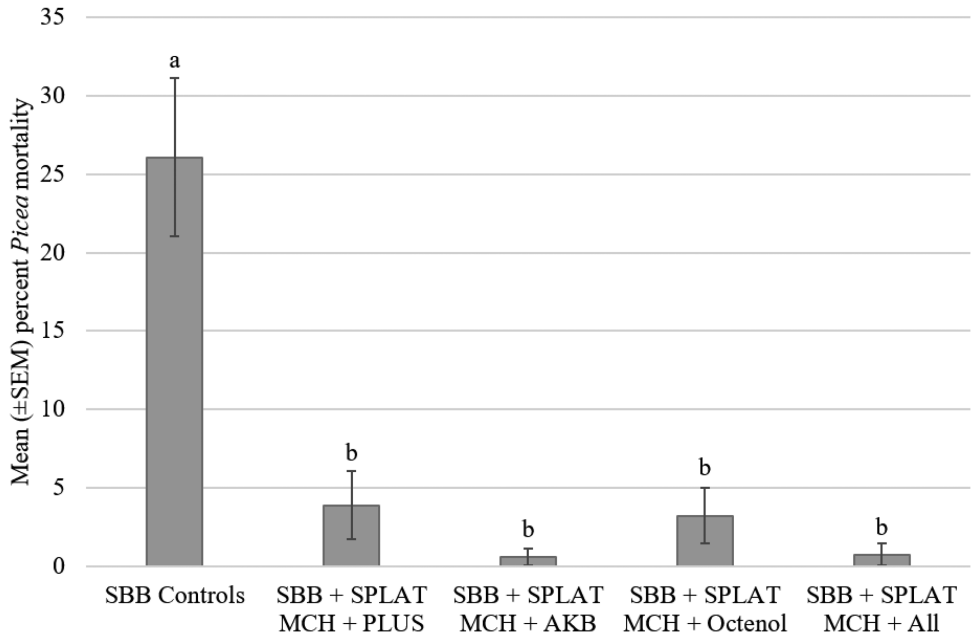

Fig. 6. Mean percent (± SEM) of *Picea* within 11.3 m of individually treated *Picea* × *lutzii* killed by *Dendroctonus rufipennis* near Tern Lake on the Chugach National Forest, Alaska, 2023. Mortality is based on the presence of crown fade. Different letters indicate significantly different means based on pairwise lsmeans tests ($\alpha = 0.05$). SPLAT MCH = a proprietary release formulation containing 10% MCH; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; All = octenol + PLUS + AKB.

Utah.

Live tree composition (based on number of trees) was 93.4 ± 2.3% *Pi. engelmannii*, 2.4 ± 0.7% subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., and 4.3 ± 2.2% lodgepole pine, *Pinus contorta* Douglas ex. Loudon, with 602 ± 32.7 trees/ha and 44.4 ± 7.9 m^2/ha of basal area. Approximately 19.0% of *Pi. engelmannii* were colonized by *D. rufipennis* at the beginning of the study. Of note, 5 *P. contorta* were also colonized by *D. rufipennis* in the study area (2 on circular plots, 3 between plots). The dbh of treated *Pi. engelmannii* was 33.5 ± 0.6 cm, ranged from 25.4 to 52.6 cm, and there were no differences in mean dbh among treatments ($\chi^2 = 1.39$, df = 4, $P = 0.85$). There were no differences in the mean density of surrounding trees among treatments ($\chi^2 = 0.77$, df = 4, $P = 0.94$).

In 2021, SPLAT MCH + PLUS, SPLAT MCH + AKB, and SPLAT MCH + GLVs reduced *D. rufipennis* colonization (strip attacks + mass attacks) of individually treated *Pi. engelmannii*

($\chi^2 = 13.64$, df = 1, $P < 0.01$, $\chi^2 = 11.95$, df = 1, $P < 0.01$, and $\chi^2 = 7.41$, df = 1, $P = 0.01$, respectively; Table 2) compared to SBB. SBB + SPLAT MCH + octenol was ineffective and not significantly different from SBB ($\chi^2 = 1.42$, df = 1, $P = 0.23$; Table 2). Despite all control trees being colonized by *D. rufipennis* in 2021, 70% (16/23) were only strip attacked, indicating a high likelihood of tree survival. This, combined with observations of *Pi. engelmannii* mortality attributed to *D. rufipennis* across the study area, suggested that *D. rufipennis* populations declined in 2021. As such, repellent treatments were reapplied in 2022 in hopes that additional attacks on control trees would occur in 2022 at levels sufficient to adequately challenge all treatments.

In 2022, all repellent treatments reduced *D. rufipennis* colonization (i.e., here we only compared 2022 colonization activity, a *Pi. engelmannii* colonized in 2021 without evidence of new attacks was ignored) compared to the control (PLUS: $\chi^2 = 13.64$, df = 1, $P < 0.01$; AKB: $\chi^2 = 13.64$, df = 1, $P < 0.01$; GLVs: $\chi^2 = 10.35$, df = 1, $P < 0.01$; octenol: $\chi^2 = 4.79$, df = 1, $P = 0.03$; Table 2). Despite a large range in the percent of *Pi. engelmannii* colonized by *D. rufipennis* (48%–74%), there were no differences among repellent treatments. Five of 7 mass-attacked control trees died in 2022, yet only 2 controls that were strip attacked in 2021 received enough new attacks in 2022 to change their status to mass attacked. Changes in colonization activity from 2021 to 2022 were investigated for each treatment; however, no significant differences were found.

Only SPLAT MCH + AKB and SPLAT MCH + octenol reduced *P. engelmannii* mortality compared to the control ($\chi^2 = 6.07$, df = 1, $P = 0.01$ for both; Table 2). This result was likely influenced by how few SBB control trees died (30%), which was quite surprising given the amount of *D. rufipennis* activity observed at the initiation of the study throughout the study area. Typically, we prefer to see mortality ≥75% in baited control trees to ensure beetle colonization pressure is strong enough to adequately challenge repellent treatments. This study fell well below this mark and thus limits the conclusions that can be drawn concerning the influence of repellent treatments on *Pi. engelmannii* survival in this study. Similarly, too few 0.041-ha circular plots were established among treatments to draw useful inferences from data collected on these plots. Of note, no tree mortality occurred in SPLAT MCH + AKB and SPLAT MCH + octenol over the 2-year period (Table 2).

While these studies were not designed to address semiochemical divergence among *D. rufipennis* haplotypes (Maroja et al. 2007), similarities in the efficacy of SPLAT MCH + PLUS and SPLAT MCH + AKB reported herein and in Audley et al. (2021) suggest similar behavioral responses between northern and Rocky Mountain haplotypes. This is encouraging from a management perspective as a single repellent treatment appears effective for the management of both haplotypes in western North America. It now appears likely that the initial tree protection study failure in 2019 in Alaska resulted from strong colonization pressure and overwhelming repellent effects. This study was implemented in a year when *D. rufipennis* activity within Denali State Park was at very high intensities (J.E.M. and C.J.F., personal observations). Repellents are less effective under high population pressures (Progar et al. 2014, Seybold et al. 2018) particularly for irruptive, tree-killing species like *D. rufipennis*.

Despite there being more actively colonized trees at the beginning of the tree protection study in Utah (19.0 ± 2.2%) than in Alaska (15.6 ± 2.2%; $\chi^2 = 64.4$, df = 1, $P < 0.01$), our results in Utah were confounded by too few SBB control trees dying. This further highlights the highly variable nature of bark beetle populations and the inherent difficulty of field-based studies involving bark beetle populations. Estimating and predicting bark beetle populations and population dynamics is particularly difficult, in part due to complexities at the tree, stand, and forest scales (Coulson 1979). However, understanding of factors that influence bark beetle outbreaks has increased. For example, the roles of stand characteristics, host availability, host suitability, and stochastic perturbations (e.g., windthrow, drought, etc.), among other factors, have been and continue to be empirically studied across different bark beetle-host systems (reviewed in Lantschner and Corley 2023). Yet an effective means of estimating population densities in a given area remains elusive. Successful field studies rely heavily on study site selection, a process that remains something of an art and is subject to the stochastic nature of bark beetle dynamics.

The efficacy of MCH alone for protecting *Picea* from *D. rufipennis* is mixed, with the consensus being that MCH alone is ineffective (Jenkins et al. 2014). However, early studies evaluated MCH doses, as informed by work on Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, where low doses and release rates are effective for tree protection. For example, Ross et al. (1996) examined doses of 6, 12, 20, 40, and 60 g of MCH/ha using a bubble capsule formulation. Total release of MCH (/ha) ranged from ~18 to ~240 mg/day. All but the 2 lowest doses reduced the percentage of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, colonized by *D. pseudotsugae*. Based on these and other studies, it is recommended that ~120 mg/ha/day of MCH be released in operational treatments for *D. pseudotsugae* (Ross 2021). For *D. rufipennis*, MCH released from bubble capsules at ~7–9 mg/day (~1.5 g/ha/day) stapled around the perimeter of 1-ha plots was ineffective for protecting *Pi. engelmannii* (Ross et al. 2004). Hansen et al. (2017) reported the

Table 2. Comparisons of percentages of treated *Picea engelmannii* colonized (strip attacks + mass attacks) and killed by *Dendroctonus rufipennis* in Utah 2021–2022. Proportions were compared using prop.test (base package) in R. Different letters within a column indicate statistical significance (α = 0.05). Changes in colonization from 2021 to 2022 within a treatment were considered; however, no significant differences were found

Treatment[a]	% Colonized 2021	% Colonized 2022[b]	% Mortality
Baited Controls	100.0A	100.0a	30.4X
SPLAT MCH + PLUS	47.8B	47.8b	13.0XY
SPLAT MCH + AKB	52.2B	47.8b	0.0Y
SPLAT MCH + GLVs	65.2B	56.5b	8.7XY
SPLAT MCH + Octenol	87.0A	73.9b	0.0Y

[a]All *Pi. engelmannii* were baited with frontalin (SBB) in 2021 only. SPLAT MCH = a proprietary release formulation containing 10% MCH by weight; PLUS = acetophenone + (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol; AKB = linalool + β-caryophyllene + (*Z*)-3-hexanol; GLVs = (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol.
[b]Only active colonization activity (i.e., evidence of new attacks during 2022) is reflected, thus a decrease in % colonized indicates trees without new attacks in 2022.

probability of severe *D. rufipennis* attacks was reduced by applying MCH bubble capsules to 1.25-ha plots, but no differences were observed among doses (20, 40, and 80 g/ha) releasing MCH at ~240–960 mg/ha/day. A single bubble capsule releasing MCH at ~12 mg/day was largely ineffective for protecting individual *Pi. engelmannii* (Hansen et al. 2017). Conversely, Audley et al. (2021) observed high levels of efficacy when MCH was released at ~147 or 294 mg/day using the SPLAT MCH formulation. In their study, SPLAT MCH alone significantly reduced the mortality of individually treated *Pi. engelmannii* and mortality of neighboring *Pi. engelmannii* on 0.041-ha plots. In addition, our release rate assays demonstrated similar levels of inhibition between SPLAT MCH alone and SPLAT MCH combined with other repellent compounds (Figs. 1 and 2). Evidence suggests that higher doses and release rates of MCH alone (i.e., than previously considered in early literature) may be effective for protecting *Picea* from *D. rufipennis*. This warrants further study in multiple hosts (e.g., *Pi. engelmannii* and *Pi.* × *lutzii*) and locations.

Further investigation of these repellent combinations to optimize efficacy, while minimizing cost, is necessary to reveal an effective tree protection tool and develop operational recommendations. Testing the effective range of inhibition (Fettig et al. 2009; i.e., the maximum distance from the repellent point source at which these semiochemicals affect beetle behavior) for SPLAT MCH combinations is an important step in elucidating stand-level doses for protecting *Picea* from *D. rufipennis*.

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