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First Report of Mating Disruption With an Aggregation Pheromone: A Case Study With *Tetropium fuscum* (Coleoptera: Cerambycidae)

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Abstract

Tetropium fuscum (F.), native to Europe and established in Nova Scotia, Canada, since at least 1990, is considered a low-to-moderate threat to spruce (*Picea* spp.) forests in North America and regulated as a quarantine pest by the Canadian Food Inspection Agency. We tested broadcast applications of the aggregation pheromone racemic (5*E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), formulated at 10% concentration in Hercon Bio-Flakes (Hercon International, Emigsville, PA), for efficacy in disrupting *T. fuscum* mating and suppressing populations. Two applications of 2.5–2.75 kg Bio-Flakes (250–275 g a.i.) per ha per season significantly reduced trap catches and mating success (2009, 2010, 2012): about 30% of females trapped in treated plots had mated compared with 60% of females trapped in untreated plots. Similar reductions in mating success were observed in 2011 with one or two 4.5 kg/ha applications of Bio-Flakes. Mean densities of *T. fuscum* colonizing sentinel bait logs or girdled trees were 36% lower in pheromone-treated plots than in untreated plots, but the difference was not statistically significant. Lack of population suppression may have been because mated females immigrated into treated plots or because populations were so high that despite a 50% reduction in mating success, absolute numbers of mated females were sufficient to infest our bait logs or trees. This is the first demonstration of insect mating disruption via broadcast application of an aggregation pheromone. Pheromone-mediated mating disruption has potential to slow the spread of invasive cerambycids by targeting low-density outlier populations near or beyond the leading edge of an infestation.

Key words: aggregation pheromone, mating disruption, Cerambycidae, *Tetropium fuscum*, invasive

Mating disruption, via the broadcast application of sex pheromones, has been successfully used to control lepidopteran pests such as the codling moth, *Cydia pomonella* (L.), and the pink bollworm, *Pectinophora gossypiella* (Saunders), in agricultural crops (Cardé and Minks 1995, Judd et al. 1997, Gut and Brunner 1998) and to slow the spread of the gypsy moth, *Lymantria dispar* L., in forests (Cameron et al. 1974, Leonhardt et al. 1996, Sharov et al. 2002, Thorpe et al. 2006, Lance et al. 2016). Pheromone-mediated mating disruption has been applied for the control of beetles, reducing damage by *Anomala orientalis* (Scarabaeidae) (Polavarapu et al. 2002, Sciarappa et al. 2005, Wenninger and Averill 2006) in blueberry crops, and *Megaplatypus mutatus* (Curculionidae: Platypodinae) in poplar plantations (Funes et al. 2011). Maki et al. (2011) provided the first evidence of the potential of mating disruption for the

control of a Cerambycid, *Prionus californicus* (Cerambycidae: Prioninae), a pest of commercial hop yards, the females of which emit a sex pheromone, 3,5-dimethyldodecanoic acid, that is highly attractive to conspecific males (Rodstein et al. 2009). Catches of male *P. californicus* in pheromone-baited traps were significantly reduced in traps that were surrounded by point sources of pheromone compared with traps surrounded by hexane (control) lures (Maki et al. 2011).

Tetropium fuscum (F.) (Coleoptera: Cerambycidae) is native to Europe, where it infests weakened or moribund Norway spruce, *Picea abies* (L.). Successfully colonized trees are reinfested each year and get progressively weaker until death in 1–5 yr (Juutinen 1955). In 1999, *T. fuscum* was discovered infesting and killing mature spruce [*Picea rubens* Sargent, *Picea glauca* (Moench) Voss, *Picea*

mariana (Miller) B.S.P.] in Halifax, Nova Scotia (Smith and Humble 2000, Smith and Hurley 2000). It was declared an official quarantine pest and was the target of an eradication program from 2000–2006 and a slow-the-spread containment program from 2007 to present [Canadian Food Inspection Agency (CFIA) 2014]. In April 2015, the regulated area was expanded to include the entire province of Nova Scotia (CFIA, 2015). Due in part to its relatively slow rate of spread (Rhainds et al. 2011) and low risk of infesting healthy spruce (Flaherty et al. 2013a,b), a 2014 pest risk analysis concluded that *T. fuscum* represented a low-to-moderate risk to spruce forests in Nova Scotia (Nova Scotia Department of Natural Resources 2014). However, due to uncertainties such as the risk that it may increase mortality rates in spruce forests under stress from abiotic factors or defoliator outbreaks (Juutinen 1955), the risk analysis recommended continued regulatory control of *T. fuscum* to reduce its artificial spread as well as implementation of direct control methods to suppress populations along the leading edge of the infestation (Nova Scotia Department of Natural Resources 2014).

Due to their subcortical feeding habits, options for suppressing populations of *T. fuscum* and other phloem- and wood-boring species are often limited to the cutting and chipping or burning of infested trees prior to brood emergence, or to the application of systemic insecticides to individual trees by stem injection or soil drench (Wang et al. 2005, Haack et al. 2010, Herms et al. 2014), neither of which is very practical at the forest level. With the relatively recent discoveries of sex and aggregation pheromones in many species of Cerambycidae (Allison et al. 2004, Hanks and Millar 2013, 2016), including *T. fuscum* (Silk et al. 2007, Sweeney et al. 2010), mating disruption may offer an alternative method for suppressing populations and slowing the spread of invasive cerambycids, as is done in the gypsy moth slow-the-spread program (Sharov et al. 2002).

Aspects of a pest's life history that favor the efficacy of pheromone-mediated mating disruption are univoltinism, monogamy, and limited mobility of mated females (El-Sayed et al. 2006, Witzgall et al. 2010). Success of suppressing a pest population via mating disruption is also more likely in low-density populations, in which competition between artificial and natural pheromone sources is reduced (El-Sayed et al. 2006, Witzgall et al. 2010) and the chance of mating success may already be low and approaching an "Allee threshold" (Tobin et al. 2009, 2011; Rhainds et al. 2015). Finally, mating disruption is likely to be most effective at suppressing small, isolated infestations, in which the probability of immigration of mated females into the treated area is low (El-Sayed et al. 2006). The gypsy moth slow-the-spread program exploits this by targeting mating disruption in low-density, isolated populations that lie beyond the leading edge of the generally infested area (Tobin et al. 2011, Lance et al. 2016). This strategy is greatly assisted by surveys with sensitive pheromone-baited traps that can detect low-density gypsy moth populations (Liebhold and Tobin 2008, Witzgall et al. 2010, Lance et al. 2016).

Certain aspects of the biology of *T. fuscum* favor the potential of its population suppression by mating disruption, and others do not. It is univoltine but not monogamous; both sexes mate more than once, and copulation can occur within hours after female emergence (Schimitschek 1929), so it is critical that pheromones be applied prior to peak adult emergence. Males emerge an average of 5 d before females (Rhainds et al. 2010), are attracted to volatiles from stressed hosts (Sweeney et al. 2004), and emit (2*S*,5*E*)-6,10-dimethyl-5,9-undecadien-2-ol (also known as fuscumol), which synergizes attraction of both sexes to stressed host volatiles (Silk et al. 2007, Sweeney et al. 2010). Thus, disruption of pheromone communication in *T. fuscum* may not only reduce mating success but may also interfere with the location of suitable hosts by females. Traps baited with fuscumol and host volatiles (ethanol, plus a blend of five monoterpenes termed spruce blend or "BSLB kairomone lure"; Sweeney et al. 2006) have been used to survey and monitor the spread of *T. fuscum* in Canada since 2007 (Cunningham 2010, Sweeney et al. 2010) and provide a means of collecting both males and females and detecting the presence of low-density outlier populations and the beginning of the flight period. Adults live for only 1–2 wk, but the adult flight period extends from May to August (Juutinen 1955), with peak activity in June and July; hence, pheromone applications would have to remain effective for at least 2 mo and preferably longer. Short-chain pheromones (12–14 carbon atoms) are less likely to be adsorbed onto foliage and persist in the environment than long-chain pheromones (18–21 carbon atoms; Gut et al. 2004, Evenden 2016), so more than one application per season of fuscumol (13 carbons) may be necessary to disrupt mating over the entire emergence period. Immigration of mated females into pheromone-treated areas is a concern because flight distances of up to 15 km and 845 m have been measured for female *T. fuscum* on laboratory flight mills and in field mark–release–recapture experiments, respectively (J.D.S. unpublished data). However, in those same experiments, the median flight distances were much shorter, <350 and <25 m in the laboratory and field, respectively. Furthermore, its habit of reinfesting host trees and its short adult life span and slow rate of spread in Nova Scotia (Rhainds et al. 2011) suggest that most mated *T. fuscum* females disperse relatively short distances.

Human transport of infested logs or firewood presents a genuine risk of increasing the rate of spread of *T. fuscum* by potentially establishing new pockets of infestation far beyond the generally infested area. Interceptions of *T. fuscum* in 2011 and 2014 in pheromone-baited traps at Kouchibouguac Park, New Brunswick, more than 150 km from the nearest known infested area (CFIA, 2015), suggest that such human-assisted movement has occurred. Although intensive surveys suggest *T. fuscum* has not established at Kouchibouguac Park, recent surveys indicate that it has established near Memramcook, New Brunswick, more than 50 km from the nearest known infested area in Nova Scotia (Ron Neville, CFIA, personal communication). We suggest that mating disruption would have the best chance of suppressing *T. fuscum* populations and slowing its spread if applied to these small, isolated infestations where both the population density and likelihood of immigration of mated females are low.

The objective of this study was to determine the efficacy of broadcast application of fuscumol for mating disruption of *T. fuscum* in spruce forests. Field trials were conducted between 2009 and 2012. We predicted that pheromone treatment would result in reduced catches of *T. fuscum* in traps baited with fuscumol + host volatiles, reduced mating success, and reduced infestation levels compared with untreated control plots.

Materials and Methods

Pheromone and Hercon Flakes

Racemic fuscumol (99.1% [sum of both enantiomers] overall purity as determined by GC-MS) was purchased from Bedoukian Research (Danbury, CT) and formulated at 10% concentration in biodegradable Hercon Disrupt Bio-Flakes by Hercon Environmental (Emigsville, PA). The flakes were shipped to the Canadian Forest Service laboratory in Fredericton, NB, and stored at −18°C until use.

Site Description

The studies were conducted near Juniper Lake (44° 43′19″ N; 63° 34′30″ W) and Sandy Lake (44° 44′33″ N; 63° 41′2″ W), Halifax Co., Nova Scotia, in conifer-dominated stands that contained mature red spruce with signs of *T. fuscum* infestation. Red spruce was the dominant tree species (38–85% of stems >10 cm diameter at breast height [dbh]), followed by balsam fir, *Abies balsamea* (L.), and red maple, *Acer rubrum* (L.) (usually >10%).

Experimental Design

Plots measured about 4 ha (3.85–4.25 ha) from 2009–2011 and 9 ha in 2012 and were laid out as approximate squares (e.g., 200 by 200 m), wherever possible, with a minimum distance between plots of about 200 m. Untreated plots of the same size served as controls in each year (Fig. 1). There were only two treatments (treated vs. untreated) each year, except in 2011, when we compared one versus two pheromone applications versus an untreated control. There were four replicates per treatment per year. Treatments were assigned randomly to plots in all years, using a completely randomized design in 2009, paired designs in 2010 and 2012, and a randomized complete block design in 2012. Plots were paired or blocked according to spatial proximity and/or similarities in stand composition and relative incidence of signs of apparent *T. fuscum* infestation (unexplained resinosis and/or exit holes on spruce trees) observed in spring surveys.

Pheromone Flake Applications

Flakes were applied at a rate of 2.5–4.5 kg/ha, depending on the year of application, and two applications were made per plot per season (Table 1). The first application was timed to coincide with the onset of flight (monitored with pheromone-baited traps), and the second application followed 3–4 wk later, when most of the fuscumol had been released from the flakes in the first application (see below). In 2011, we compared the efficacy of one application at the onset of beetle flight (30 May) versus two applications per season (30 May, 20 June). Thus, the total amount of fuscumol applied per ha per season ranged from 500 g/ha in 2012 to 900 g/ha in 2011.

The Bio-Flakes were applied aerially from a gas-powered motorized rotary-spreader attached to a hopper suspended beneath a helicopter. The spreader was calibrated to deliver the flakes at a rate of 10 kg/min. As plots varied slightly in size, so did the amount of flakes required per plot, so the latter were weighed and assigned to individual plots ahead of time. For each plot, the hopper was loaded with the required load of flakes for that plot only. The helicopter was guided by a navigation/recording unit (AG-NAV GPS Precision Navigation, Barrie, ON) programmed to follow flight lines spaced 20 m apart in 2009–2010 and 2012 and 14 m apart in 2011. The pilot flew alternate lines, applying flakes to the odd-numbered lines first, then the even-numbered lines, and then flew two additional lines in the center of the block in case any flakes remained in the hopper.

Efficacy of Mating Disruption

We measured efficacy of mating disruption by comparing treated and control plots for: 1) mean numbers of *T. fuscum* (males, females, and total) captured per trap per plot in traps baited with pheromone + host volatiles (see below); and 2) the mean percentage of *T. fuscum* females captured in traps that had successfully mated.

Black-panel intercept traps (Alpha Scents Inc, West Linn, OR; Sweeney et al. 2006) were baited with an ultra-high release rate (UHR) BSLB kairomone lure (also known as "spruce blend"), a UHR ethanol lure (ConTech Inc, Delta, BC, now Scotts Canada),

and a fuscumol lure. The fuscumol lures consisted of a 0.2-ml thin-walled, clear, dome-capped polymerase chain reaction tube (Axygen Scientific Inc, CA, USA) containing 15 mg of racemic fuscumol, with a 1-mm-diameter hole drilled in the cap (Silk et al. 2007). Release rates of fuscumol, BSLB kairomone, and ethanol were 80–800 µg/d (Sweeney et al. 2010), 2 g/d, and 275 mg/d, respectively (Sweeney et al. 2006). Fuscumol lures were replaced after 8 wk; the kairomone and ethanol lures were not replaced. Collecting cups contained 0.5 liters of trapping solution that consisted of saturated salt (NaCl) solution with 1–2 drops of unscented dish detergent.

From 2009–2011, traps were spaced 50 m apart along diagonal transects across each plot, starting about 30 m inside the plot corner. There were five traps per plot along a single transect in 2009 and nine traps per plot along two bisecting diagonal transects in 2010–2011. In 2012, we placed 13 traps per plot, spaced 70–100 m apart, with all traps at least 50 m inside the plot edge (Supp. Fig. A [online only]). In each year, traps were set up in the first week of May, checked weekly until the end of July, then once in mid-August, and again at the end of August. Captured insects were stored in 70% ethanol (2009) or at −10°C in a freezer (2010–2012) until processed. *Tetropium* were identified to species and sex (Yanega 1996, Smith and Humble 2000) and voucher specimens retained in the Atlantic Forestry Centre collection.

Mating status of females captured in traps was determined by dissecting each female to remove the spermatheca, mounting it on a slide in glycerol, gently crushing it under a cover slip, and examining it for presence of sperm at 1,000× magnification under oil immersion.

Efficacy of Population Suppression

We measured efficacy of population suppression by comparing treated and control plots for mean density of *T. fuscum* larvae and adults per m^2 surface area in five decks of spruce bait logs per plot (2009–2010) and/or in 10–12 randomly located girdled red spruce trees per plot (2010–2012). Each bait log deck consisted of six red spruce logs (1.2-m-long by 21–38-cm-diameter) stacked three on the bottom, two in the middle, and one on top. Decks were spaced about 50 m apart and 25 m distant from the nearest pheromone-baited trap, along the same diagonal transect. Logs were sourced on site by felling red spruce with full green crowns and no signs of *T. fuscum* infestation (e.g., no unexplained resin or exit holes on the stem) in mid-April. The log decks were covered with fiberglass window screening to protect them from *T. fuscum* oviposition prior to pheromone application. The screening was removed on the day of the first pheromone application to expose bait logs to *T. fuscum* attack for the duration of the flight season.

Flaherty et al. (2011) showed that establishment and survival of *T. fuscum* were greater in live girdled trees than in cut trees (bait logs), so girdled trees were used in 2010–2012 to increase the probability of successful colonization and provide a more conservative test of efficacy of pheromone application for *T. fuscum* suppression. Trees for girdling were randomly selected from red spruce greater than 18 cm dbh with no signs of infestation. Each plot was divided into about 400 individually numbered 10 by 10-m quadrats, and a random number table was used to select 12 quadrats. The red spruce tree nearest the center of each quadrat was girdled 2.5 cm deep in the sapwood about 30 cm above the ground in mid-April. Flaherty et al. (2011) showed that red spruce that had been girdled in a similar fashion were significantly moisture-stressed about 4 wk post-girdling and very susceptible to *T. fuscum* infestation.

In mid-September, we collected the bottom three logs of each deck and felled the girdled trees and cut a 1.2-m-long basal bolt
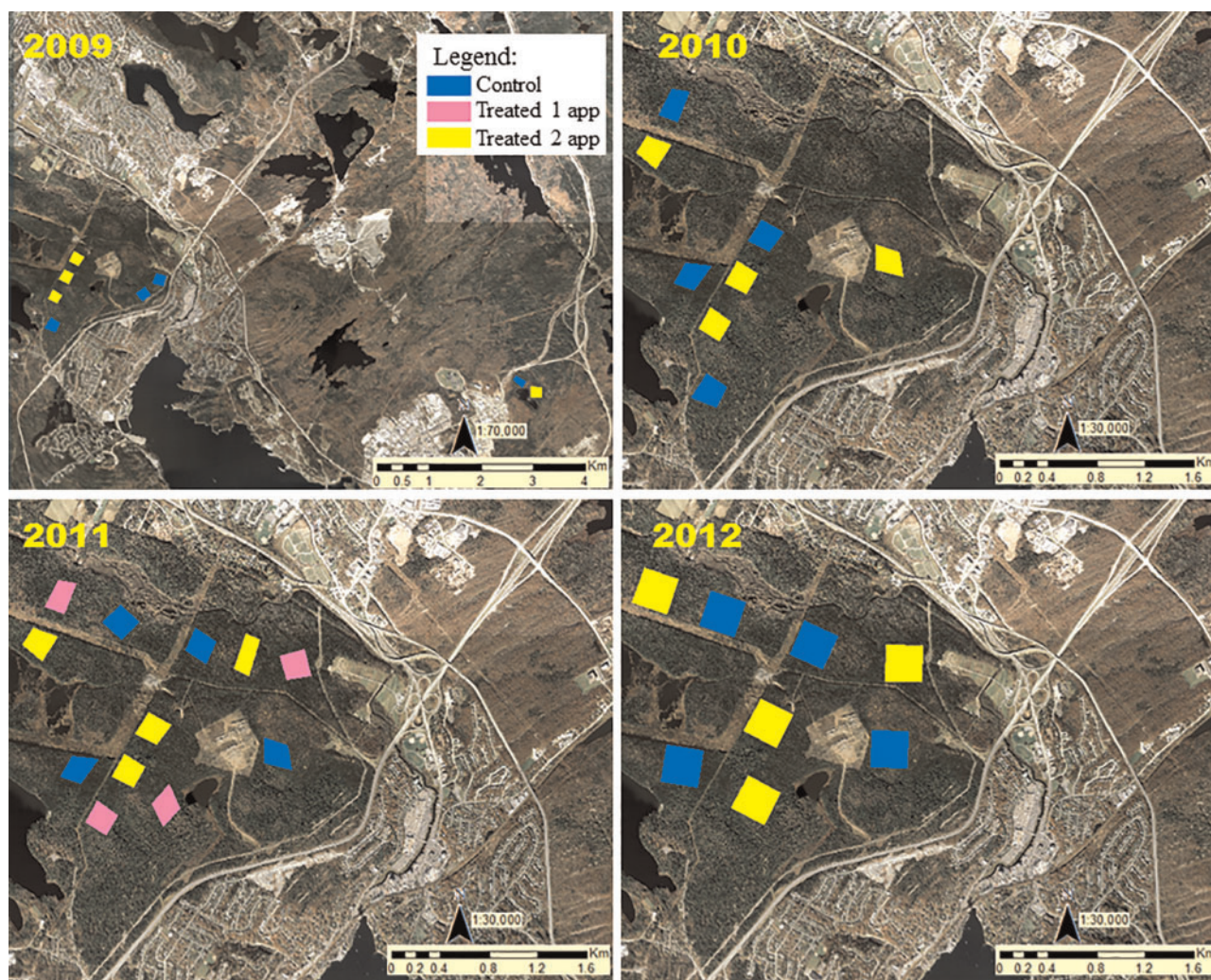
Fig. 1. Location of experimental plots for aerial applications of fuscumol formulated in Hercon Bio-Flakes in 2009 (the six plots on the left are near Sandy Lake, the two plots on the right are near Juniper Lake) and 2010–2012 (near Sandy Lake) in forests located near Bedford, Nova Scotia. Plots received zero (Control, all years), one (Treated 1 App., 2011 only), or two (Treated 2 App., all years) applications of fuscumol per season.

Table 1. Summary of methods used 2009–2012 near Halifax, Nova Scotia, testing application of Hercon flakes formulated with 10% fuscumol for mating disruption of *T. fuscum*

Year	Product	kg per ha	Applications per season (dates)
2009	Bio-Flake	2.75	2 (26 May, 18 June)
2010	Bio-Flake	2.75	2 (18 May, 9 June)
2011	Bio-Flake	4.50	1 vs. 2 (30 May, 20 June)
2012	Bio-Flake	2.50	2 (23–24 May, 20 June)

There were four replicate plots per treatment in each year.

from each tree. Each log was cut into two bolts, one about 90 cm in length and the other about 30 cm in length. The length and mean diameter of each bolt were recorded, and its surface area estimated using the formula for a cylinder. The shorter bolts were stored either outdoors (as late as mid-March) or in a walk-in freezer at $-2°C$ until they could be set up for rearing to estimate the density of adult *T. fuscum* emerging per m^2 (see below). The longer bolts were stored outdoors until late November and then milled and peeled to estimate the density of larvae per m^2.

Estimating *T. fuscum* larval densities

Each bolt was milled into slabs (8–10-mm-thick by 90-cm-long) using a portable band saw (Wood-Mizer LT40 hydraulic, Wood-Mizer Canada, Lindsay, ON), the numbers of *Tetropium* pupal cells in the sapwood were counted and recorded for each bolt, and mature *Tetropium* larvae (prepupae) were collected from pupal cells. Bark was peeled from a subsample of 8–10 slabs per log, 4–5 slabs taken from one side of the log and 4–5 slabs taken from the opposite side. All Cerambycid larvae exposed at the phloem–xylem interface were collected. The total area of the bark removed from each log was recorded. All Cerambycid larvae and prepupae were immersed in hot water (80–100°C) for 1–2 min to maintain color and shape (Martin 1977), preserved in 70% ethanol, and identified to subfamily. *Tetropium* larvae were identified to genus using keys in Craighead (1923). All *Tetropium* spp. larvae collected from pupal cells and most larvae collected under the bark were mature and could be identified as either *T. fuscum* or *Tetropium cinnamopterum* Kirby based on the morphology of their caudal spines; those of *T. cinnamopterum* are sharply pointed and arise from a common base, whereas those of *T. fuscum* are blunt and not fused at the base (Flaherty et al. 2012). Very few immature *Tetropium* spp. larvae were observed and all were under the bark; these could not be

Table 2. Mean (± SE) numbers of male, female, and total *T. fuscum* captured per trap per plot, post application, in pheromone-treated vs. untreated plots near Halifax, Nova Scotia, 2009–2012

Year	n	T. fuscum	1 App.	2 App.	Control	F^a	df	P
2009	4	Males	–	2.3 ± 0.4	2.6 ± 0.8	0.51	1,6	0.3
2009	4	Females	–	2.5 ± 1.0	2.8 ± 0.4	0.09	1,6	0.77
2009	4	Total	–	4.8 ± 1.3	5.4 ± 0.7	0.14	1,6	0.72
2010	4	Males	–	2.8 ± 1.3	4.4 ± 1.4	0.86	1,3	0.42
2010	4	Females	–	3.4 ± 1.7	5.2 ± 1.8	0.63	1,3	0.49
2010	4	Total	–	6.2 ± 2.9	9.5 ± 3.1	0.68	1,3	0.47
2011	4	Males	4.5 ± 1.6	3.0 ± 1.8	5.7 ± 1.9	1.59	2,6	0.28
2011	4	Females	6.3 ± 2.3	3.6 ± 1.4	5.8 ± 1.8	1.57	2,6	0.28
2011	4	Total	10.7 ± 3.9	6.6 ± 3.1	11.5 ± 3.6	1.15	2,6	0.38
2012	4	Males	–	3.2 ± 0.3	9.2 ± 1.7	10.5	1,3	**0.05**
2012	4	Females	–	4.3 ± 0.8	7.9 ± 1.3	3.97	1,3	0.14
2012	4	Total	–	7.6 ± 1.0	17.1 ± 2.8	13.9	1,3	**0.04**
2009–2012	16	Males	–	2.7 ± 0.5	5.4 ± 0.9	8.59	1,27	**<0.01**
2009–2012	16	Females	–	3.3 ± 0.6	5.4 ± 0.8	8.21	1,27	**<0.01**
2009–2012	16	Total	–	6.0 ± 1.0	10.8 ± 1.7	7.25	1,27	**0.01**

Treated plots received one (1 App.) or two applications (2 App.) per season of Hercon flakes formulated with 10% fuscumol at rates of 2.75 kg/ha (2009–2010), 4.5 kg/ha (2011), or 2.5 kg/ha (2012). *P* values for significant effects in bold.

[a]Results from generalized linear mixed model (SAS/STAT, PROC GLIMMIX) with either Poisson or negative binomial distribution, whichever had the best fit (lowest value for AICc).

positively identified to species, so we estimated the proportion of immature *Tetropium* larvae that were *T. fuscum* versus *T. cinnamopterum* based on the proportions we observed in the prepupal larvae in the same girdled tree or log deck. We then summed the number of *T. fuscum* larvae per m² under the bark plus the number of *T. fuscum* pupal cells per m² in the sapwood to give an estimate of total *T. fuscum* larvae per m² in each log or girdled tree.

Estimating *T. fuscum* adult densities emerging from logs

Each short bolt was placed inside a Lexan or Plexiglass cage (45.8 by 45.8 by 45.8 cm) with two fine-mesh (<1 mm) windows (5 by 33.5 cm) and incubated at 20–21°C and 40% RH for 12 wk in containment facilities at Atlantic Forestry Centre. Emergence was recorded 5 d per wk, and the total numbers of adult *T. fuscum* that emerged per bolt were used to estimate the mean number of adults emerging per m² from log decks or girdled trees in each plot.

Data Analyses

Data were analyzed with generalized linear mixed models (PROC GLIMMIX) using SAS/STAT software (SAS/STAT, Version 9.2 of the SAS System for Windows. Copyright 2002–2008, SAS Institute Inc, Cary, NC). Pheromone treatment was a fixed effect, and blocks were treated as random effects for years 2010–2012. Count data, i.e., mean numbers of *T. fuscum* adults (males, females, totals) per trap per plot and mean numbers of *T. fuscum* (larvae, adults) per m² per plot in bait logs or girdled trees, were modeled with both Poisson and negative binomial distributions (log link) and results reported from the model-distribution with the lowest value of Akaike's information criterion corrected for small sample sizes (AICc). The Laplace method of estimating model parameters was used, as recommended when count means are sometimes <5 (Bolker et al. 2008). Data on female mating success (proportion mated of total females captured in traps) were modeled with a binomial distribution (logit link) by using the number of mated females per plot and total number of females per plot that were collected in pheromone-baited traps; for illustrative purposes, these data are reported as mean percentage of females mated per plot.

Data for each response variable were first analyzed separately by year. Then, for data on trap catch and mating success, we pooled data across years for plots that received two pheromone applications per season versus none (i.e., data from the 2011 plots that received only one pheromone application were omitted) in two ways: 1) data from 2010–2012 were pooled and analyzed with blocks as random effects; and 2) data from 2009–2012 were pooled and analyzed with years as random effects. Results, in terms of significance of pheromone treatment (α = 0.05), did not differ between the two methods, so we report results from the latter method that pooled all of the data. For data on *T. fuscum* larval and adult densities in logs and trees, we pooled the data in three ways: 1) data on *T. fuscum* densities in bait logs from 2009 and 2010 were pooled and analyzed with year as a random effect; 2) data on *T. fuscum* densities in girdled trees from 2010, 2011 (2 applications), and 2012 were pooled and analyzed with blocks as a random effect; and 3) data from both bait logs and girdled trees from 2009–2012 were pooled and analyzed with year as a random effect; in this analysis, we averaged the number (of larvae or adults) per m² per plot from both bait logs and girdled trees in 2010. Standard errors are reported for all means.

## Results

Efficacy of Mating Disruption

Overall mean catch per trap per plot (2009–2012 pooled data) was significantly lower in pheromone-treated plots than in control plots for males, females, and total *T. fuscum* ($F_{1,27} > 7.2$, $P \leq 0.01$; Table 2). Within individual years, significant reductions in mean trap catches in pheromone-treated plots were observed in 2012 only (Table 2). Seasonal phenology of *T. fuscum* adults based on weekly catches in traps showed that flight began in late May and continued to late August, with most activity within June and July (Fig. 2).

The proportion of females that had successfully mated was significantly lower in pheromone-treated plots than untreated plots, both for pooled data (treated: 30.4 ± 3.2%; untreated: 60.8 ± 2.2%; $F_{1,27} = 89.9$, $P < 0.0001$) and within each year (Fig. 3). In 2011, there was no difference in mating success between plots treated with 4.5 kg Bio-Flakes per ha once per season versus twice (Fig. 3).
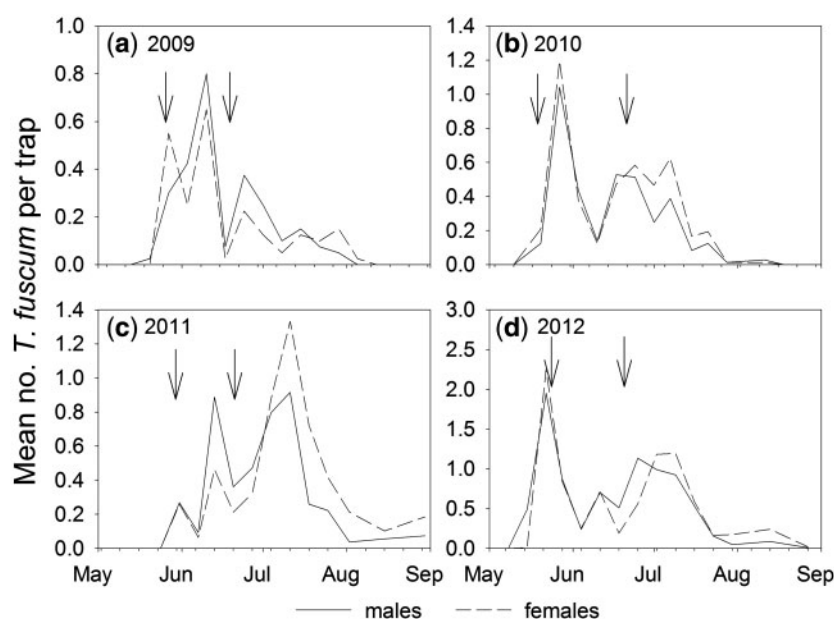
Fig. 2. Mean catch per trap per week of male and female *T. fuscum* in traps baited with fuscumol, spruce blend, and ethanol near Halifax, Nova Scotia, and dates of pheromone applications in (**a**) 2009, (**b**) 2010, (**c**) 2011, and (**d**) 2012. Arrows indicate dates of application of Hercon Bio-Flakes formulated with 10% racemic fuscumol.
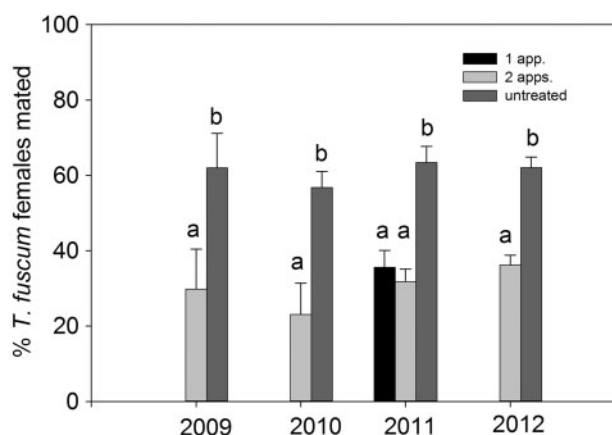
Fig. 3. Mean percentage (± SE) per plot of *T. fuscum* females that had successfully mated among those captured in pheromone-baited traps in plots treated with one or two applications per season of Hercon Bio-Flakes formulated with 10% racemic fuscumol or untreated. Within year, bars with different letters were significantly different. Data were analyzed by generalized linear model (2009) or generalized linear mixed model (blocks random in 2010, 2011, 2012; SAS PROC GLIMMIX) using a binomial distribution and logit link; response variable was y/n, where y = number of mated females per plot and n = total number of females per plot. 2009: $F_{1,6} = 6.62$, $P = 0.04$; 2010: $F_{1,3} = 23.8$, $P = 0.02$; 2011: $F_{2,8} = 14.1$, $P = 0.002$; 2012: $F_{1,3} = 36.5$, $P = 0.01$.

Efficacy of Population Suppression

The mean numbers of larvae and adults per m² per plot in bait logs and girdled trees were highly variable (Tables 3 and 4) and were not significantly affected by pheromone treatment in any year, except 2011, in which mean density of adults differed between plots that received one versus two pheromone applications, but neither differed from that in control plots (Table 4). When data were pooled across all years, mean densities of larvae and adults were about 36% lower in treated plots than in control plots, but differences were not significant (larvae: $F_{1,27} = 2.16$, $P = 0.15$; adults: $F_{1,27} = 1.342$, $P = 0.26$; Tables 3 and 4). Densities of both larvae and adults were

greater in girdled trees than in bait logs in 2010 (Tables 3 and 4), supporting the findings of Flaherty et al. (2011), who suggested girdled spruce trees provide more suitable host material for *T. fuscum* larval establishment and survival than do bait logs.

Discussion

To our knowledge, this study provides the first demonstration that aggregation pheromone (as defined by Wertheim et al. 2005: "...compound(s) causing aggregative behavior in conspecifics of both sexes or in the same sex as the emitter") can be used to disrupt mating among feral females and reduce attraction of both sexes to pheromone baits. We provide data from 4 yr of forest field trials that show that broadcast applications of racemic fuscumol, a synthetic aggregation pheromone of *T. fuscum*, significantly reduced response to pheromone-baited traps and female mating success. About 60% of female *T. fuscum* captured in pheromone-baited traps in untreated plots were mated compared with only 30% in pheromone-treated plots. In related research, Sanchez-Husillos et al. (2015) showed that mass trapping with traps baited with the male-produced aggregation pheromone, 2-undecyloxy-1-ethanol (also known as monochamol), plus the kairomones, ipsenol and 2-methyl-3-buten-2-ol, successfully suppressed populations of the pinewood nematode vector *Monochamus galloprovincialis* Olivier (Cerambycidae: Lamiinae) in field trials.

Mating disruption, defined as broadcast application of synthetic pheromone sources to interfere with mate location and reduce female mating success, is a well-established management tactic to control lepidopteran pests (Judd et al. 1997, Thorpe et al. 2006, Witzgall et al. 2010). In recent years, the approach has been successfully applied to nonlepidopteran pests that also rely on female-produced pheromone for mate location, including beetles in the families Scarabaeidae (Sciarappa et al. 2005) and Cerambycidae (Maki et al. 2011), as well as Hemiptera (Walton et al. 2006, Vacas et al. 2009), Diptera (Samietz et al. 2012), and Hymenoptera (Martini et al. 2002). Mating disruption has also been successfully

Table 3. Mean (± SE) numbers of *T. fuscum* larvae per m² surface area in red spruce bait logs and girdled trees in plots treated with zero (control), one, or two applications of Hercon Bio-Flakes formulated with 10% racemic fuscumol at a rate of 2.75–4.5 kg/ha, near Halifax, Nova Scotia, 2009–2012

Year	Host type	Treated 2 App.	Treated 1 App.	Control	F^a	df	P
2009	Log	2.3 ± 1.3	–	3.4 ± 1.1	0.51	1,6	0.50
2010	Log	2.6 ± 1.1	–	2.4 ± 0.7	0.02	1,3	0.89
2009–2010 pooled	Log	2.4 ± 0.8	–	2.9 ± 0.6	0.31	1,13	0.59
2010	Tree	15.7 ± 4.4	–	18.3 ± 10.3	0.78	1,3	0.44
2011	Tree	24.2 ± 14.6	30.4 ± 12.1	34.7 ±7.9	1.41	2,6	0.32
2012	Tree	21.4 ± 6.2	–	42.2 ± 8.9	4.12	1,3	0.11
2010–2012 pooled	Tree	17.8 ± 5.2	–	27.9 ± 5.3	4.02	1,11	0.07
2009–2012 pooled	Both	13.9 ± 4.2		21.8 ± 4.8	2.16	1,27	0.15

[a]Results from generalized linear mixed model (SAS/STAT, PROC GLIMMIX) with either Poisson or negative binomial distribution, whichever had the best fit (lowest value for AICc).

Table 4. Mean (± SE) numbers of *T. fuscum* adults emerging per m² surface area from red spruce bait logs and/or girdled trees in plots treated with zero (control), one, or two applications of Hercon Bio-Flakes formulated with 10% racemic fuscumol at a rate of 2.75–4.5 kg/ha, near Halifax, Nova Scotia, 2009–2012

Year	Host type	Rate kg/ha	Treated 2 App.	Treated 1 App.	Control	F^a	df	P
2009	Logs	2.75	3.3 ± 1.7	–	5.8 ± 3.4	0.77	1,6	0.42
2010	Logs	2.75	1.0 ± 0.3	–	1.1 ± 0.6	0.03	1,3	0.87
2009–2010 pooled	Logs	2.75	2.1 ± 0.9	–	3.5 ± 1.8	0.76	1,13	0.40
2010	Trees	2.75	25.7 ± 9.3	–	22.4 ± 10.4	0.9	1,3	0.46
2011	Trees	4.5	16.7 ± 6.4b	33.8 ± 6.2a	24.7 ± 10.2ab	5.2	2,6	0.05
2012	Trees	2.5	37.1 ± 11.1	–	67.1 ± 19.2	2.93	1,3	0.19
2010–2012 pooled	Trees	2.5–4.5	22.4 ± 5.2	–	34.5 ± 9.8	2.71	1,11	0.13
2009–2012 pooled	Both	2.5–4.5	17.6 ± 4.8	–	27.3 ± 8.0	1.34	1,27	0.26

[a]Results from generalized linear mixed model (SAS/STAT, PROC GLIMMIX) with either Poisson or negative binomial distribution, whichever had the best fit (lowest value for AICc). Means followed by different letters differed significantly (Tukey–Kramer comparison of least square means, α = 0.05).

implemented for the ambrosia beetle *Megaplatypus mutatus* (Curculionidae), an insect that relies on male-produced sex pheromone (strictly attractive to females) for mate location (Funes et al. 2011). Although we observed significant reductions in female mating success, we were unable to completely shut down mating in pheromone-treated plots; about 30% of females were mated in treated plots compared with about 60% in untreated plots. This may be due in part to the fact that *T. fuscum* adults emerge sexually mature and can mate within hours of emergence from their host. The beetle's habit of reinfesting host trees year after year (Juutinen 1955) could very well result in a proportion of females that mate and oviposit on the host from which they emerged. In such situations, the aggregation pheromone may play less of a role in *T. fuscum* mate location than close-range mechanisms such as contact pheromones (Silk et al. 2011). Efficacy may also have been reduced near the boundaries of our field plots where the number of Bio-Flakes were lower than near the center of plots (Supp. Fig. C [online only]), or during periods of the flight season when concentrations of fuscumol in treated plots may have been relatively low; e.g., in 2011, there were still many *T. fuscum* active in late July and August, more than 30 d following the second application of fuscumol (Fig. 1). However, the fact that mating success in 2011 was similar in plots treated once versus twice that season does not support the latter argument.

There was no consistent significant effect of the pheromone applications on densities of *T. fuscum* in bait logs or girdled trees (Tables 3 and 4). The lack of significant population suppression in treated plots, despite reduced mating success, may be due to immigration of mated females from untreated areas that surrounded the

treated plots. Due to logistical constraints, it was not feasible to use either very large plots or small isolated populations to resolve this problem. However, potential problems with immigration of mated females would be less of a concern if mating disruption were applied to isolated infestations established far beyond the leading edge of the infestation. Another explanation for insignificant reductions in infestation levels in pheromone-treated plots may be that absolute densities of *T. fuscum* were so high, that despite the significant reduction in the percentage of females mated, there were still enough to locate and infest the girdled trees and bait log decks.

According to theory, the efficacy of mating disruption should increase as pest population density decreases. Our test area was moderately infested with *T. fuscum*, according to catches in pheromone-baited traps, that is, mean catches per trap per season of 5–15 beetles compared with 1–3 beetles observed in in low-density populations (J.D.S. unpublished data). We predict efficacy of mating disruption would be greater if fuscumol were applied to low-density populations of *T. fuscum* near or beyond the fringe of its range in Nova Scotia where mating success is already low (Rhainds et al. 2015), but this remains to be tested.

Exactly how elevated levels of pheromone interfere with insect mating success is not always clear, but several mechanisms have been proposed, including camouflage of natural pheromone plumes, competition between artificial and natural point sources of pheromone (i.e., false-trail following), and desensitization of response to pheromone through habituation or sensory adaptation (Bartell 1982, Cardé and Minks 1995). Pheromone-mediated mating disruption may also delay mating, which has been shown to significantly reduce female fecundity and fertility in moths (Knight 1997,

Fadamiro and Baker 1999, Mori and Evenden 2013). Because fuscumol by itself is not a potent attractant but instead synergizes attraction of both sexes when combined with spruce host volatiles, we do not think the point sources of fuscumol likely competed with calling males, except for flakes that happened to lodge on stressed spruce. We speculate it is more likely that the synthetic fuscumol interfered with *T. fuscum* mating by camouflaging the plumes from calling males or by desensitizing responses of both sexes to pheromone. However, we must emphasize that the exact mechanisms involved here are unknown.

Our study demonstrates the potential of broadcast applications of pheromone for helping to contain or slow the spread of an invasive cerambycid. Chances of success of such a strategy would be improved by targeting low-density, isolated populations that may have established as a result of human-assisted movement, and by sanitation, i.e., cutting and disposal of infested trees, at such outlier sites.

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