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NOTE

Trap trees: an effective method for monitoring mountain pine beetle activities in novel habitats

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Abstract: Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) has recently expanded its range into the lodgepole pine forests in Alberta, Canada. However, it is unknown whether semiochemical tools developed in the beetle's historical range are suitable for monitoring MPB in the new environment. Thus, we conducted a 3-year study to test new MPB monitoring tools in Alberta. A field trial selected a combination of MPB pheromones and two host volatiles. Using this combination, we baited different numbers of trees in triangular, square, or rectangular formations (spatial arrangements of trees) to determine how the densities of baited trees affect MPB attraction. Three plots, each made up of three formations, were arranged in a linear transect at various distances between formation boundaries. The proportion of baited trees mass-attacked was highest in the square formation. However, the proportion of spillover trees mass-attacked (attacks on non-baited trees) was lower when formations were 1 km apart compared with 4 or 8 km apart. In a follow-up test of the square formation alone, there was no difference in trap tree effectiveness between distances of 8 and 12 km. We suggest that four baited trees spaced 50 m apart in a square formation at a 12 km distance can be used in the field.

Key words: bark beetle pheromones, *Dendroctonus ponderosae*, host volatiles, insect invasion, beetle management.

Résumé : Le dendroctone du pin ponderosa (DPP; *Dendroctonus ponderosae* Hopkins) a récemment agrandi son aire de répartition dans les forêts de pin tordu en Alberta, au Canada. Cependant, on ne sait pas si les outils semiochimiques développés dans son aire de répartition historique sont appropriés pour le suivi du DPP dans ce nouvel environnement. Par conséquent, nous avons réalisé une étude d'une durée de 3 ans pour tester les nouveaux outils de suivi du DPP en Alberta. Un essai sur le terrain a permis de sélectionner des phéromones du DPP combinées à deux composés volatiles produits par l'hôte. Avec cette combinaison, nous avons appâté différents nombres d'arbres disposés en triangle, carré ou rectangle (disposition spatiale des arbres) pour déterminer de quelle façon la densité des arbres appâtés influence l'attraction du DPP. Trois parcelles, chacune composée de trois formations, ont été établies le long d'un transect linéaire en variant la distance entre la limite des formations. La proportion des arbres appâtés ayant subi une attaque massive était la plus élevée dans la formation carrée. Cependant, la proportion des arbres non appâtés ayant subi une attaque massive due à un effet de débordement était plus faible lorsque les formations étaient distantes de 1 km comparativement à 4 ou 8 km. Dans un test subséquent portant seulement sur la formation carrée, il n'y avait pas de différence dans l'efficacité des arbres pièges entre des distances de 8 et 12 km. Nous suggérons que quatre arbres appâtés espacés de 50 m dans des formations carrées distancées de 12 km soient utilisés sur le terrain. [Traduit par la Rédaction]

Mots-clés : phéromones de scolytes, *Dendroctonus ponderosae*, composés volatiles produits par l'hôte, invasion d'insecte, gestion du dendroctone.

Introduction

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins (Col: Curculionidae, Scolytinae)) outbreaks have killed millions of mature pine trees, primarily lodgepole pines (*Pinus contorta* Douglas), in western North America over the last 10 years (Safranyik et al. 2010). In western Canada, MPB outbreaks began in lodgepole pine forests in central British Columbia in 1999 and invaded the eastern edge of the lodgepole pine range in north-central Alberta in 2006 (Safranyik et al. 2010). MPB is now established in the hybrid lodgepole pine – jack pine (*Pinus banksiana* Lamb.) forests and was detected in the jack pine forests in eastern Alberta in 2016 (Alberta Agriculture & Forestry (AAF) 2016). Improved semiochemical tools and deployment methods are needed at the periphery of this recent expansion to detect and monitor MPB at low densities in these novel habitats.

MPB has a complex life history, with beetle pheromones and host chemicals facilitating beetle aggregation and colonization on host trees (Wood 1982). Female beetles initiate the attack, and if a host is acceptable, they release the aggregation pheromone *trans*-verbenol that attracts both sexes of beetles. Responding males mate with the females and release the aggregation pheromone *exo*-brevicomin that attracts mainly females (Pureswaran et al. 2000). The mixture of both male and female aggregation pheromones serves as a powerful attractant. At this stage, volatile host chemicals, mainly monoterpenes that are released along with beetle aggregation pheromones from attacked trees, increase beetle attraction to host trees (Borden et al. 2008). The aggregation is required for the depletion of host tree defenses, successful host colonization, and beetle reproduction at high densities (Safranyik et al. 2010). In the later stages of host colonization, aggregation

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pheromone production declines and beetles instead produce frontalin and verbenone — anti-aggregation pheromones that mediate the number of MPB arriving to the host (Pureswaran et al. 2000). Following mating, female beetles lay eggs within the phloem, and these eggs develop into larvae that overwinter, mature to adults, and then emerge to attack live trees, thus repeating the cycle.

Pheromone baits attached to either flight-intercept or funnel traps or trees (hereafter trap trees) are commonly used as operational tools for beetle management in beetle-affected forests (Borden et al. 2008). In general, beetle traps baited with semiochemicals are used to monitor the beetle flight period within an area, whereas baited trees are used to concentrate and contain local beetle populations on certain trees in an area. This latter operational tool is currently being used to monitor beetle presence in Alberta. Briefly, in this tactic, three mature pine trees, about 50 m apart in a triangular formation, baited with a two-component MPB bait (*trans*-verbenol and *exo*-brevicomin) are set up every 8 to 9 km in the zone of highly or extremely susceptible stands. Baited trees and nearby non-baited trees are inspected for signs of attacks at the end of the beetle flight period. Tree baiting in this manner is a straightforward, cheap, and logistically simple monitoring method. Baited trees also help concentrate MPB attacks into a defined area on or around the bait sites by attracting the emergent brood from nearby infested stands or beetles dispersing from distant forests (Borden 1986; Gray and Borden 1989). However, the efficacy of commercially available baits for monitoring MPB populations in novel habitats has previously not been tested. Furthermore, it is unclear whether the current MPB bait and current baited tree conformation and deployment distance on the landscape are effective for monitoring low-density MPB populations in novel habitats.

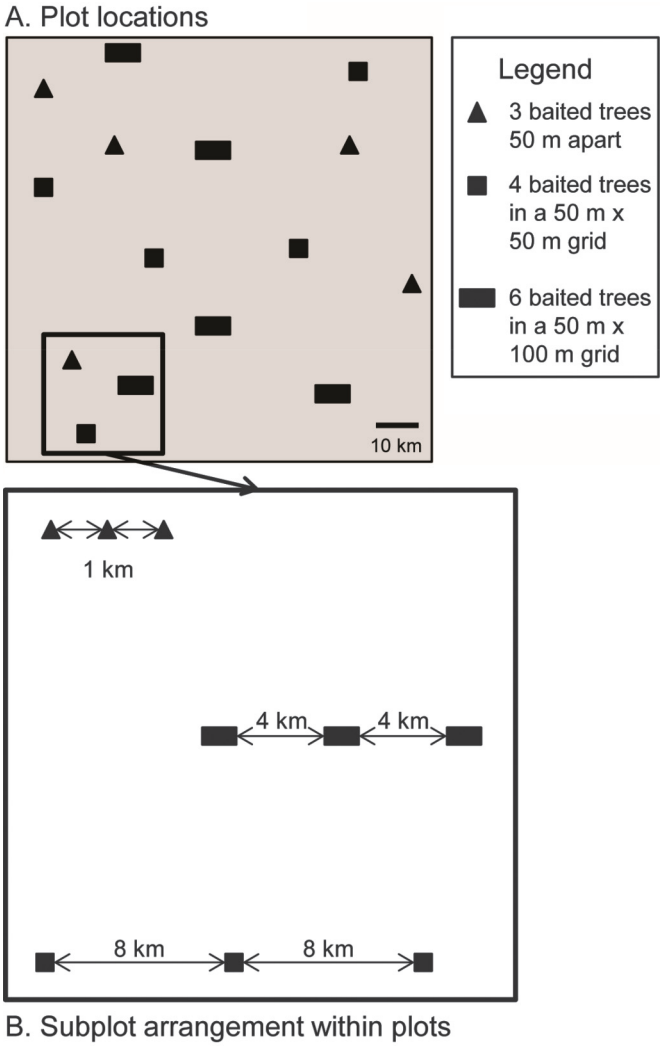
Thus, our primary objectives were to (*i*) assess and attempt to improve the currently available commercial MPB baits to monitor low-density beetle populations in novel habitats, (*ii*) develop an efficient field protocol for the deployment of trap trees to monitor and detect these populations, and (*iii*) determine whether trap trees can be used to survey beetle colonization in novel habitats.

Materials and methods

Determining the optimum attractant

We compared attraction of MPB to various baits using flight-intercept traps (Advanced Pheromone Technologies, Marylhurst, Oregon, USA) near Swan Hills (54°33.7′N, 115°30.4′W), Alberta, from 14 July to 18 August 2014. We tested the standard MPB bait (*trans*-verbenol, *exo*-brevicomin plus terpinolene) alone or in combination with several host- and beetle-produced chemicals that could potentially increase attraction of MPB to the aggregation pheromones (Hughes 1973; Sakai and Toruyamasaki 1991; Miller and Lindgren 2000; Pureswaran et al. 2000; Kashiwagi et al. 2006; Borden et al. 2008; Erbilgin et al. 2014). The six treatments were as follows: (1) standard MPB bait alone or in combination with (2) 3-carene, (3) 3-pinen-2-ol, (4) myrcene, (5) myrtenol, or (6) quercivorol. Traps were suspended from 2 m long poles, placed 15 m apart, and organized into treatment blocks. Blocks were set 100 m from each other. Captured beetles were removed from the traps every 4 days. The location of the treatments within blocks was rotated clockwise by moving the position of each trap including the bait at every collection date. All baits are formulated to last 40–50 days in field conditions (Synergy Semichemicals Inc., Burnaby, B.C., Canada). Release rates of *trans*-verbenol, *exo*-revicomin, 3-carene, 3-pinen-2-ol, myrcene, myrtenol, and quercivorol per 24 h at 20 °C (quercivorol at 25 °C) were determined by Synergy Semiochemicals and are approximately 120 μg, 1.4 mg, 140 mg, 2 mg, 175 mg, 1.5 mg, and 3 mg, respectively. Pheromones were delivered in bubble caps that contained liquid bait in a reservoir with an impervious backing and a thin plastic membrane heat-sealed over the bubble, and monoterpene hydrocarbons were in sealed 5 mL low-density polyethylene vials.

Fig. 1. Schematic diagram showing relative locations of (A) plots and (B) subplots. Lodgepole pine (*Pinus contorta*) dominated areas that were identified using geographic information system and ground truth were randomly assigned formation and distance combination treatments.



Developing a trap-tree system

Trees baited with the standard MPB bait plus myrcene were used to bait trees in the remaining 2 years of the project. In 2015, we used a grid pattern with different densities of trap trees to investigate how MPB attraction is affected by the number of baited trees per trap tree formation and the distance between trap trees (Fig. 1). Trap trees were arranged in three formations at the following densities: (*i*) three baited trees spaced 50 m apart arranged in a triangular formation, a modification of the current protocol used by the Alberta Government (Alberta Government 2016); (*ii*) four baited trees spaced 50 m apart in a square formation; and (*iii*) six baited trees spaced 50 m apart arranged in a rectangular formation (50 m × 100 m). Each formation was considered a subplot and a plot consisted of three subplots (i.e., three square formations) arranged in a linear transect with a distance of 1, 4, or 8 km between subplot (subreplicates) borders to evaluate the optimum distance between subplots. We kept the maximum distance between subplots at 8 km because that approximates the current distance used in Alberta. Each formation and distance combination was randomized and repeated three times in different

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locations in Whitecourt (54°16.3′N, 116°13.0′W), Fox Creek (53°57.0′N, 116°50.9′W), and Swan Hills (54°34.9′N, 115°29.7′W) in lodgepole pine dominated forests, yielding 81 subplots and 351 baited trees. Plots were separated by a minimum of 10 km.

To determine the most efficient and effective trap tree system, the results of the 2015 study determined which distance treatments were tested in 2016. The 2015 experiment revealed that the square trap tree formation was best because it was more effective at concentrating beetle attacks in a relatively small area (See Results section for details). In 2016, we selected 18 sites within the same general study area as the first trap tree experiment and tested the square formation at two inter-subplot distances: 8 km and 12 km. We attempted to replicate each distance three times on the landscape (e.g., 8 km – 8 km – 8 km), but due to lack of suitable stands, we set up two replicates of the 8 km treatment and three replicates for the 12 km treatment. All treatments were applied at random. A total of 72 trees were baited. Plots were separated by a minimum of 15 km.

In both experiments, mature lodgepole pine trees (>80 years old with an average diameter at breast height (DBH) > 25 cm) were baited. Baits were placed at least 2 m from the ground on the main stem of trees on the northern aspect. All baits were attached prior to MPB flight (7–10 July 2015 and 19–24 July 2016) and retrieved at the end of the flight season (1–9 September 2015 and 29–31 August 2016).

At the end of the flight season, all baited pine trees and all pine trees within a 50 m radius of each baited trap tree were examined for MPB attacks. We recorded the DBH of all trees within each of three variable-radius plots (basal area factor = 6 metric) per subplot, using baited trees (randomly selected in the square and rectangular formations) as plot centres. Stand basal area, density, and diameter distributions were calculated for pine and all other tree species. Further, all pine trees were categorized as non-attacked, attacked (<31.25 attacks·m^{-2}), and mass-attacked (≥31.25 attacks·m^{-2}) by counting the number of attacks as evidenced by pitch tubes and frass within the portion of the stem 1 to 2 m from the ground (Raffa and Berryman 1983).

Data analysis

A Kruskal–Wallis test was used to determine the attractiveness, measured as mean number of captures per trap day, of the baits to MPB using flight-intercept traps. This test was bootstrapped using within-group resampling and 10 000 iterations from which a P value was calculated as the proportion of non-significant test iterations.

For the field experiment in 2015, chi-squared (χ^2) tests were used to evaluate two-way contingency tables constructed from a treatment (either formation or distance treatment) variable and a response variable (attack status of trap trees (i.e., attacked or non-attacked), or mass-attack status of trap trees, or spillover trees). Chi-squared tests were also used to evaluate the proportion of spillover trees (relative to all spillover trees) in formation and distance treatments separately. Differences between treatment levels were tested for significance using pairwise χ^2 tests with a Bonferroni-adjusted α (0.017). Variation in mean MPB attack density on trap trees and spillover trees among formation and distance treatments was tested for significance using mixed-effects analysis of covariance (ANCOVA), with formation, shape, and lodgepole pine basal area and density as fixed effects and plot designation as a random effect. Separate linear mixed-effects models for response variables of the mean number of spillover trees and MPB attack density on spillover trees were used to test their statistical relationship to fixed (mean MPB attack density on trap trees and lodgepole pine basal area and density) and random (plot designation) factors. Response variables were log(x + 1) transformed as needed to satisfy models assumptions. When used, these transformations satisfied model assumptions. Differences in mean lodgepole pine basal area and density were analyzed using separate two-way ANOVAs each testing formation and distance treatment main effects and formation–distance interactions.

Table 1. Mean (±standard error (SE)) and total mountain pine beetle (MPB; *Dendroctonus ponderosae*) captured per trapping day in traps baited with different chemical lures in Alberta.

Treatment	Mean captures per trap per day (±SE)	Total captures per trap day
Standard MPB lure (*trans*-verbenol, *exo*-brevicomin plus terpinolene)	0.6 (±0.2)	3.0
Standard MPB lure + 3-carene	0.5 (±0.2)	3.3
Standard MPB lure + 3-pinenol-2-ol	0.4 (±0.1)	1.3
Standard MPB lure + myrcene	0.8 (±0.3)	7.4
Standard MPB lure + myrtenol	0.5 (±0.1)	3.6
Standard MPB lure + quercivorol	0.5 (±0.1)	1.8

For the 2016 field experiment, differences in mean MPB attack density on trap trees and spillover trees between distance treatments were tested for statistical significance using Mann–Whitney U tests. These tests were also used to assess differences in lodgepole pine basal area and density between treatments, and tests were bootstrapped in the same manner as described above. Differences in mean lodgepole pine basal area and density between distance treatments were tested for significance using bootstrapped Mann–Whitney U tests as above.

All analyses were performed within the R software environment version 3.3.1 (R Core Team 2016). Mixed-model ANCOVAs were performed using functions provided in R packages "nlme" version 3.1-128 (Pinheiro et al. 2016).

Results

Determining the optimum attractant

There was no statistical difference among bait treatments in mean catch of MPB in flight-intercept traps with baits (P = 0.963), although traps baited with the standard MPB bait plus myrcene captured 51%–82% more beetles in total than traps baited with other baits (Table 1).

Developing a trap tree system

Pine basal area and density of stands did not vary statistically among formations (triangle, square, or rectangle) (P = 0.549) or distances (1, 4, or 8 km) (P = 0.651), indicating similar stand structure among treatments. In 2015, 92% of all trap trees were colonized by MPB. The proportion (calculated as the number of attacked trap trees in each treatment out of the total number of trap trees among treatments) of trap trees attacked did not differ among formation and distance treatments (P = 0.987) (Table 2A).

Mean MPB attack density per subplot ranged from 0.16 to 60.59 attacks·m^{-2} of bark and was positively related to pine basal area ($F_{[1,51]}$ = 8.47, P = 0.005) but did not differ significantly among formation (P = 0.131) and distance (P = 0.867) treatments and was not related to pine density (P = 0.225). Overall, 21% of trap trees were mass-attacked by MPB, and the proportion (calculated as the number of mass-attacked trees in each treatment out of the total number of trap trees among treatments) of trap trees that were mass-attacked significantly differed among trap tree formation treatments ($\chi^2_{[2]}$ = 13.67, P = 0.001). This proportion of trees within each treatment was similar in the triangular (0.28) and square (0.32) formations, which were significantly greater than that of the rectangular formation (0.13).

A total of 224 spillover trees were attacked by MPB in the study sites, and the number varied significantly among formation and distance treatments ($\chi^2_{[4]}$ = 35.90, P < 0.001; Table 2B). The proportion (calculated as the number of spillover trees in each treatment out of the total number of spillover trees among treatments) of spillover trees differed among formations ($\chi^2_{[2]}$ = 22.13, P < 0.001) and was 28% and 129% greater in the rectangular than in

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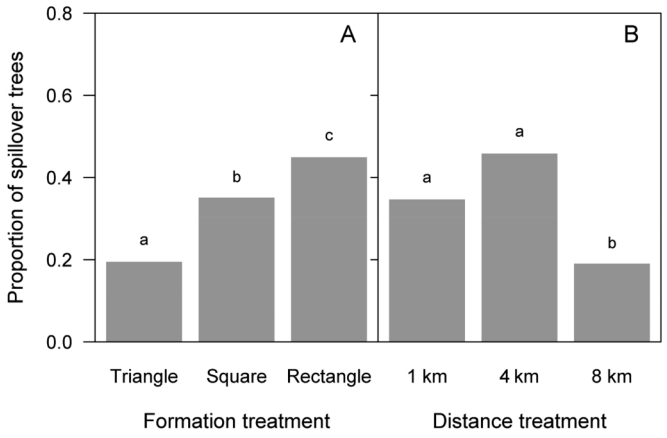
Table 2. The total number (proportion) of (A) baited and (B) non-baited spillover trees attacked by mountain pine beetle (MPB; *Dendroctonus ponderosae*) per site formation (columns) and distance (rows) treatments in Alberta, Canada.

	Total no. (proportion) of trees attacked		
Distance	Rectangle	Square	Triangle
(A) Baited trees			
1 km	50 (0.94)	35 (0.97)	24 (0.89)
4 km	41 (0.76)	31 (0.97)	24 (0.89)
8 km	49 (0.92)	35 (0.97)	27 (1.00)
Total (316)	140 (0.88)	101 (0.97)	75 (0.93)
(B) Non-baited spillover trees			
1 km	55 (0.26)	10 (0.30)	13 (0.54)
4 km	32 (0.30)	51 (0.41)	20 (0.32)
8 km	14 (0.35)	18 (0.33)	11 (0.46)
Total (224)	101 (0.30)	79 (0.34)	44 (0.44)

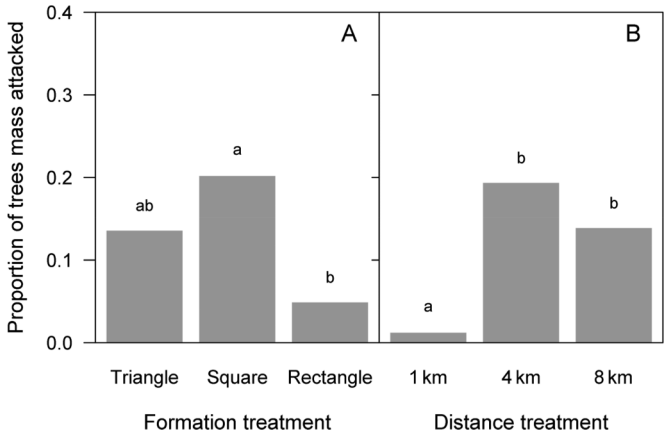
Fig. 2. The proportion of spillover (non-baited and attacked by mountain pine beetle [*Dendroctonus ponderosae*]) trees by (A) bait site formation and (B) distance treatments in 2015. Proportions were calculated as the number of spillover trees in each treatment out of the total number of spillover trees among treatments. Bars with different letters significantly differ as indicated by pairwise, Bonferroni-adjusted χ^2 tests using counts of spillover trees.



the square and triangular formations, respectively (Fig. 2A). The proportion of spillover trees also differed among distance treatments ($\chi^2_{[2]} = 24.33$, $P < 0.001$) and was 80% and 140% greater in the 1 km and 4 km treatments, respectively, than in the 8 km treatment (Fig. 2B). Furthermore, the number of spillover trees in each site was positively associated with the mean MPB attack density on trap trees ($F_{[1,52]} = 22.65$, $P < 0.001$). The number of spillover trees per trap tree did not differ among formation or distance treatments.

The mean attack density on spillover trees did not differ significantly among formation or distance treatments but was positively associated with the pine basal area covariate ($F_{[1,50]} = 10.22$, $P = 0.002$) and mean MPB attack density on trap trees ($F_{[1,50]} = 14.57$, $P < 0.001$). The proportion (calculated as the number of mass-attacked trees in each treatment out of the total number of spillover trees in the respective treatment) of spillover trees that were mass-attacked differed significantly within trap tree formation ($\chi^2_{[2]} = 9.92$, $P = 0.007$) and was about three times greater in the square formation than in the rectangular formation (Fig. 3A). The proportion of mass-attacked spillover trees also differed significantly among distance treatments ($\chi^2_{[2]} = 13.95$, $P < 0.001$) and was >10 times greater in the 8 km and 4 km treatments than in the

Fig. 3. The proportion of mass-attacked spillover (non-baited and attacked by mountain pine beetle [*Dendroctonus ponderosae*] at densities indicative of beetle mass attack) trees by (A) bait site formation and (B) distance treatments. Proportions were calculated as the number of mass-attacked trees in each treatment out of the total number of spillover trees in the respective treatment. Bars with different letters significantly differ as indicated by pairwise, Bonferroni-adjusted χ^2 tests using counts of mass-attacked trees.



1 km treatment (Fig. 3B). This proportion did not differ between the 4 km and 8 km treatments (Fig. 3B).

In 2016, 92% of trap trees were attacked by MPB (95% and 91% in the 8 km and 12 km distance treatments, respectively), and the average attack density did not differ between treatments ($P = 0.910$). Mass attacks occurred on 21% of trap trees, with 30% of trees attacked in the 12 km treatment compared with 16% in the 8 km treatment, but that difference was not significant ($P = 0.730$). Lodgepole pine basal area ($P = 0.302$) and density ($P = 0.884$) did not differ between distance treatments.

Six spillover trees were attacked in each distance treatment with no difference in the mean attack density of MPB between treatments ($P = 0.921$). Spillover trees were not mass-attacked by MPB because the beetle attack densities did not exceed 12.0 attacks·m^{-2} of bark.

Discussion

Our findings indicate that addition of a host volatile to the current MPB bait can increase the total number of MPB caught in novel habitats. Although our results were not statistically significant, flight-intercept traps baited with the standard MPB bait (*exo*-brevicomin, *trans*-verbenol plus terpinolene) plus myrcene caught more beetles than any other combinations, supporting the results of Borden et al. (2008) in British Columbia, Canada. Furthermore, when the bait is deployed in conjunction with a modified trap tree configuration on the landscape, it can effectively monitor low-density beetle populations and concentrate attacks in a discrete area. In both 2015 and 2016, over 90% of trees baited with the standard MPB bait plus myrcene had one or more MPB attacks. In 2015, numbers and proportions of mass-attacked trap trees were similar between the square and triangular formations, but the square formation had greater proportions of trees with mass attacks than the triangular formation. The square formation at 8 km distance had the lowest spillover attacks on neighbouring non-baited trees compared with shorter distance treatments but was the same as the 12 km distance treatment. Below, we argue that trap trees can be used in three possible management activities targeting MPB.

Trap trees can concentrate beetle attacks by attracting them into baited stands and preventing them emigrating from them

We found that beetles colonized over 90% of all baited trees in both consecutive years, and of those attacks, 21% were mass-attacked. The majority of spillover attacks occurred within a 10 m

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radius to baited trees, and relatively few non-baited trees were attacked and fewer of those were mass-attacked. These results demonstrate that tree baiting was successful for increasing beetle immigration into and arrestment within the baited stands, supporting the conclusion of earlier studies in British Columbia (Borden 1986; Gray and Borden 1989). We suspect that baiting can influence bark beetle dispersal behaviour by two possible mechanisms. First, the continuous release of attractive compounds from the baits on trees likely overrides the effect of anti-aggregation pheromones produced by mated beetles (i.e., swamping) (Borden 1986; Borden et al. 1993), which results in more attacked trees and higher attack densities on the baited than non-baited trees. Second, baited trees may create a flight corridor for beetles within a forest stand rather than allowing beetles to be more dispersed in stands without baits, resulting in a higher concentration of beetle attacks on baited trees in a confined area.

Baited trees can be used to detect beetles at low and high population densities

We found that MPB attacks varied from 0.16 to 60.59 attacks·m^{-2} of bark area in both years, possibly reflecting beetle population sizes in the surrounding forest stands. During tree selection for baiting, we avoided stands with active beetle infestations within a 50 m radius of the baited trees and thus conclude that almost all beetles that colonized baited and non-baited trees immigrated from neighbouring stands. Under the canopies of mature lodgepole pine stands, MPB tends to select suitable hosts nearby (Safranyik et al. 1992; Barclay et al. 1998), and thus trees with low attack densities might reflect low MPB population density. In contrast, mass attacks might be a result of immigration of beetles from neighbouring forest stands with high beetle density (Borden et al. 1983*a*). Although the attractive range of trap trees is unknown, release–recapture experiments with traps baited with *trans*-verbenol, *exo*-brevicomin, and myrcene showed that MPB can fly up to 750 m from their point of release, although the majority disperse within shorter distances (Safranyik et al. 1992; Barclay et al. 1998).

Tree baiting can be used to help detect beetle colonization in novel habitats

A large portion of trees was attacked in both study years. Even though we did not compare the efficacy of baited traps with trap trees, the latter are usually considered superior for attracting beetles because they provide better visual cues for long-distance beetle attraction (Borden et al. 1983*b*; Ryker and Libbey 1982). Furthermore, trap trees provide additional chemical cues, as a result of pheromone production by arriving beetles and the continuous release of host volatiles, for attraction, culminating in accelerated tree colonization (Campbell and Borden 2006). Considering that aerial monitoring cannot detect beetle-attacked trees until the year after attacks have occurred, trap trees may at least provide a simple management tool to detect and monitor MPB activities in novel habitats in the year of beetle attacks.

The operational success of trap trees for monitoring MPB activities requires strong attractants. Adding myrcene to the standard MPB bait increased the total number of beetles caught. Myrcene is common monoterpene of western pines (Gijzen et al. 1993) and can be a strong synergist of MPB pheromone (Borden et al. 2008). Having an effective MPB bait can improve the efficacy of MPB monitoring activities and increase the efficacy of operational control programs. A trap-tree program can be considered successful if no or few non-baited trees occurring in close proximity to the baited trees are attacked by MPB. This may significantly reduce the costs of tree removal at the end of the trap-tree program. It must also be kept in mind that although it is an effective method, trap trees may also pose a risk of starting a bark beetle outbreak if all baited and surrounding non-baited trees attacked are not removed prior to emergence of beetle offspring in the summer.

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