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Predicting *Dendroctonus pseudotsugae* (Coleoptera: Curculionidae) Antiaggregation Pheromone Concentrations Using an Instantaneous Puff Dispersion Model

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ABSTRACT An instantaneous puff dispersion model was used to assess concentration fields of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, antiaggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), within a 1-ha circular plot. Several combinations of MCH release rate and releaser spacing were modeled to theoretically analyze optimal deployment strategies. The combinations of MCH release rate and releaser spacing used in the modeling exercise were based on results of previous field studies of treatment efficacy. Analyses of model results suggest that a release rate up to six times the initial standard, at a correspondingly wider spacing to keep the total amount of pheromone dispersed per unit area constant, may be effective at preventing Douglas-fir beetle infestation. The model outputs also provide a visual representation of pheromone dispersion patterns that can occur after deployment of release devices in the field. These results will help researchers and practitioners design more effective deployment strategies.

KEY WORDS Douglas-fir beetle, Scolytinae, MCH, 3-methylcyclohex-2-en-1-one, pheromone plume

Throughout the range of Douglas-fir, *Pseudotsuga menziezii* (Mirbel) Franco, in western North America, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae), periodically kills trees (Furniss and Carolin 1977, Schmitz and Gibson 1996). At low population densities the beetle preferentially colonizes trees that have recently died or those that are stressed from fire, disease, or other causes (McMullen and Atkins 1962, Furniss 1965, Rudinsky 1966). When favorable breeding sites become abundant after windstorms, wildfire, defoliator outbreaks, extended drought, or other disturbances, populations can reach high densities and successfully overcome the defenses of live trees (Cornelius 1955, Furniss et al. 1979, Wright et al. 1984). These outbreaks can last from one to several years depending upon geographic location, stand conditions, weather, additional natural disturbances, and management actions.

Impacts on resource management goals can be minimized before these large outbreaks through silvicultural activities such as stand density management, and sanitation and salvage harvesting (Lejeune et al. 1961, Williamson and Price 1971, Schmitz and Gibson 1996). During outbreaks, silvicultural treatments are usually less effective because of the time it takes for implementation and, in the case of thinning, the lag time for residual trees to respond to the treatment. In contrast, pheromone-based treatments work quickly in the Douglas-fir beetle system and are effective at reducing Douglas-fir beetle impacts on resource management objectives by preventing or reducing tree mortality in key stands across the landscape (Ross et al. 1996; Ross and Daterman 1997a, b). In particular, 3-methylcyclohex-2-en-1-one (MCH), the antiaggregation pheromone of the Douglas-fir beetle, can be used to protect high-value trees and stands until populations decline to endemic levels (Ross et al. 2006). MCH has been used operationally throughout the western United States since 2000.

Most MCH treatments to date have involved application of a bubble capsule formulation at a recommended rate of 30-g active ingredient per hectare, or approximately 75 capsules per hectare. Deployment of MCH bubble capsules requires personnel to walk through the area undergoing treatment and place MCH dispensers on an approximate 11.5-m grid pat-
tern (Ross et al. 2006). To reduce the cost associated with personnel manually applying MCH, Ross et al. (2002) investigated deploying fewer release devices with higher release rates while keeping the total MCH mass released per treated area constant. They compared three treatment arrangements on 1-ha circular plots. The mass of MCH released remained constant for the three arrangements, however, the spacing and release rate per point differed. The three treatment arrangements were the established initial standard (1×) and two higher release rates with correspondingly wider spacing, 3× and 9× the initial standard. The higher release rates were achieved by placing three or nine MCH bubble capsules together at individual release points. The initial standard and 3× treatments were equally effective at reducing Douglas-fir beetle infestation, but the 9× treatment did not significantly reduce infestation compared with the untreated control plots (Ross et al. 2002). More recently, the efficacy of the 3× treatment was confirmed on larger plots that represented an operational treatment arrangement (Ross and Wallin 2008). The question remains whether an intermediate release rate and spacing combination between the 3× and 9× treatments would effectively prevent Douglas-fir beetle infestation. Identification of the optimal combination of release rate and spacing would reduce overall treatment costs by minimizing the labor required to treat a given area.

We can theoretically explore the MCH concentration fields and plume dilution resulting from the different deployment arrangements using an instantaneous puff dispersion model. This model was developed to simulate time-averaged and 1-s ‘instantaneous’ subcanopy semiochemical concentration fields (Strand et al. 2009). In this paper, we use the model in conjunction with the results from the Ross et al. (2002) field study to accomplish the following objectives: (1) to simulate the three MCH concentration fields resulting from the Ross et al. (2002) treatments to investigate why the 9× treatment failed to prevent colonization on live trees; (2) to explore potential combinations of release rate and releaser spacing and resulting MCH concentration fields between the 3× and 9× treatment arrangements; and (3) to determine the feasibility of conducting further field tests to see if the release rate and distance between MCH bubble capsules can be increased beyond the maximum recommended 3× release rate spaced on a 20-m grid (Ross and Wallin 2008).

Materials and Methods

Model Description. An instantaneous puff model (Peterson et al. 1990, Strand et al. 2009) was used to simulate MCH release, transport, and spread within the 1-ha treatment circles described by Ross et al. (2002). This three-dimensional (3-D) Gaussian puff model releases a puff from every MCH release point every second. The puffs are then transported downwind and dispersed according to the wind field and turbulence characteristics. The turbulence characteristics were calculated from the three components of the measured wind speed (N-S, E-W, and vertical), which were used as input data. The concentration within each puff is calculated using the Gaussian puff equation as described in Strand et al. (2009).

The instantaneous puff model, designed for subcanopy pheromone plume transport and dispersion, was evaluated during development (Strand et al. 2009) using concentrations of a pheromone surrogate (sulfur hexafluoride) measured during subcanopy surrogate pheromone field studies (Thistle et al. 2004, 2011). These field studies used between 45 and 60 chemical samplers (Krasnec et al. 1984), yielding 30-min data, in concentric circles in the near field (0–30 m in all directions) around a source of tracer gas. The samplers were deployed in the canopy trunk space. Monitoring included elevated samplers as well as four 3-D sonic anemometers to measure winds at 10 Hz and to describe the turbulent flow field. One high-frequency trace gas monitor (Benner and Lamb 1985) was also deployed to gather tracer data at 1 Hz. Each test yielded 40–60 h of canopy trunk space dispersion data as well as detailed wind observations to understand the airflow. Detailed measurements of canopy density were also made with both LI-COR (LI-3000; LI-COR, Lincoln, NE) and hemispherical photography. The complete field tests were done in seven different canopy/stand conditions.

Description of the Previous MCH Field Study. The field study involved five replications of four treatments in a randomized complete block design (Ross et al. 2002). Circular 1-ha plots were located at least 200 m apart in mixed conifer stands with a large component of mature Douglas-fir near trees containing Douglas-fir beetle brood. Plots were installed in the spring before beetle flight. Treatments included three MCH release rate and spacing combinations and an untreated control. The three different release rates were achieved by attaching 1, 3, or 9 bubble capsules at each release point spaced 5, 15, and 44 m, respectively, around the plot perimeters. Bubble capsules contained 400 mg of MCH and were designed to release the pheromone throughout the beetle flight period (Phero Tech, Delta, BC, Canada; now part of Conotech Enterprises Inc., Victoria, BC, Canada). Releasers were attached to the north sides of trees, snags, or shrubs at an approximate height of 2 m. Aggregation pheromone-baited multiple-funnel traps with a low release rate lure were placed at each plot center to provide a standard source of attraction. After beetle flight ended, plots were surveyed to gather stand and infestation data. All Douglas-fir ≥20 cm diameter at breast height in the center 0.3 ha circle on each plot were inspected and classified as mass-attacked or unattacked based on the presence or absence of large amounts of boring dust on the lower bole. The percentages of Douglas-fir trees that were mass-attacked were subjected to analysis of variance (ANOVA) after arcsine square-root transformation.

Model Setup and Simulated Pheromone Release Rate. The 120 × 120 × 8-m modeling domain was set to encompass a 1-ha circle and simulated 30-min av-
because release rate depends upon the temperature and 8 (first day at 25°C in a constant temperature cabinet) to as high as 11 mg/d/capsule (MCH at the same rate (Ross and Wallin 2008). Predictions. Both formulations are designed to release rates ranging from as low as 1.23 mg/d/capsule (sea-son long field average) to as high as 11 mg/d/capsule (MCH treatment patterns were investigated: the three combinations of release rate and releaser spacing between the 3× and 9× patterns, which were treatments 4×, 6×, and 8× (Table 1).

All previous field studies with MCH bubble capsules have used one of two commercially available formulations. Both formulations are designed to release MCH at the same rate (Ross and Wallin 2008). Previous publications have reported different release rates ranging from as low as 1.23 mg/d/capsule (season long field average) to as high as 11 mg/d/capsule (first day at 25°C in a constant temperature cabinet) because release rate depends upon the temperature and time period over which it is measured (Ross and Daterman 1994, 1995; Ross et al. 1996; Ross and Wallin 2008). In the analyses discussed herein our intent was to compare the relative impact of different combinations of release rate (individual or multiple bubble capsules per release point) and releaser spacing to the resulting pheromone concentration fields. Consequently, the specific release rate per bubble capsule was not critical to our analyses as long as it was a realistic rate. We chose to use 7 mg/d/capsule, a 2 wk average at 25°C in a constant temperature cabinet, (Ross and Daterman 1994) as the initial standard in our modeling because this is likely near the actual release rate on warm afternoons when beetles are actively colonizing host trees during the first month or two after bubble capsules are deployed in the field. For the noninitial-standard treatments, the modeled release rate was increased by the corresponding number of times above the initial standard (multiple bubble capsules), for example, 3× treatment had 21 mg/d release rate per release point, 6× treatment had 42 mg/d release rate per release point, etc., so the total released mass per treatment was held constant. The MCH release points encompassed a 1-ha circular plot and concentrations were assessed at the center point of the plot (Fig. 1).

We also used the model to predict pheromone concentrations with a deployment arrangement more typical of management practices. To visualize a gridded treatment pattern, we modeled the concentration field produced by 75 MCH bubble capsules in a 1-ha square. We modeled the following arrangement patterns: one MCH capsule every 11.5-m (initial recommendation), three MCH capsules every 20-m, and nine MCH capsules approximately every 35-m (Fig. 2). Because of the mathematics of the 9× treatment grid only 72 capsules were used in the hectare. The 120 × 120 × 8-m modeling domain encompassed the 1-ha treated plot and concentrations were sampled on a 5 × 5 × 2-m (length × width × height) sampling grid.

**Meteorological Input Data.** The model is driven by high frequency (10 Hz) wind and turbulence data. Based on extensive data collection and previous experiments, which show a direct correlation between subcanopy turbulence and stand canopy density (Thistle et al. 2011), a turbulence regime typical of a conifer canopy of similar density was imposed. These data were selected from previous subcanopy surrogate pheromone dispersion studies (Thistle et al. 2004) and the input data were selected from the available data-sets that best matched the stand density and crown closure conditions of the mixed conifer stand where Ross et al. (2002) conducted their study. The 3-D wind speed data collected during a 2001 subcanopy dispersion study in a ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, forest near La Pine, OR, was the best fit to the mixed conifer canopy. The meteorological data used were collected from 1630 to 1700, 20 June 2001; the average temperature and wind speed during that time were 26°C and 0.21 m/s, respectively. The 1630–1700 time frame was selected because this represents a time of day during which peak Douglas-fir

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**Table 1.** Three treatments (initial standard, 3×, and 9×) used in the field to assess the efficacy of MCH for preventing colonization of live trees by the Douglas-fir beetle (Ross et al. 2002) on 1-ha circular plots and three additional hypothetical treatments (4×, 6×, and 8×)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. MCH release points</th>
<th>Distance between MCH release points (m)</th>
<th>No. MCH capsules per release point</th>
<th>Release rate per release point (mg/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial standard</td>
<td>72</td>
<td>5</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>3×</td>
<td>24</td>
<td>15</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>9×</td>
<td>8</td>
<td>44</td>
<td>9</td>
<td>63</td>
</tr>
<tr>
<td>4×</td>
<td>18</td>
<td>21</td>
<td>4</td>
<td>28</td>
</tr>
<tr>
<td>6×</td>
<td>12</td>
<td>30</td>
<td>6</td>
<td>42</td>
</tr>
<tr>
<td>8×</td>
<td>9</td>
<td>39</td>
<td>8</td>
<td>56</td>
</tr>
</tbody>
</table>

*These treatments were modeled with an instantaneous puff dispersion model to gain insight into the dispersion physics resulting from the different release rate and releaser spacing combinations.

*Release rate of 7 mg/d was used based on 2-wk avg. MCH release rate at 25°C (Ross and Daterman 1994).
beetle flight would normally occur, challenging the pheromone plume. Although the meteorological conditions during the MCH field study undoubtedly differed from the data we used in the model, our intent was not to predict the actual pheromone concentration fields but to compare the concentration fields resulting from the alternative release rate and spacing combinations. Using the available dataset for a stand similar to the mixed conifer stands in the field study allowed us to meet this objective.

**Results**

The 30-min averaged MCH concentrations at the center of the 1-ha treated plots varied little with different pheromone release rates and corresponding releaser spacing: 0.0027 µg/m³ for the 1×, 3×, 4×, and 6× treatments; 0.0024 µg/m³ for the 8× treatments and 0.0025 µg/m³ for the 9× treatment. This is not surprising because the total MCH mass released per treated area was the same for all treatments. Despite this apparent uniformity, the overall concentration field across the treated domain changed considerably when the pheromone release rates per point and the releaser spacing were increased (Fig. 3). The initial standard treatment provided a uniform circle of higher MCH concentrations around the plot. This uniform circle progressively shifts toward an irregular circle consisting of varying MCH concentrations as the distance between releasers increases. This shift occurs despite the total released MCH mass remaining constant. The overall differences among the initial standard, 3×, and 4× treatments are subtle, while the concentration field for the 6× treatment begins to diverge from the initial standard, and concentration fields for the 8× and 9× treatments clearly deviate from the initial standard (Fig. 4).

The 30-min MCH concentration field gives a snapshot of the average concentration field that an insect population might experience, but an individual insect responds to concentration fluctuations on the order of 1-s or less. The 1-s MCH concentration values at the center of the 3×, 4×, 6×, 8×, and 9× treatments were subtracted from the initial standard to explore the deviations of these arrangements from the initial standard on a small time-scale (Fig. 5). Treatments 3× and 4× are nearly identical to the initial standard and treatment 6× does not substantially differ, while treatments 8× and 9× have concentration fluctuations that range both higher and lower than the initial standard. The concentration fluctuations at the center of treatments 8× and 9× differ widely from the initial standard despite their similar 30-min averaged concentration values. The spacing of the MCH bubble capsules, which changes the potential for the individual MCH pheromone plumes to overlap, causes different concentration fluctuations per treatment arrangement. The difference in occurrence of higher concentration values in the initial standard compared with treatments 8× and 9× is also evident in frequency histograms of the 1-s concentration values (Fig. 6). These concentration histograms further demonstrate the im-

![Fig. 2. Model domain and source arrangement for a gridded pattern of one MCH capsule every 11.5-m (top); three MCH capsules every 20-m; and nine MCH capsules approximately every 35-m. In total, 75 capsules were used in the first two cases and, because of mathematics, 72 capsules in the last case. The square around the sources indicates the 1-ha plot. The x and y axes show distance (m).](image)
Efficacy. The efficacy of pheromone treatments is a function of the concentration field generated by the release of the pheromone, plume movement and concentration, stand density and structure, as well as insect population density and biology (Fares et al. 1980). The transport and spread of a pheromone plume under a forest canopy is complex. Individual plumes produced at each bubble capsule undergo plume transport in the direction of the mean wind field. The width of the plume (horizontally and vertically) is determined by mechanical and thermal turbulent mixing. Mechanical turbulence shreds the plume into narrow strands as air currents pass through the forest stems and underbrush (Thistle et al. 2004) and thermal turbulence, generated by the heterogeneous heating of the forest floor, moves the pheromone vertically (Baldocchi et al. 2000). The pheromone concentration field is dependent on canopy density, which in turn through thermal and mechanical turbulent mixing impacts the rate of plume dilution (Edburg et al. 2010). Thistle et al. (2011) have consistently found higher surrogate pheromone concentrations at downwind distances in dense canopy stands compared with more open canopy stands. Turbulent mixing within a canopy is a complex process that may limit the efficacy of releaser spacing on concentration fluctuations at a finer time-scale at the center of the treated area.
The difference in 1-s MCH concentration values at the center of the treated plots. The 3×, 4×, 6×, 8×, and 9× treatments were subtracted from the initial standard (1×) treatment. Positive values indicate the initial standard treatment concentrations are greater and negative values indicate the initial standard treatment concentrations are lower.

Fig. 4. Scatter plot of the 30-min averaged MCH concentration values for the entire domain (x, y, z data-points). The initial standard treatment (1×) is on the x-axis (concentration μg/m³) and 3× (top left), 4× (top right), 6× (middle left), 8× (middle right), 9× (bottom left) are on the y-axis (concentration μg/m³). The light gray line is the 1:1 line.

Fig. 5. The difference in 1-s MCH concentration values at the center of the treated plots. The 3×, 4×, 6×, 8×, and 9× treatments were subtracted from the initial standard (1×) treatment. Positive values indicate the initial standard treatment concentrations are greater and negative values indicate the initial standard treatment concentrations are lower.
Fig. 6. Histograms of the 1-s concentration values, which were binned into groups of 0.001 μg/m³ and counted. The y-axis shows the number of values within each bin, the x-axis shows the bin. The central left histogram with arrows radiating from it is the initial standard treatment with, going clockwise starting top left, treatments 3×, 4×, 6×, 8×, and 9× surrounding it. The gray bar plot between each histogram is the difference between the standard and that treatment. There is a clear change in frequency of higher concentration values between the 6× and 8× treatments.
of the treatment by diluting the concentration field below the behaviorally significant concentration minimum.

Dilution of the pheromone concentration field is minimized when several releasers are placed in the treated area. Multiple releaser points allow for the individual plumes to overlap, increasing the concentration. In the Ross et al. (2002) field study, the 9× treatment pattern did not successfully protect against Douglas-fir beetle infestation. The results from that field study illustrate that there is a minimum MCH concentration value that is critical to maintain to prevent colonization. The modeled MCH concentration fields for the 8× and 9× treatments show an incursion of lower concentration values into the treated circle and both of these treatments have an irregular circle of varying MCH concentrations, markedly different from the concentration fields produced with lower release rates and closer spacing of releasers (Fig. 3). In addition, the modeled 1-s concentration values at the center of the treated units further illustrate the difference the spacing of the bubble capsules can create (Fig. 5), despite little variation in the 30-min average concentration value at the same location. The model results indicate that the Ross et al. (2002) wide spacing of the 9× releasers allowed for dilution of the concentration field, because of less overlapping of the plumes. This occurred at more times and places within the treated plot than the treatments that used lower pheromone release rates and closer spacing. Identification of the behaviorally significant concentration would contribute greatly to our ability to interpret the results of model outputs and field efficacy trials.

Influence of Wind and Capsule Spacing. The mean wind direction and velocity and bubble capsule spacing influenced the uniformity of the pheromone concentration field. On the upwind side of the treated area, the pheromone is pushed away diluting concentrations near the upwind edge and increasing concentrations on the downwind edge (Fig. 3). In addition to this edge dilution effect, the combination of wind and wide spacing of the pheromone release devices can introduce ‘fingers’ of lower pheromone concentrations or pheromone-free air into the treated area. This dilutes the interior concentration field. Both the edge and finger dilution effects are important considerations for operational management practices. Meteorological parameters, such as the prevailing wind direction, typical wind speed, and atmospheric stability, and forest canopy density should be considered when determining the distance between MCH bubble capsules and their distribution relative to the boundary of the area to be protected. For example, as spacing between releasers increases, they will need to be placed farther beyond the boundary of the area to compensate for the edge and finger dilution effects. When treatment unit boundaries are adjacent to clear cuts or forest roads, it may be best to space the releasers closer together along those boundaries.

A regular grid distribution of MCH bubble capsules releasing at 3× the initial standard and spaced every 20-m is the highest release rate and widest spacing of releasers currently recommended for preventing Douglas-fir beetle infestation of forest stands (Ross and Wallin 2008). We used the model to visually examine this spacing, a denser array and an array equivalent to the 9× treatment arrangement (Fig. 7). As in Fig. 3, the predominant wind direction shift is evident and even magnified with the gridded arrangement.

![Concentration map](image_url)
The winds shift the concentration field by ≈10-m. The concentration contours for the hectare modeled with the dense array are uniform and there is no obvious grid pattern in the concentration field. In addition, there is a uniform area of higher concentration values and fingers of lower concentration values do not extend into this zone. The hectare modeled with the $3 \times$ deployment pattern displays gridded ‘hot spots’ with fingers of lower concentration values between the deployment pattern displays gridded ‘hot spots’ with fingers of lower concentration values between the MCH bubble capsule locations; however, a zone of high concentration values is apparent on the downwind side of the hectare. The $9 \times$ treatment has clearly defined hot spots and fingers of lower concentration values throughout the treated hectare. Ross et al. (2002) found spacing of the releasers to play a dominant role in the efficacy of the treatment. These modeling results help to visualize the role of releaser spacing.

**Further Field Testing.** Knowing the threshold concentration that prevents the Douglas-fir beetle from initially landing on a tree and beginning a colonization attempt would allow us to more fully interpret the concentration fields resulting from the different treatments. For example, it may be that MCH concentrations as low as 0.001 $\mu g/m^3$ are all that is required to deter the insect from landing and beginning to excavate a gallery. If this were the case, then there is sufficient MCH concentration coverage in all the grid treated treatments, except for the wind drift (Fig. 7). Alternatively, if the threshold concentration were closer to 0.01 $\mu g/m^3$ then only a denser array of releasers would provide sufficient coverage to deter a colonization attempt. Knowledge of the threshold concentration is important for further understanding the combined impact of wind, turbulence, and deployment patterns on the overall concentration fields and treatment efficacy.

While the time-averaged MCH concentration values from the circular arrangements varied little, the 1-s concentration fluctuations displayed a large difference between the initial standard and the $8 \times$ and $9 \times$ treatments (Figs. 4 and 6). The minimal difference between the initial standard and known effective $3 \times$ treatment and the yet untested $6 \times$ treatment justifies further exploration in the field to test the efficacy of spacing the MCH bubble capsules further apart. Refining operational treatments to the highest effective release rate and widest spacing of releasers would minimize treatment costs resulting in the most efficient treatments and, potentially, lead to wider use of MCH applications.

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