

Review

Applied Chemical Ecology of Spruce Beetle in Western North America

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Abstract

Spruce beetle (*Dendroctonus rufipennis* (Kirby)) is a major cause of spruce (*Picea* spp.) mortality in western North America. We synthesized the literature on the chemical ecology of spruce beetle, focusing on efforts to reduce host tree losses. This literature dates back to the mid-20th century and focuses on spruce beetle populations in Alaska, U.S., western Canada, and the central and southern Rocky Mountains, U.S. Spruce beetle aggregation pheromone components include frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), seu-denol (3-methyl-2-cyclohexen-1-ol), MCOL (1-methyl-2-cyclohexen-1-ol), and verbenene (4-methylene-6,6-dimethylbicyclo[3.1.1]hept-2-ene). The attraction of spruce beetle to one aggregation pheromone component is enhanced by the co-release of other aggregation pheromones and host compounds (e.g., α -pinene). Several baits that attract spruce beetles are commercially available and are used for survey and detection, population suppression, snag creation, and experimental purposes. The antiaggregation pheromone is MCH (3-methyl-2-cyclohexen-1-one), which has been evaluated for reducing colonization of felled spruce since the 1970s. Beginning in the early 2000s, MCH has been evaluated for protecting live, standing spruce from colonization by and mortality attributed to spruce beetle. With a few exceptions, significant reductions in levels of spruce beetle colonization and/or spruce mortality were reported. More recent efforts have combined MCH with other repellents (e.g., nonhost compounds) in hope of increasing levels of tree protection. Today, several formulations of MCH are registered for tree protection purposes in the U.S. and Canada.

Keywords: attractant; *Dendroctonus rufipennis*; MCH; *Picea engelmannii*; *Picea glauca*; *Picea x lutzii*; pheromone; repellent; semiochemical



Academic Editor: Qing-He Zhang

Received: 16 May 2025

Revised: 24 June 2025

Accepted: 2 July 2025

Published: 3 July 2025

Citation: Fettig, C.J.; Audley, J.P.; Munson, A.S. Applied Chemical Ecology of Spruce Beetle in Western North America. *Forests* **2025**, *16*, 1103. <https://doi.org/10.3390/f16071103>

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1. Introduction

Spruce beetle (*Dendroctonus rufipennis* (Kirby)) (Coleoptera: Curculionidae) is a major cause of spruce (*Picea* spp.) mortality in western North America [1]. All North American species of spruce and known hybrids of spruce are potential hosts, with large-diameter, mature trees preferred (Figure 1). Preferred host species in western North America include Lutz spruce (*P. x lutzii* Little) and white spruce (*Picea glauca* (Moench) Voss) in Alaska, U.S., white spruce and Engelmann spruce (*P. engelmannii* Parry ex. Engelm.) in western Canada, and Engelmann spruce in the central and southern Rocky Mountains, U.S. The distribution of spruce beetle is transcontinental, with three major genetic groups isolated

since the Pleistocene [2]. Two groups extend from Alaska to Newfoundland, Canada, and a third occurs in the Rocky Mountains. Spruce beetle populations can quickly transition from endemic to epidemic levels when favorable weather (warm, dry) and host conditions occur [1]. Historically, most spruce beetle epidemics were incited by windthrow events that resulted in abundances of downed spruce, with compromised defenses. Phloem temperatures and moisture conditions in large (>30.5 cm dbh, diameter at 1.37 m), windthrown spruce are conducive to brood survival, which can lead to epidemics once the availability of suitable windthrown trees is exhausted (by decay or colonization by spruce beetle or other bark beetles [3,4]) and beetles transition to colonizing live spruces. In recent decades, warming [5,6] and droughts [7,8] have incited notable spruce beetle epidemics in western North America.



Figure 1. Faded Lutz spruce (*Picea x lutzii*) colonized and killed by spruce beetles (*Dendroctonus rufipennis*) along the Funny River, Alaska, U.S. Photo credit: C.J. Fettig, USDA Forest Service.

Female spruce beetles initiate attacks during late spring and early summer. Upon selecting a host, females release aggregation pheromones (see Section 3) that attract males and other females to the host tree. Positive density-dependent feedback occurs at high population densities, resulting in mass attacks (hundreds to thousands of beetles/host) that can overwhelm the defenses (resin) of even healthy trees [9] (Figure 2). However, too many spruce beetles within a host results in high levels of intraspecific competition, negatively affecting spruce beetle populations. The release of an antiaggregation pheromone (see Section 4) by females and males serves to limit attack densities and reduce intraspecific competition. Spruce beetle completes 0.33–1 generations per year. During the late 20th and early 21st centuries, warming resulted in higher proportions of univoltine beetles in some populations [6,10–14].



Figure 2. A healthy Engelmann spruce (*Picea engelmannii*) colonized by spruce beetles (*Dendroctonus rufipennis*) in Utah, U.S. Resin is the primary defense of spruces against spruce beetle attacks as pioneering (female) beetles are often drowned or immobilized in resin. Monoterpenes in resin (e.g., α -pinene and β -pinene) are also highly toxic to spruce beetles at high doses and after prolonged exposure [15,16]. Photo credit: C.J. Fettig, USDA Forest Service.

Below, we have synthesized information on the use of semiochemicals (a compound or mixture of compounds that affects the behavior of receiving individuals) for the management of spruce beetles in western North America. We focus on advances in the use of semiochemical repellents for tree protection.

2. Management of Spruce Beetle

Substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of spruce mortality attributed to spruce beetles. Suppression addresses current infestations and includes the use of insecticides (bole sprays and systemic injections), semiochemicals (see Sections 3 and 4), sanitation harvests, or a combination of these and other treatments. Prevention reduces the probability and severity of future infestations by reducing the abundance of susceptible host trees. For more information on spruce beetle management, we encourage the reader to consult syntheses by Jenkins et al. [13] on spruce beetle in the central and southern Rocky Mountains and by Bleiker and Brooks [14] on spruce beetle in Canada.

3. Semiochemical Attractants

Spruce beetle aggregation pheromone components include frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), seudenol (3-methyl-2-cyclohexen-1-ol), MCOL (1-methyl-2-cyclohexen-1-ol), and verbenene (4-methylene-6,6-dimethylbicyclo[3.1.1]hept-2-ene) [17]. Frontalin, produced by females [18,19] and males [19], was first demonstrated to induce spruce beetle attacks by Dyer and Chapman [20]. Seudenol, produced by females [21] and in lesser amounts by males [22], was first detected by Vité et al. [23]. MCOL, produced by females, was first identified by Borden et al. [24] and has a synergistic effect on spruce beetle attraction in the presence of frontalin [25,26]. Verbenene, produced by females, was first identified in spruce beetles by Gries et al. [27].

The attraction of spruce beetles to one aggregation pheromone component is enhanced by the co-release of other aggregation pheromones and host compounds. For example, in Alaska, Werner [28] demonstrated that α -pinene, β -pinene, camphene, and 3-carene enhanced spruce beetle attraction to frontalin. In Utah, U.S., Ross et al. [26] found that MCOL increased spruce beetle attraction to frontalin and α -pinene by almost 10 times. The enantiomeric specificity of chiral aggregation pheromone components, and the quantity of aggregation pheromone(s) produced and released by spruce beetles, may vary among different populations. However, differences in the experimental methods (e.g., pheromone isolation methods) and analyses used among relevant studies could explain some of these differences. Isitt et al. [19] reported that the quantity of MCOL produced by spruce beetles varies widely across its geographic range. Some enantiomers of MCOL may be inhibitory to spruce beetles [19,24,25].

Aggregation pheromones and host compounds are used in baits (Table 1), which often include frontalin, MCOL, and one or more host compounds (e.g., α -pinene, β -pinene, camphene, and/or 3-carene). Baits applied to host trees to induce spruce beetle colonization often exclude host compounds, which are naturally emitted by the host tree.

Table 1. Common semiochemicals used in research and management of spruce beetles (*Dendroctonus rufipennis*) in western North America.

Compound	Emitter	Application
Attractants		
Aggregation pheromones		
Frontalin	<i>D. rufipennis</i>	Baits
MCOL	<i>D. rufipennis</i>	Baits
Seudenol	<i>D. rufipennis</i>	Baits
Host compounds		
Terpenes	<i>Picea</i> spp. and others	Baits
Inhibitors		
Antiaggregation pheromone		
MCH	<i>D. rufipennis</i>	Repellent for tree protection
Nonhost compounds		
Acetophenone	Common plant volatile, several <i>Dendroctonus</i> spp.	Used in combination with other repellents for tree protection (experimental use only)
β -caryophyllene	Common plant volatile	Used in combination with other repellents for tree protection (experimental use only)
linalool	Common plant volatile	Used in combination with other repellents for tree protection (experimental use only)
(E)-2-Hexen-1-ol (Z)-2-Hexen-1-ol (Z)-3-hexanol	Green leaf volatiles	Used in combination with other repellents for tree protection (experimental use only)
AKB		
linalool β -caryophyllene (Z)-3-hexanol	Described above	Repellent for tree protection (experimental use only)

Table 1. Cont.

Compound	Emitter	Application
PLUS		
Acetophenone	Described above	Repellent for tree protection (experimental use only)
E-2-hexen-1-ol		
Z-2-hexen-1-ol		

3.1. Use of Semiochemical Attractants in Trapping for Survey, Detection, and Experimental Purposes

Traps are used for survey, detection, and evaluating spruce beetle responses to olfactory stimuli (Figures 3 and 4). In most cases, two-component (frontalin and α -pinene) or three-component (frontalin, MCOL, and spruce terpenes) baits are used. Three-component baits capture more spruce beetles than two-component baits [26], which may be advantageous for some uses. Traps should be placed at least 15 m from susceptible host trees to reduce spillovers (i.e., whereby spruce beetles are attracted to traps but colonize adjacent host trees), which is indicative of epidemic spruce beetle populations [29]. Mark-and-recapture studies in Alaska demonstrate that spruce beetles can fly long distances (up to 600 m) and orient in the direction of prevailing winds [30].



Figure 3. A 12-unit multiple-funnel trap [31] baited with frontalin, MCOL, and spruce terpenes to assess the effects of semiochemical repellents (in yellow circle) on spruce beetles (*Dendroctonus rufipennis*) in Alaska, U.S. Photo credit: C.J. Fettig, USDA Forest Service.

Some invertebrate predators are attracted to spruce beetle aggregation pheromones [32,33] and may be captured and killed in attractant-baited traps. For example, Bentz and Munson [34] reported that 64% of traps employed for the mass trapping of spruce beetles (see Section 3.3) in Utah caught more clerid beetles (*Thanasimus dubius* (F.) and *T. undulatus* (Say)), common bark beetle predators, than spruce beetles. Caution should be taken to limit the bycatch of these and other natural enemies. Screen filters can be placed on collection cups to prevent predators larger than spruce beetles from entering the collection cup.

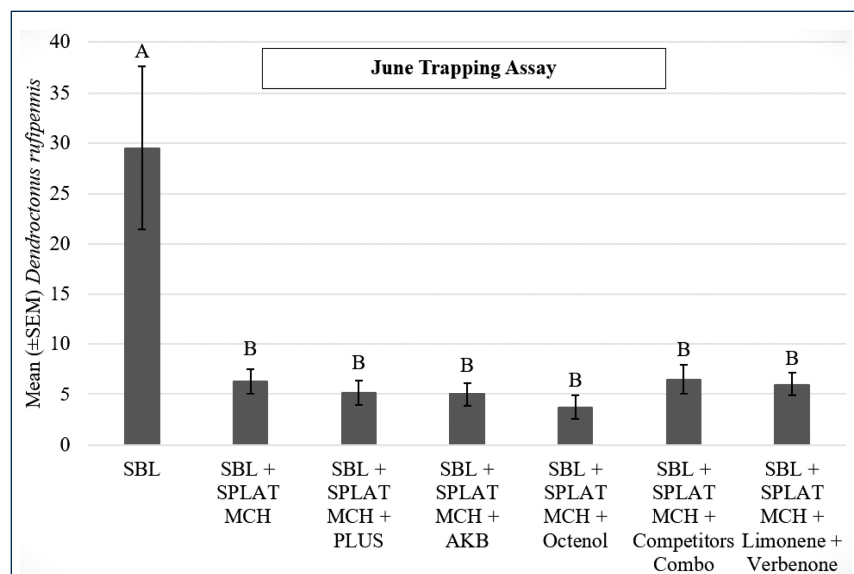


Figure 4. Mean ($\pm$ SEM) daily number of spruce beetles (*Dendroctonus rufipennis*) caught in 12-unit multiple-funnel traps baited with frontalinal, MCOL, and spruce terpenes (SBL) in Alaska, U.S. SPLAT MCH = 10% MCH by weight (ISCA Inc., Riverside, CA, USA); PLUS = acetophenone + (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol [35]; AKB = linalool + β -caryophyllene + (Z)-3-hexanol [36,37]; competitors combo = *exo*-brevicomin + *endo*-brevicomin + ipsdienol + ipsenol. Different letters among treatments indicate significantly different means. Adapted from Audley et al. [38].

3.2. Use of Semiochemical Attractants in Trapping for Forecasting Levels of Spruce Mortality

Although multiple-funnel traps are used to monitor spruce beetle populations, the relationships between trap catches and levels of spruce mortality have not been adequately studied. Hansen et al. [29] studied spruce beetle catches in 16-unit multiple-funnel traps baited with frontalinal and α -pinene in Utah. Although model predictions had large variances, the authors argued that trap catches could be used to estimate relative levels of Engelmann spruce mortality, expressed as “phases”. Captures of >842 spruce beetles/season (late May to mid-August, single trap) represented a transition between endemic (<2 mass attacked trees/ha) and epidemic phases (≥ 2 mass attacked trees/ha) [29]. In Colorado, U.S., Negrón and Popp [39] found that spruce beetle catches in 12-unit multiple-funnel traps baited with frontalinal and α -pinene were positively correlated with Engelmann spruce mortality in the current year, but did not provide reliable estimates of spruce mortality across years.

3.3. Use of Semiochemical Attractants in Mass Trapping for Population Suppression

Mass trapping is the least effective method of suppressing spruce beetle populations and is not widely used. Bentz and Munson [34] reported that mass trapping, sanitation harvesting, the burning of spruce beetle-infested trees, and trap trees (see Section 3.4) reduced the number of Engelmann spruce infested by spruce beetles by 91% in Utah. Sixteen-unit multiple-funnel traps were baited with frontalinal and α -pinene. A total of 36,109 spruce beetles were captured over a two-year period; however, the effects of mass trapping cannot be distinguished from the other treatments. Hansen et al. [40] compared naturally baited (fresh Engelmann spruce) traps, multiple-funnel traps baited with frontalinal and α -pinene, and fallen trap trees in regard to their ability to suppress spruce beetle populations in Utah. All methods caught similar numbers of spruce beetles, but multiple-funnel traps resulted in higher levels of spillover. Trees colonized by spruce beetles as a result of spillover could interfere with suppression tactics and should be promptly treated or removed.

3.4. Use of Semiochemical Attractants on Trap Trees for Population Suppression

Trap trees can be effective for suppressing spruce beetle populations on a localized basis [41,42]. Uninfested spruces are felled or left standing and baited. Felled trap trees attract (capture) more spruce beetles than standing trap trees [43]. Once trap trees are fully colonized (late summer), they must be burned or debarked to kill the brood, or removed from the site [13]. It is important that this occurs prior to the emergence of spruce beetles from trap trees. Baited, toxic trap trees incorporate the use of insecticides, which eliminate the need for treatment or removal, but they are not widely used. Negrón et al. [44] found that carbaryl had no effect on the number of spruce beetle attacks, egg galleries, or other life stages on felled trap trees in Colorado, although carbaryl is highly toxic to spruce beetles and effective for protecting live spruce from spruce beetles. In their study, the trap trees were divided into two sections, with one section sprayed with carbaryl and the other left unsprayed [44].

Like mass trapping, trap trees are most effective when combined with other suppression tactics. The number of trap trees required to control spruce beetle infestations has not been adequately studied, but likely varies with population density, host density, and the diameter of trap trees. Larger and higher numbers of trap trees are required for higher spruce beetle population densities. Jenkins et al. [13] recommended one trap tree per two to three naturally infested spruce. In British Columbia, Canada, Shore et al. [45] baited 9-ha plots with frontalin and α -pinene at 50-m intervals for the pre-harvest containment of spruce beetles, with the goal of harvesting infested spruce before beetle emergence occurred. Overall, >4 times as many spruce beetle attacks occurred on baited plots than unbaited plots [45].

3.5. Use of Semiochemical Attractants for Snag Creation

Snags provide feeding substrates, nesting and roosting sites, and other important habitats for wildlife. Snags may be created in some forests by placing baits on individual spruce to induce colonization by spruce beetles.

3.6. Use of Semiochemical Attractants for Baiting Spruce for Experimental Purposes

Baits are used for a variety of experimental purposes. Most common is baiting spruce to test the efficacy of semiochemical repellents (Figure 5) or insecticides. The efficacy of treatments is based on comparisons of attack densities and/or levels of spruce mortality between treated and untreated spruce.



Figure 5. Engelmann spruce (*Picea engelmannii*) baited with frontalin (black pouch within yellow circle) to assess the efficacy of SPLAT MCH (gray dollop within blue circle) + *Acer* kairomonal blend (white pouch) [36,37] for reducing mortality attributed to spruce beetles (*Dendroctonus rufipennis*) in Utah, U.S. Photo credit: J.P. Audley, University of California.

4. Semiochemical Repellents

The antiaggregation pheromone 3-methyl-2-cyclohexen-1-one (MCH) was first discovered in spruce beetle by Rudinsky et al. [46] (Table 1). Female spruce beetles generally do not release MCH until after a male spruce beetle enters the gallery, while MCH is present in both sexes of emerging adults [46]. In addition to MCH, the antennae of spruce beetles detect several other compounds, including 1-octen-3-ol, *trans*-verbenol, verbenone, nonanal, *exo*-brevicomin, *endo*-brevicomin, and acetophenone [47], several of which have been found to be inhibitory in trapping assays. For example, in British Columbia, Poland and Borden [48] reported that *exo*-brevicomin and *endo*-brevicomin reduced spruce beetle captures in 12-unit multiple-funnel traps baited with frontalinal and α -pinene by up to 42%. Moreover, *exo*-brevicomin and *endo*-brevicomin are aggregation pheromones of the sympatric *Dryocoetes affaber* (Mannerheim) [49]. Of note, 1-octen-3-ol has been detected in female spruce beetles [47,50] and may be an antiaggregation pheromone component. Pureswaran and Borden [50] reported that 1-octen-3-ol had no effect on spruce beetle catches in baited 12-unit multiple-funnel traps, but that 1-octen-3-ol reduced baited trap catches to levels no longer significantly different from unbaited traps (which catch few beetles). The addition of 1-octen-3-ol to MCH had no effect on spruce beetle catches in 12-unit multiple-funnel traps baited with frontalinal, MCOL, and spruce terpenes in Alaska [38] (Figure 4, octenol).

Developing semiochemical repellents for bark beetles is a multifaceted challenge, requiring the identification and synthesis of semiochemicals; the development of release devices to diffuse semiochemicals into the forest environment at biologically meaningful doses; and the screening of semiochemicals through the use of olfactometer, electroantennogram, trapping, and tree protection assays in multiple locations, years, and beetle populations [51]. The situation is further complicated by the need to work in remote areas that are often difficult and costly to access. Once a promising semiochemical repellent has been identified, there are still substantial regulatory hurdles at multiple levels of government that must be addressed before a product is commercialized for tree protection in the U.S. and Canada.

4.1. Use of Semiochemical Repellents for Reducing Colonization of Downed Spruce

Kline et al. [52] demonstrated that MCH reduced the number of spruce beetles collected in traps baited with small (30.5 cm in diameter and 25.4 cm long) Engelmann spruce logs that were infested with unmated female spruce beetles by 99% in Idaho. As a result, the authors recommended more intensive study of MCH to reduce the colonization of downed spruce. Lindgren et al. [53] reported that MCH reduced spruce beetle attack densities by 85%, and brood production by 79%–88%, on felled Engelmann spruce in Montana, U.S. In their study, MCH was released from bubblecaps (Figure 6A) stapled along the stems of felled Engelmann spruce at ~3-m intervals. Each bubblecap released ~1–3 mg of MCH/d [53]. Similar results have been observed for felled spruce in Alaska [54]. Despite these and other data demonstrating the value of MCH for reducing colonization of downed spruce, the efficacy of treating downed spruce to reduce colonization and mortality of nearby live standing spruce, which differs from directly treating live standing spruce (Table 2), has not been adequately studied.

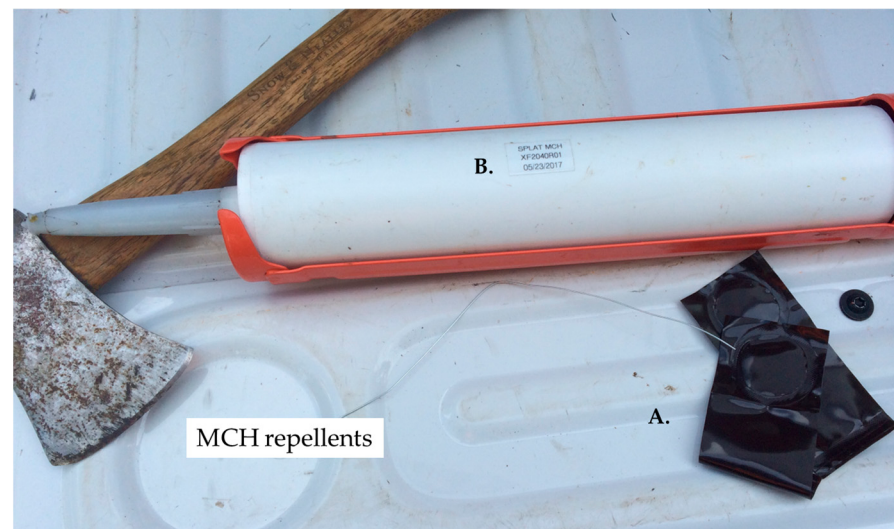


Figure 6. (A) MCH bubblecaps and (B) an early prototype of SPLAT MCH. Several formulations of MCH are registered for tree protection in the U.S. and Canada. Photo credit: C.J. Fettig, USDA Forest Service.

4.2. Use of Semiochemical Repellents for Reducing Colonization and Mortality of Live Standing Spruce

Holsten et al. [55] provided the first evidence of the use of MCH to protect live standing spruce (Table 2). In their study, in Alaska, MCH was released from Med-e-Cell devices (used for chronic drug infusions in humans) containing a small battery-operated pump and storage reservoir. These devices provided timed releases of MCH (2.6 mg/d, regardless of the abiotic conditions) onto a collection pad, from which MCH evaporated into the forest environment. MCH reduced the number of newly attacked Lutz spruce by 87% [55]. The authors commented that “beetle pressure” was low at the beginning of their study (<1 attacked tree/ha). Repellents are most effective at low (endemic) to moderate (incipient) bark beetle populations. Ross et al. [56] found that the percentage of Engelmann spruce ≥ 20 cm dbh that were mass attacked by spruce beetles was not significantly different between MCH-treated (52.7% mass attacked) and untreated plots (68.3% mass attacked) in Utah (Table 2). These attack levels (in a single year) are extremely high. For example, the largest recent spruce beetle epidemic in Utah began in the Manti-LaSal National Forest in 1986 and by 1998 (12 years later) 73% of Engelmann spruce >12.7 cm dbh had been killed [60]. Ross et al. [56] treated 1-ha circular plots with 180 MCH bubblecaps along the perimeter of the plots. Today, it is recognized that semiochemical repellents exert relatively short-range inhibition in bark beetles. For example, Audley et al. [59] demonstrated that the maximum inhibition of spruce beetles was statistically constant to 4 m from repellent sources (several treatments) in Alaska and 12 m in Colorado. The radius of a 1-ha circular plot is ~ 56.4 m, likely leaving interior portions of the plot unprotected by MCH. The lack of efficacy reported by Ross et al. [56] may be attributed to the extremely high spruce beetle populations observed during their study and the lack of MCH bubblecaps applied to the interior portions of the plots.

Table 2. Peer-reviewed literature on the efficacy of semiochemical repellents for protecting spruce (*Picea* spp.) from colonization and mortality attributed to spruce beetle (*Dendroctonus rufipennis*) in western North America, 2000–2025.

Publication	Type of Study	Location	Host	Repellent Treatments ¹	Doses	Release Rates/ Device ⁴	Total Release/d ⁵	Inhibitory Effect ⁶
Holsten et al. [55]	Areawide (0.2 ha)	AK	<i>P. x lutzii</i>	MCH (Med-e-Cell device ²)	125/ha	2.6 mg/d	325 mg/ha	Reduction in number of attacked spruce.
Ross et al. [56]	Areawide (1 ha)	UT	<i>P. engelmannii</i>	MCH	180/ha	7 or 9 mg/d (varied by device)	1480 mg/ha	NS
Hansen et al. [57]	Areawide (0.79 ha)	UT	<i>P. engelmannii</i>	MCH + isophorone + sulcatone	40/ha of each repellent	12 mg/d, 6.5 mg/d, and 35 mg/d, respectively	2140 mg/ha	Reduction in the probability of mass attacked spruce.
Hansen et al. [36]	Areawide (0.64 ha)	NM, UT	<i>P. engelmannii</i>	MCH	20/ha, 40/ha or 80/ha	12.0 mg/d	240, 480, or 960 mg/ha	Reductions in the probability of severe attacks; no differences among doses.
Hansen et al. [36]	Individual tree	NM, UT	<i>P. engelmannii</i>	MCH, AKB ³ , and MCH + AKB	1/tree of each repellent, according to treatment	12.0 mg/d and undetermined (AKB)	Unknown	Reductions in the probability of mass attacks. Spruce treated with MCH or AKB were more likely to be mass attacked than those treated with MCH + AKB.
Hansen et al. [37], Experiment 2017	Individual tree	CO, UT	<i>P. engelmannii</i>	MCH + AKB	1/tree of each repellent	12.0 mg/d and 65 mg/d, respectively	77 mg/tree	Reductions in the probability of severe attacks on treated spruce and on spruce within 10 m of treated spruce.
Hansen et al. [37], Experiment 2018	Individual tree	AK	<i>P. glauca</i>	MCH, MCH + AKB, MCH + AKB + sulcatone, double-dose MCH + AKB	1/tree of each repellent, according to treatment except for 2 times for double dose	12 mg/d (MCH), 65 mg/d (AKB), 35 mg/d (sulcatone)	12–154 mg/tree, depending on treatment	NS in regard to treated trees, but reductions in the probability of severe attacks on spruce within 10 m of treated spruce.
Hansen et al. [37], Experiment 2018	Individual tree	CO, NM, UT, WY	<i>P. engelmannii</i>	MCH + AKB, MCH + AKB + sulcatone, double-dose MCH + AKB	1/tree of each repellent, according to treatment except for 2 times for double dose	12 mg/d (MCH), 65 mg/d (AKB), 35 mg/d (sulcatone)	77–154 mg/tree, depending on treatment	Reductions in the probability of severe attacks on treated spruce and on spruce within 10 m of treated spruce.
Hansen et al. [37]	Areawide (0.64 ha)	CO, UT	<i>P. engelmannii</i>	MCH + AKB	30/ha of each	12 mg/d and 65 mg/d, respectively	2310 mg/ha	Reductions in the probability of severe attacks.
Audley et al. [58]	Individual tree	WY	<i>P. engelmannii</i>	3.5 g MCH (SPLAT MCH, SPLAT3.5), SPLAT3.5 + AKB, SPLAT3.5 + PLUS ³ , 7 g MCH (SPLAT MCH, SPLAT7), SPLAT7 + AKB, and SPLAT7 + PLUS	SPLAT3.5 = two 17.5 g dollops/tree, SPLAT7 = four 17.5 g dollops/tree, 1/tree of other repellents	SPLAT3.5 (147 mg/d), SPLAT7 (294 mg/d), AKB (60 mg/d), acetophenone (103 mg/d), GLV (20 mg/d)	147–417 mg/tree, depending on treatment	Reductions in mortality of treated spruce and of spruce within 11.3 m of treated spruce; no differences among treatments.

Table 2. Cont.

Publication	Type of Study	Location	Host	Repellent Treatments ¹	Doses	Release Rates/ Device ⁴	Total Release/d ⁵	Inhibitory Effect ⁶
Audley et al. [38]	Individual tree	AK	<i>P. x lutzii</i>	7 g MCH (SPLAT MCH, SPLAT7) + AKB, SPLAT7 + PLUS, SPLAT7 + octenol, and SPLAT7 + octenol + PLUS + AKB	SPLAT7 = four 17.5 g dollops/tree, 1/tree of other repellents	SPLAT7 (294 mg/d), AKB (60 mg/d), acetophenone (103 mg/d), GLV (20 mg/d), octenol (58 mg/d)	354–535 mg/tree, depending on treatment	Reductions in mortality of treated spruce and of spruce within 11.3 m of treated spruce; no differences among treatments.
Audley et al. [38]	Individual tree	UT	<i>P. engelmannii</i>	7 g MCH (SPLAT MCH, SPLAT7) + AKB, SPLAT7 + PLUS, SPLAT7 + octenol, and SPLAT7 + GLVs	SPLAT7 = four 17.5 g dollops/tree, 1/tree of other repellents	SPLAT7 (294 mg/d), AKB (60 mg/d), acetophenone (103 mg/d), GLV (20 mg/d), octenol (58 mg/d)	354–417 mg/tree, depending on treatment	Only SPLAT MCH + AKB and SPLAT MCH + octenol reduced mortality of treated spruce. Effects on nearby spruce were not determined.
Audley et al. [59]	Individual tree	AK	<i>P. x lutzii</i>	1 g, 3 g, and 7 g MCH (SPLAT MCH and bubblecaps)	SPLAT 1 g = one 10 g dollops/tree, SPLAT 3 g = three 10 g dollops/tree, SPLAT 7 g = four 17.5 g dollops/tree, 1, 3, or 7 bubblecaps/tree	SPLAT 10 g dollops (14 mg/d), SPLAT 17.5 g dollop (46 mg/d), and 1 bubblecap (17 mg/d)	14–184 mg/tree, depending on treatment	Reductions in mortality of treated spruce. Effects on nearby spruce were not determined.
Audley et al. [59]	Individual tree	AK	<i>P. x lutzii</i>	3.5 g MCH (SPLAT MCH, SPLAT3.5), SPLAT3.5 + AKB, SPLAT3.5 + PLUS, 7 g MCH (SPLAT MCH, SPLAT7), SPLAT7 + AKB, and SPLAT7 + PLUS	SPLAT3.5 = two 17.5 g dollops/tree, SPLAT7 = four 17.5 g dollops/tree, 1/tree of other repellents	SPLAT3.5 (147 mg/d), SPLAT7 (294 mg/d), AKB (60 mg/d), acetophenone (103 mg/d), GLV (20 mg/d)	147–417 mg/tree, depending on treatment	Reductions in mortality of treated spruce and of spruce within 11.3 m of treated spruce; no differences among treatments.
Audley et al. [59]	Individual tree	CO	<i>P. engelmannii</i>	3.5 g MCH (SPLAT MCH, SPLAT3.5), SPLAT3.5 + AKB, SPLAT3.5 + PLUS, 7 g MCH (SPLAT MCH, SPLAT7), SPLAT7 + AKB, and SPLAT7 + PLUS	SPLAT3.5 = two 17.5 g dollops/tree, SPLAT7 = four 17.5 g dollops/tree, 1/tree of other repellents	SPLAT3.5 (147 mg/d), SPLAT7 (294 mg/d), AKB (60 mg/d), acetophenone (103 mg/d), GLV (20 mg/d)	147–417 mg/tree, depending on treatment	Reductions in mortality of treated spruce and of spruce within 11.3 m of treated spruce; no differences among treatments.

¹ Release devices are bubblecaps or pouches, unless otherwise specified. ² Medical device developed for chronic drug infusions. ³ AKB = Acer kairomonal blend (linalool + β -caryophyllene + (Z)-3-hexanol) [36,37], PLUS = acetophenone + (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol [35], GLV = (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol. ⁴ Methods for assessing release rates varied by study. Release is passive (except for Med-e-Cell) and depends on temperature and time since deployment. ⁵ Represents the release of all repellents. ⁶ Significant inhibitory effect compared to the control. NS = not statistically significant (no effect).

Following the work by Ross et al. [56], limited research occurred on MCH and other spruce beetle repellents for years due to declines in spruce populations (especially in Alaska) and the occurrence of a large mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic. The mountain pine beetle epidemic diverted research efforts from spruce beetle to mountain pine beetle. Spruce beetle populations began increasing again in several western U.S. states in 2013, with an ongoing epidemic in Alaska affecting >650,000 ha since 2016. With the resurgence in spruce beetle activity came a resurgence in research on spruce beetle repellents (Table 2). The experimental methods used varied widely among studies and, as such, we encourage the reader to consult each publication listed in Table 2 for more information. Some publications report levels of colonization (e.g., “attacked”, “strip attacked”, “mass attacked”, “severely attacked”, etc.), while others include levels of spruce mortality. The former is based on the distribution and density (attacks/m²) of spruce beetle attacks observed on the bole the year the study was initiated. The latter requires waiting about one year to confirm tree mortality based on the presence (dead) or absence (live) of crown fade, which we feel is important given the overall objective is to reduce levels of spruce mortality attributed to spruce beetles. Furthermore, in our own research, we have occasionally misclassified trees as “mass attacked” (indicative of eminent mortality), despite our collective experiences of conducting these types of studies in several bark beetle-host systems. For studies that provided estimates of both spruce beetle colonization and spruce mortality, we focused on mortality (Table 2).

Hansen et al. [57] suggested that MCH was effective for protecting Engelmann spruce from spruce beetles in Utah. In their study, mass attacks were >30 times more likely on Engelmann spruce in control plots compared to plots treated with MCH + isophorone + sulcatone and lethal trap trees (Table 2), although the effects of each treatment could not be distinguished. This led Hansen et al. [36] to evaluate MCH at three doses (240, 480, or 960 mg/ha) for the areawide protection of Engelmann spruce in New Mexico and Utah (Table 2). MCH bubblecaps were stapled to the north aspects of tree boles, at a height of ~2 m, in a grid pattern. All doses of MCH reduced the severity of spruce beetle attacks [36]. In related efforts, MCH, an *Acer* kairomone blend (AKB; linalool, β -caryophyllene, and (Z)-3-hexanol), and MCH + AKB were evaluated in individual tree studies in New Mexico and Utah [36]. AKB was included on the basis of AKB being inhibitory to spruce beetles in trapping assays [36,37]. All repellent treatments reduced the probability of mass attacks on individual Engelmann spruce, but MCH + AKB was most effective. This led the authors to conclude that MCH alone was a “marginal” areawide and individual tree protectant, but that deploying MCH with other repellents, such as AKB, increases its efficacy [36].

Hansen et al. [37] evaluated repellents (MCH, MCH + AKB, MCH + AKB + sulcatone) in individual tree assays in Engelmann spruce in Colorado and Utah (2017), white spruce in Alaska (2018), and Engelmann spruce in Colorado, New Mexico, Utah, and Wyoming (2018) (Table 2). All repellent treatments reduced the probability of severe attacks on treated spruce and on spruce within 10 m of treated spruce, with the exception of the study in Alaska. In Alaska, no effect was observed on treated spruce, but there was a significant reduction in the probability of severe attacks on spruce within 10 m of treated spruce [37]. Spruce within 10 m of control spruce were 4.2–6.9 times more likely to be in a higher-severity attack class. Collectively, the research by Hansen et al. [36,37,57] identified several spruce beetle repellents suitable for spruce protection, with MCH + AKB being the most promising.

Following the development of SPLAT Verb (10.0% active ingredient (verbenone) by weight; ISCA Inc., Riverside, CA, USA) for protecting pines from mountain pine beetles [61], a SPLAT formulation containing MCH was developed (SPLAT MCH, 10.0% active ingredient (MCH) by weight; ISCA Inc.; Figure 6B). SPLAT MCH was first evaluated for individual tree and areawide protection of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)

Franco) from the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in Idaho and New Mexico [62]. SPLAT MCH was as effective as MCH bubblecaps for protecting individual Douglas-fir, the latter considered a highly effective treatment for reducing host tree losses to Douglas-fir beetles [63]. For spruce beetles, SPLAT MCH was first evaluated at two doses (35 and 70 g of SPLAT MCH/tree) alone and combined with AKB and PLUS (acetophenone, (E)-2-hexen-1-ol, and (Z)-2-hexen-1-ol) for protecting Engelmann spruce in Wyoming [58] (Table 2). PLUS was identified by Fettig et al. [35] for western pine beetle (*Dendroctonus brevicornis* LeConte) and when combined with verbenone (the antiaggregation pheromone component of western pine beetle) yields sufficient inhibition of western pine beetle to impart protection of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), while verbenone alone is ineffective. All repellent treatments significantly reduced the mortality of treated spruce and of spruce within 11.3 m of treated spruce [58] (Figure 7C,D). Additional research by Audley et al. [38] confirmed the efficacy of these treatments on Lutz spruce in Alaska, but on Engelmann spruce in Utah, only SPLAT MCH + AKB and SPLAT MCH + octenol were effective (Table 2). The effects on nearby spruce were not determined in the Utah study, as spruce beetles were already colonizing trees when the study was being established [38].

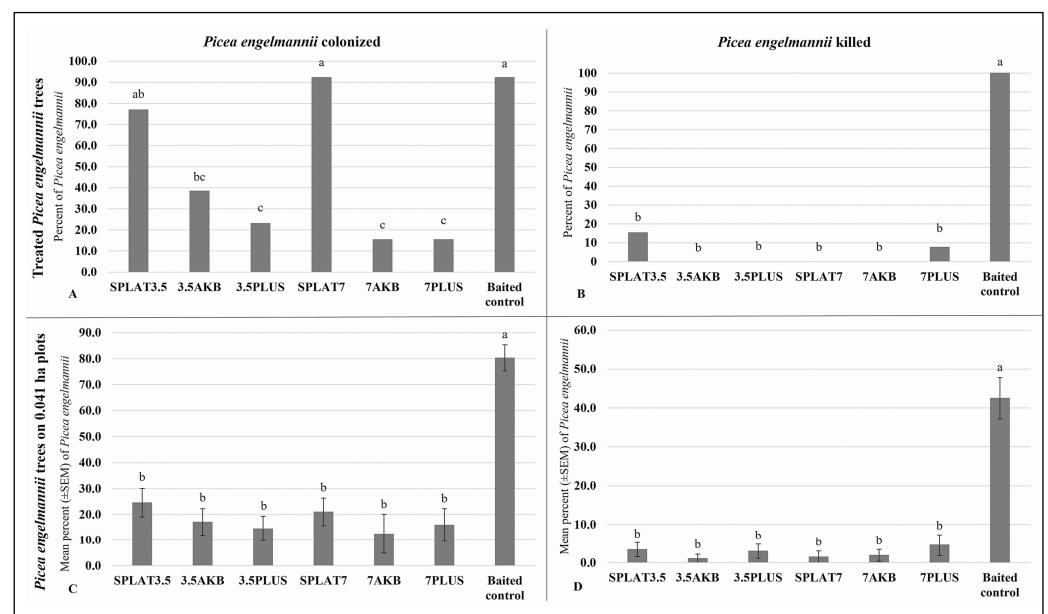


Figure 7. Percentage of Engelmann spruce (*Picea engelmannii*) baited with frontalinal that were (A) colonized and (B) killed by spruce beetles (*Dendroctonus rufipennis*) and mean percentage ($\pm$ SEM) of Engelmann spruce within 11.3 m of individually treated Engelmann spruce that were (C) colonized and (D) killed by spruce beetles in Wyoming, U.S. SPLAT MCH = 10% MCH by weight (ISCA Inc., Riverside, CA, USA) at 3.5 g or 7 g of MCH (35 or 70 g of SPLAT Verb); AKB = linalool + β -caryophyllene + (Z)-3-hexanol [36,37]; PLUS = acetophenone + (E)-2-hexen-1-ol + (Z)-2-hexen-1-ol [35]. Within each subfigure, different letters among treatments indicate significantly different means. Adapted from Audley et al. [58].

Audley et al. [59] evaluated two doses of MCH (35 and 70 g of SPLAT MCH/tree) alone and combined with AKB and PLUS for protecting Lutz spruce in Alaska and Engelmann spruce in Colorado (Table 2). All repellent treatments significantly reduced the mortality of treated spruce and of spruce within 11.3 m of treated spruce. In a related study, SPLAT MCH and Synergy Shield MCH Double Bubblecaps (Synergy Semiochemical Corp. Delta, BC, USA) were evaluated at three doses (1, 3, and 7 g of MCH/tree) for protecting individual Lutz spruce in Alaska [59]. The effects on nearby spruce were not determined due to time constraints. All repellent treatments significantly reduced the mortality of treated

spruce [59] (Figure 8). Across all three of the studies by Audley et al. [59], only two (of 300) repellent-treated spruce died, while 47%–80% mortality occurred in the controls.

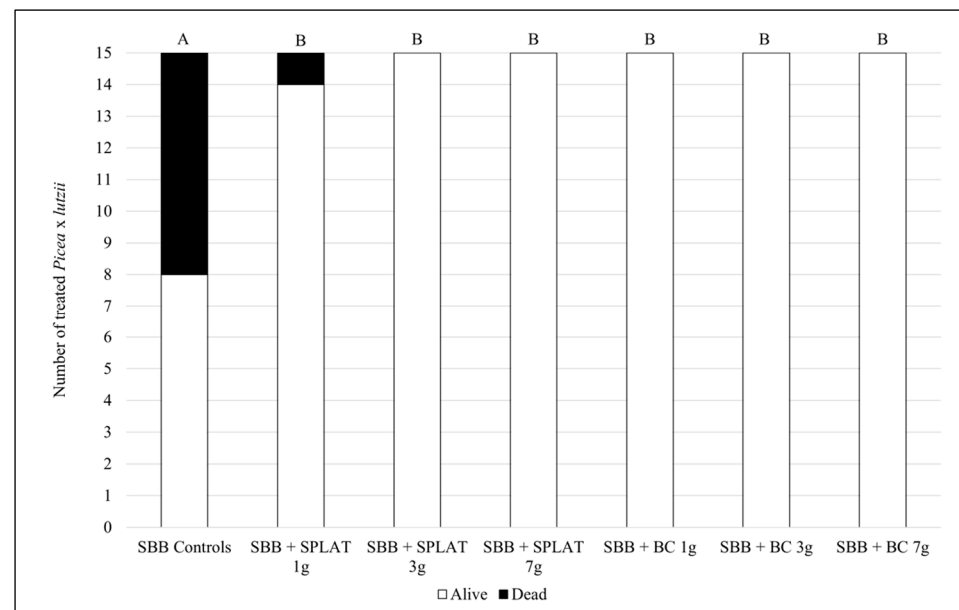


Figure 8. Number of Lutz spruce (*Picea x lutzii*) baited with frontalinal that were killed by spruce beetles (*Dendroctonus rufipennis*) in Alaska, U.S. SPLAT = SPLAT MCH (ISCA Inc., Riverside, CA, USA); BC = Synergy Shield MCH Double Bubblecaps (Synergy Semiochemical Corp. Delta, BC, Canada); g = grams of active ingredient (MCH). Different letters among treatments indicate significantly different means. Modified from Audley et al. [59].

5. Conclusions

Much progress has been made in identifying and developing semiochemicals for the management of spruce beetles in western North America (Tables 1 and 2). Spruce beetle aggregation pheromone components include frontalinal, seudenol, MCOL, and verbenene. Their attraction to these aggregation pheromone components is enhanced by the co-release of host terpenes. Effective baits are available, inexpensive, and used for survey and detection, population suppression, snag creation, and research purposes. The availability of baits has furthered the understanding of the ecology of spruce beetle by providing a means of attracting and manipulating beetles for experimental study. Semiochemical attractants, unlike semiochemical repellents, do not need to be registered with the U.S. Environmental Protection Agency (EPA) or the Health Canada Pest Management Regulatory Agency.

The antiaggregation pheromone of spruce beetle is MCH (3-methyl-2-cyclohexen-1-one). Several formulations of MCH are registered for tree protection purposes in the U.S. and Canada, while SPLAT MCH is currently under review by the EPA. We found only one peer-reviewed study [56] on MCH (or MCH + other repellents) that failed to demonstrate efficacy for spruce protection, while two other studies showed efficacy for only some of the repellent treatments that were evaluated [38] or at one of two spatial scales investigated [37] (Table 2). The findings by Ross et al. [56] are likely explained, in part, by the extreme spruce beetle population (based on the numbers of spruce that were mass attacked) and the insufficient distribution of MCH bubblecaps/unit area. Recent efforts have focused on comparing MCH alone to MCH + other repellents (e.g., AKB and PLUS) in hope of increasing treatment efficacy. A challenge is that these additional repellents would require registration by regulatory agencies. Research by Audley et al. [38,58,59] in Alaska, Colorado, and Wyoming, showed that all repellents evaluated significantly reduced the mortality of treated spruce and of spruce within 11.3 m of treated spruce. The data shown

in Figure 7B are particularly promising, as 100% of the control trees were killed by spruce beetles, while several of the repellent treatments experienced no mortality. The next logical step is to evaluate the efficacy of these treatments at larger spatial scales (e.g., 1-ha plots).

Only one study on spruce beetles compared MCH bubblecaps to SPLAT MCH [59], and no differences in spruce mortality were observed among the repellent treatments (Figure 8). An advantage of SPLAT MCH is that it degrades (within 2 years, depending on abiotic conditions) and, thus, SPLAT MCH, unlike MCH bubblecaps, does not need to be retrieved from the field following its application. The use of SPLAT MCH, a flowable matrix, also allows for flexibility in applying different doses (dollops, Figure 4) at different rates and spacings/unit area [61]. For individual tree protection, an application rate of 70 g of SPLAT MCH/tree is proposed (for labelling) and, for areawide protection, 700 g to 5 Kg of SPLAT MCH/acre (1.7–12.4 kg/ha) is proposed. A MCH human health and ecological risk assessment on forest use patterns (for bubblecaps) is available [64]. Other methylcyclohexanones similar in molecular structure to MCH have been shown to repel bees, e.g., [65], which has been expressed as a concern by some individuals. However, a study of MCH bubblecaps and SPLAT MCH on forest pollinators (bees) in Idaho and Montana found no detrimental effects [66]. While semiochemical repellents may not provide the same level of spruce protection as insecticides, semiochemical repellents can be applied to larger and/or environmentally sensitive areas, with less restrictions and fewer regulatory concerns. Technical assistance concerning the use of semiochemicals for the management of spruce beetles can be obtained in relevant areas from Forest Health Protection (USDA Forest Service) entomologists, state forest entomologists, and county extension agents in the U.S., and provincial entomologists in Canada.

Author Contributions: Conceptualization, C.J.F.; investigation, C.J.F., J.P.A. and A.S.M.; writing—original draft preparation, C.J.F. and J.P.A.; writing—review and editing, C.J.F., J.P.A. and A.S.M.; project administration, C.J.F. All authors have read and agreed to the published version of the manuscript.

Funding: This work received no external funding.

Acknowledgments: We thank numerous colleagues who have shaped our thinking on the chemical ecology of bark beetles. In particular, John Borden (JHB Consulting), Matt Hansen (USDA Forest Service, retired), and Jason Moan (Alaska Division of Forestry and Fire Protection) have influenced our research on semiochemical repellents for spruce beetle. We thank Shakeeb Hamud (USDA Forest Service, retired) for his assistance with literature searches and three anonymous reviewers for their critiques. We dedicate this publication to Chrissy Howell (USDA Forest Service, retired), whose support and encouragement over the years has been invaluable.

Conflicts of Interest: The authors declare that there are no conflicts of interest.

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