C. P. Alexander review[1]

Thirty-five years of pheromone-based mating disruption studies with *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae)

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Abstract—The Canadian registration in 2007 of Disrupt SBW Micro-Flakes®, a pheromone-based product for control of spruce budworm, *Choristoneura fumiferana* (Clemens), paved the way for large-scale trials to test the practicality of mating disruption as a commercial pest management strategy. We review results from field and laboratory experiments on pheromone-based mating disruption of spruce budworm conducted from 1974 to 2008. Application of pheromone from the ground or the air consistently reduced the orientation of males toward pheromone sources. Mating disruption also reduced the mating success of caged or tethered females in 15 of 16 field studies where this parameter was recorded, but had only a limited effect on the mating success of feral females. No consistent difference in the density of egg masses in control and treated plots was observed, which has often been attributed to immigration of gravid females into pheromone-treated plots. Laboratory studies suggest that false-trail following is the predominant mechanism underlying mating disruption in spruce budworm. The enhanced mating success of females with increasing population density suggests that mating disruption should target low-density emergent populations during the initial phase of an outbreak. Constraints that may limit the potential of mating disruption as a management tool include (1) difficulties associated with obtaining accurate sampling estimates at low population density to forecast the onset of outbreaks, (2) potential behavioral adaptations by which females enhance their mating success when the atmosphere is treated with pheromone, and (3) long-range dispersal of females by flight.

Résumé—L'homologation canadienne en 2007 des micro-flocons Disrupt SBW®, un produit dérivé de phéromones pour la lutte contre la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clemens), a ouvert la voie à des essais à grande échelle pour tester l'utilité pratique de la perturbation de l'accouplement comme stratégie commerciale de lutte intégrée contre les ravageurs. Nous passons en revue ici les résultats des expériences sur le terrain et en laboratoire de perturbation des accouplements à l'aide de phéromones chez la tordeuse des bourgeons de l'épinette de 1974 à 2008. L'épandage de la phéromone au sol ou dans les airs réduit de manière constante l'orientation des mâles vers les sources de phéromone. La perturbation des accouplements a aussi abaissé le succès des accouplements chez des femelles tenues en cage ou en suspension dans 15 des 16 études de terrain dans lesquelles on a tenu compte de cette variable; elle n'a cependant qu'un effet limité sur le succès de l'accouplement de femelles sauvages. On n'observe aucune différence constante dans la densité des masses d'œufs entre les parcelles témoins et expérimentales, ce qui a

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souvent été attribué à l'immigration de femelles gravides dans les parcelles traitées à la phéromone. Les études en laboratoire indiquent que la poursuite de fausses pistes est le mécanisme principal sous-jacent à la perturbation de l'accouplement chez la tordeuse des bourgeons de l'épinette. L'augmentation du succès de l'accouplement des femelles en fonction de l'accroissement de la densité de la population laisse croire que la perturbation de l'accouplement devrait cibler des populations émergentes de faible densité durant la phase initiale d'une épidémie. Les contraintes qui peuvent limiter le potentiel de la perturbation des accouplements comme outil de gestion incluent (1) la difficulté d'obtenir des estimations justes par échantillonnage aux faibles densités de population afin de prédire le début d'une épidémie, (2) les adaptations comportementales potentielles par lesquelles les femelles augmentent le succès de leurs accouplements lors d'épandages aériens de la phéromone et (3) la dispersion au vol des femelles sur de grandes distances.

Introduction

The mating system of moths (Lepidoptera) is usually characterized by females releasing trace amounts of pheromone to attract males for copulation (Greenfield 1981; Phelan 1997). When a male perceives a pheromone source that is above a physiological threshold, he flies upwind toward the source in zigzagging movements (anemotactic orientation) before "locking on" to the pheromone plume in the late stage of orientation as he gets closer to a calling female (Marsh *et al.* 1978; Sanders 1997). Traps baited with synthetic pheromone are used as to monitor the abundance and seasonal occurrence of moth pests (McNeil 1991). Pheromones have also been used to control populations directly, either through mass trapping of males to reduce the mating success of females (Taschenberg *et al.* 1974) or through mating disruption by interfering with male orientation toward calling females (Gaston *et al.* 1967; Beroza and Knipling 1972). In Lepidoptera, mating disruption research outnumbers mass trapping research by a factor of four to one (El-Sayed *et al.* 2006). An approach based on the annihilation of males attracted to pheromone sources ("lure and kill") has been explored (El-Sayed *et al.* 2009) but not as thoroughly as mass trapping and mating disruption (El-Sayed *et al.* 2006). Even though direct removal of males from the reproductive pool is theoretically more effective than mating disruption, the major drawbacks of mass trapping or "lure and kill" are the high cost and large number of pheromone-baited traps needed in operational programs (Byers 2007; Yamanaka 2007; Teixera *et al.* 2010). Mass trapping and "lure and kill" may be most effective in the context of eradicative measures against invasive species with low population density and limited spatial distribution (El-Sayed *et al.* 2006, 2009).

Commercial mating disruption programs predominantly target pests in heavily managed, high-value settings such as vineyards or orchards (Cardé and Minks 1995; Welter *et al.* 2005; Witzgall *et al.* 2010). Because immigration of gravid females into areas treated with pheromone severely reduces the practicality of mating disruption, successful programs are usually conducted over a broad geographic range, *e.g.*, area-wide management programs performed at regional rather than local scales (Welter *et al.* 2005; Witzgall *et al.* 2008). Another advantage of large-scale applications is that they substantially facilitate increased concentration and homogeneous diffusion of the air with pheromone (Witzgall *et al.* 2010). The positive association between the size of areas treated and the efficacy of mating disruption suggests this approach has excellent potential for controlling forest defoliators over large landscapes (Overhulser *et al.* 1980; Hulme and Gray 1994; Leonhardt *et al.* 1996; Martini *et al.* 2002; Thorpe *et al.* 2007).

High insect density is another factor that constrains the effectiveness of mating disruption (Webb *et al.* 1990; Cardé and Minks 1995; Witzgall *et al.* 2008). At a mechanistic level, the relationship between population density and the level of mating suppression is mediated by the physiological processes underlying mating disruption. Four major mechanisms have been proposed to explain how mating disruption works: (1) sensory fatigue (adaptation or habituation) of male pheromone receptors, (2) camouflage of female pheromone plumes in a background of high pheromone concentration, (3) imbalance of sensory input when the ratio of background pheromone components is different from that produced by calling females, and (4) false-trail following by male moths to synthetic pheromone sources that compete with plumes produced by calling females (Bartell 1982; Cardé and Minks 1995).

The first three mechanisms can be grouped as noncompetitive processes (Miller *et al.* 2006a) that do *not* imply a direct relationship between population density and the level of mating suppression, although an increased rate of random mate encounters at high density may be associated with high female mating success (Mosimann 1957; Barclay and Judd 1995). False-trail following, in contrast, implies that the efficacy of mating disruption is a function of the ratio of calling females to synthetic pheromone sources, *i.e.*, a low level of mating suppression is expected at high population density (Barclay and Judd 1995; Cardé and Minks 1995; Miller *et al.* 2006a). Competitive attraction of synthetic pheromone sources appears to be a leading cause of mating disruption in a majority of moth species (Miller *et al.* 2006b; see also Miller *et al.* 2010), although the different mechanisms are not exclusive but rather interact with each other (Cardé and Minks 1995; Sanders 1997).

The chemical structure, formulation (distribution system), and concentration of the synthetic pheromone are key components of mating disruption. For example, using the pheromone blend most attractive to males may or may not enhance the efficacy of mating disruption (see references in Evenden *et al.* 1999a); analogs of pheromone or antagonist blends may also result in effective mating disruption (Evenden *et al.* 1999b). Mating disruption is expected to bring about female mating failures if the aerial concentration of pheromone exceeds a threshold value; estimating the relationship between pheromone emission rate and male response in the field, however, is extremely challenging (Vacas *et al.* 2011).

The occurrence of inverse density-dependent mating success of females on a small scale in field populations of insects (Rhainds 2010) suggests that males may be disoriented by pheromone plumes simultaneously released by numerous calling females, in a context that is reminiscent of "natural mating disruption" (Rhainds *et al.* 1999). Selective pressures to enhance mate encounters in response to high pheromone concentrations may thus have existed over a long evolutionary time, and these preexisting adaptations may limit the application of mating disruption. Female moths are physiologically capable of recognizing their conspecific sex pheromone, *i.e.*, auto-detection (McNeil 1991; DeLury *et al.* 2005; Stelinski *et al.* 2006; Yang *et al.* 2009), and numerous examples of behavioral phenotypic plasticity in response to fluctuations in pheromone concentration have been reported (McNeil 1992; Groot *et al.* 2009), including modification of the calling behavior (Lim and Greenfield 2006; Yang *et al.* 2009), oviposition strategy (den Otter *et al.* 1996; Weissling and Knight 1996; Harari *et al.* 2011), foraging activities of mate-seeking females (Birch 1977; Weissling and Knight 1995), and incidence of flight dispersal (Palaniswamy and Seabrook 1978; Sanders 1987; Pearson *et al.* 2004). Males exhibit distinct mate location strategies as a function of population density, *e.g.*, at corresponding low and high concentrations of pheromone (Richerson *et al.* 1976; Elkinton and Cardé 1983; Cardé and Hagaman 1984), which may in turn influence the outcome of mating disruption. Behavioral adaptations to alleviate the negative effect of high atmospheric pheromone concentration in high-density populations are among the key factors that influence the efficacy of mating disruption (McNeil 1992; Cardé and Minks 1995).

The eastern spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), is the most serious pest in Canadian boreal forest stands of balsam fir and spruce (*Abies balsamea* (L.) Mill. and *Picea* A. Dietr. (Pinaceae)) (Morris 1963). Spruce budworm population dynamics are characterized by extreme variation in temporal abundance from endemic populations with very low numbers of larvae to epidemic populations in which larvae are so abundant as to completely defoliate and kill trees. Currently (2012), only two insecticides registered in Canada are used to limit defoliation by spruce budworm: microbial formulations of *Bacillus thurigiensis kurstaki* Berliner (*Btk*) (Bauce *et al.* 2004; Cai *et al.* 2010) and the ecdysone agonist Mimic® 240 LV (Tebufenozide) (Cadogan *et al.* 1998). Reliance on this limited number of options is problematic because the intensity and range of spruce budworm outbreaks are expected to increase in the future with trends of global warming (Gray 2008). Mating disruption studies resulted in commercial registration in Canada in 2007 of the pheromone-based product, Hercon Disrupt Micro-Flakes® SBW (http://pr-rp.pmra-arla.gc.ca/PR_SOL/pr_web.ve1?p_ukid=12247) (Kettela and Silk 2005), but the practicality of implementing a mating disruption control program on an operational scale remains unclear. The objectives of this review are to consolidate the literature on spruce budworm mating disruption (including unpublished technical reports and a summary of the different experiments posted at http://atl.cfs.nrcan.gc.ca/sprucebudworm) and provide a contextual framework for mating disruption as a management tool for spruce budworm.

Reproductive biology of spruce budworm

Eggs are laid by mated females on host plant foliage in early summer. Females have an average fecundity of ~200 eggs but lay only about 80% of their eggs (Thomas *et al.* 1980). After hatching, first instars construct a hibernaculum on foliage in which they molt and then overwinter as second instars. Larval development resumes in late spring, and individuals develop through six instars prior to pupation on the host plant. Adults emerge in late June or early July. The emergence of males usually precedes that of females (Bergh *et al.* 1988; Eveleigh *et al.* 2007).

Females release a blend of 95:5 *E*:*Z*-11 tetradecenal (5–40 ng/female) to attract males for mating; the *E* isomer was initially identified as a pheromone component (Weatherston *et al.* 1971), and the synergistic activity of the *Z* isomer was demonstrated subsequently (Silk *et al.* 1980; Silk and Kuenen 1988). Females start calling on the first night following their emergence and remain attractive for up to 12 days (Sanders and Lucuik 1972; Miller and McDougall 1973). In epidemic populations, most females mate on the day of emergence (Outram 1973). Sexual attractiveness is lower for mated females than for virgin females (Sanders and Lucuik 1972). Nearly 100% of females mate at least once during their lifetime in high-density populations (Greenbank *et al.* 1980), but mating success is lower in sparse populations (Sanders and Lucuik 1972; Outram 1973; Kipp *et al.* 1995). Although some females mate repeatedly over their lifetime (up to four times), the majority of females (usually >90%) mate only once (Outram 1971, 1973; Miller 1979).

The neural inhibition of pheromone production among mated females involves the transfer of sperm by males during copulation (Delisle and Simard 2002). Mated females lay their eggs in batches and sometimes disperse above the forest canopy between oviposition bouts. The enhanced dispersal of females in response to their conspecific pheromone (Sanders 1987) suggests density-dependent dispersal, although the relationship between population density and the incidence of dispersal in field populations of spruce budworm is unclear (Greenbank *et al.* 1980). Well-fed females full of mature eggs are usually incapable of extended flight before oviposition (Wellington and Henson 1947). Comparatively light-weight females that have fed on poor-quality foliage are more capable of extended flight (Blais 1953). Virgin females without mating opportunities lay unfertilized eggs (Wallace *et al.* 2004), which may be a physiological adaptation to reduce abdominal weight and facilitate flight. Dispersal by flight may be an adaptation to enhance mating success: 30% (106 of 342) of females sampled at ground level were unmated compared with none of 154 females sampled above the plant canopy in one study (Outram 1973). Dispersal is more prevalent among females than males (Greenbank *et al.* 1980; Eveleigh *et al.* 2007) and massive immigration by gravid females affects local population dynamics (Miller and McDougall 1973; Miller 1979). Mark–recapture studies indicate that mature males respond to the first (nearest) source of pheromone they encounter and have a daily survival rate of 0.67 (Sanders 1983). Molecular analysis revealed a high level of gene flow among spruce budworm populations across broad latitudinal and longitudinal ranges, likely due to a high incidence of female dispersal (Harvey 1996; see also Weber *et al.* 1996).

Laboratory studies on spruce budworm mating disruption

Numerous laboratory and wind-tunnel studies on spruce budworm pheromone communication have yielded valuable information on the mechanisms of mating disruption and parameters that may affect its efficacy (Sanders 1997). The effect of pheromone on spruce budworm has been evaluated using physiological (electroantennograms) and behavioral (wing fanning, flight take-off, orientation toward pheromone sources, or calling females) responses.

Synthetic sources of pheromone interfere with the orientation of males toward calling females and the level of disruption increases with the concentration of pheromone (Schmidt *et al.* 1980a; Sanders 1982, 1996, 1998; Ponder *et al.* 1986). Most experiments tested a blend approximating the ratio produced by females (95:5 *E*:*Z*-11 tetradecenal), but some experiments also evaluated the effect of pheromone analogs or different ratios of *E*:*Z*-11 tetradecenal. In general, the orientation of males was most suppressed by blends corresponding to the natural pheromone of spruce budworm (Schmidt *et al.* 1980a; Ponder *et al.* 1986; Sanders 1995), although when pheromone was presented to males in small flasks, pure *E*- and *Z*-11 tetradecenal were equally effective in reducing the subsequent mating success of females (Schmidt *et al.* 1980a). The level of suppression increased with the concentration of pheromone for a range of 100 μg to 1 mg active ingredient (AI) or 125 ng/h to 1 μg/h (Schmidt *et al.* 1980a; Ponder *et al.* 1986). Three analogs of pheromone showed some behavioral activity in the laboratory, 10-(Cyclopent-1-en-1-yl)-decanal, (1:1)-*E*-*Z*-11,13-tetradecadienal, and (1:1)-*E*-*Z*-12-tetradecenal (Schmidt *et al.* 1980a; Ponder *et al.* 1986).

The predominant mechanism underlying mating disruption appears to be false-trail following (competitive attraction between synthetic pheromone sources and calling females), at least when the pheromone release rates approximate that of a calling female as indicated by (1) the higher level of male disorientation when synthetic pheromone was released from discrete sources rather than in a uniform concentration (Sanders 1982), (2) the similar response of males previously exposed or not to high doses of pheromone (Sanders 1985, 1996), and (3) the orientation of males toward synthetic sources of pheromone (Sanders 1995). At pheromone concentrations above 20 ng/m^3, sensory fatigue appears to be involved in the disorientation of males (Sanders 1996). Sensory fatigue may also be at play when an "unnatural" blend of 50:50 *E*:*Z*-11 tetradecenal is used as a mating disruptant (Sanders 1997). Mating disruption may be most effective when the pheromone is released from a few point sources with a high concentration rather than from numerous point sources with a low concentration of pheromone (Sanders 1982; see Alford and Silk (1983) for a similar result in the field). Mating disruption is not likely to suppress female mating success to near-zero levels, because a high proportion of males eventually locate a calling female even when the concentration of pheromone is high (Sanders 1995, 1997, 1998). The mating success of females maintained in cages was independent of population density in the absence of pheromone but increased with density when the air was treated with pheromone (Ponder *et al.* 1986).

Electroantennograms revealed that females perceived their conspecific pheromone at an amplitude of approximately two-thirds that of males (Palaniswamy and Seabrook 1978; Palaniswamy *et al.* 1979). Female spruce budworms also responded to high concentrations of pheromone by altering their calling behavior and increasing flight dispersal; for virgin females, the effect was documented only for individuals >3 days old (Palaniswamy and Seabrook 1978, 1985; Sanders 1987). In other experiments, however, neither the concentration of pheromone nor the density of conspecific females had any effect on the calling behavior of spruce budworm females (Sanders and Lucuik 1972; Sanders 1995).

Field studies on spruce budworm mating disruption

The logistics and main findings of 21 field studies on mating disruption are summarized in Tables 1 and 2. Ground or aerial trials have been conducted at spatial scales ranging from 0.001 to 400 ha in Ontario, Quebec, New Brunswick, and Nova Scotia in Canada and Maine in the United States. The feasibility of mating disruption was first demonstrated on a small scale by applying pheromone from the ground. Operational mating disruption programs must rely on aerial application to be practical because of the large areas of forests infested by spruce budworms. It is inherently difficult to conduct replicated mating disruption trials for forest defoliators due to the large spatial scale and high monetary cost involved. Because of these constraints, few field studies on spruce budworm mating disruption have been replicated in a true statistical sense (see Trudel *et al.* 2009 for an exception) and none have rigorously evaluated the effect of environmental variables (*e.g.*, forest composition or spruce budworm density) on the effectiveness of mating disruption. Despite these limitations, sufficient mating disruption studies have been

Table 1. Summary of mating or communication disruption experiments conducted in the field to target spruce budworm.

						Variables		
Experiment	Year	Site	*N*	Area	Release rate	Dependent	Independent	Mating disruption
Pheromone applied from the ground								
1	1974	ON	1	1600 m^2	Not specified	♂ ORIENT (FBT)	POS	YES
2	1978	NB	1	16 m^2	330–1800 mg/ha/h	♀ MS (CF)	PD	YES
3	1981	NB	4	113 m^2	6–84 mg/ha/h	♀ MS (CF)	PD, SR	YES
4	1981	NB	2	100 m^2	10 mg/ha/h	♀ MS (TF)	PS	YES
5	1982	NB	3	500 m^2	21 mg/ha/h	♀ MS (FBT)	PS, ET	YES
6	1989	NB	1	1 ha	110 g/ha	♂ ORIENT (PT, FBT)		YES
Pheromone applied from the air								
7	1975	ON	1	12 ha	7.4 g/ha	♂ ORIENT (FBT)	POS	YES
						♀ OVIP (EC)		
8	1977	ON	1	9–250 ha	3–30 mg/ha/h	♂ ORIENT (PT, FBT)		YES
						♀ MS (FBT)		YES
						♀ OVIP (EC, LC)		YES
9	1978	NB	1	400 ha	0.1–20 mg/ha/h	♂ ORIENT (PT, FBT)	ET, VP	YES
		NS	1	400 ha		♀ MS (TF, CF)	ET, PD	YES
						♀ MS (WF)		NO
						♀ OVIP (EC, LC, EP)		NO
10	1980	ME	1	9–145 ha	50–500 g/ha	ORIENT (PT)		YES
						♀ MS (WF)		NO
						♀ OVIP (EC, FR)		NO
11	1981	ON	1	30 ha	100 g/ha	♂ ORIENT (PT)	VP	YES
						♀ MS (CF)	PD	YES
						♀ MS (WF)		NO
						♀ OVIP (EC, FR)	ET	NO
12	1983	ON	1	3 ha	148 g/ha	♂ ORIENT (PT)		YES
13	1985	NB	1	3 ha	140 g/ha	♀ MS (CF)	BS	YES
14	1987	NB	1	16 ha	96 g/ha	♂ ORIENT (PT)	ET	YES
						♀ OVIP (EC, EP)		NO
15	1988	NB	1	25 ha	20–90 g/ha	♂ ORIENT (PT, FBT)		YES
						♀ OVIP (EC)		NO
16	1996	NB	1	2 ha	100 g/ha	♀ MS (CF)	ET	YES

Table 1. *Continued*

17	2000	NB	1	4 ha	5 g/ha	♀ MS (CF)	ET, VP	YES
18	2001	NB	1	5 ha	25–75 g/ha	♀ MS (CF)	YES	
19	2004	ON	1	8 ha	25–50 g/ha	♂ ORIENT (PT)		YES
						♀ MS (CF, WF)	ET	YES
						♀ OVIP (EC)		YES
20	2005	ON	1	25 ha	25 g/ha	♂ ORIENT (PT)	PT	YES
						♀ MS (CF)		YES
						♀ MS (WF)		NO
						♀ OVIP		YES
21	2008	QC	4	50	35 g/ha	♂ ORIENT (PT, FBT ET)		YES
						♀ MS (PBT)		
						♀ OVIP (EC, LC)		

Notes: For different parameters and studies, the effect of pheromone treatment or lack thereof was summarized as a YES or NO. Detailed results are provided in the Appendix (http://atl.cfs.nrcan.gc.ca/sprucebudworm). The logistics of aerial applications are detailed in Table 2.

References for different experiments: 1, Sanders (1976); 2, Schmidt and Seabrook (1979); 3, Palaniswamy *et al.* (1982); 4–5, Alford and Silk (1983); 6, Kipp *et al.* (1990); 7, Sanders (1976); 8, Sanders (1979); 9, Miller (1979) and Schmidt *et al.* (1980b); 10, Dimond *et al.* (1984); 11, Sanders and Silk (1981); 12, Seabrook and Kipp (1986); 13, Kipp *et al.* (1987); 14, Seabrook and Baskerville (1988); 15, Seabrook (1989); 16, Lonergan *et al.* (1997); 17, Silk and Kettela (2001); 18, Silk and Kettela (2002); 19, Kettela and Silk (2005); 20, Kettela *et al.* (2006); 21, Trudel *et al.* (2009).

The efficacy of pheromone-based disruption is evaluated using three parameters: (1) orientation of males toward females (♂ ORIENT: captures of males in traps baited with synthetic pheromone or virgin females); (2) mating success of females (♀ MS: presence or absence of spermatophore in the reproductive tract of tethered, caged, or feral females); and (3) reproduction of females (♀ OVIP: counts of eggs or second instars).

Abbreviations in parentheses represent the methodology used to assess the dependent variables. FBT, female baited traps; PT, pheromone traps; TF, tethered females; CF, caged females; WF, wild (feral) females; EC, egg count on foliage; LC, L2 count on foliage; EP, egg masses per pupa; FR, fertility rate.

The independent variables represent parameters that affected the efficacy of mating disruption; an empty space indicates that no effect was reported. POS, spatial position in the forested stand; ET, emergence time; BS, body size of females; VP, vertical position in the canopy; PS, number of pheromone point sources; PD, population density; SR, sex ratio.

Table 2. Logistics of spruce budworm mating disruption trials in which the pheromone was applied from the air.

Experiment	Product	Tank mix	Aircraft equipment	Application
7	National Cash Registered microCap	H_2O Mini-drift Rhoplex B-15	Stearman (1)	Boom & Nozzle T-Jet
8	Conrel fibers	Polybutene sticker	Cessna 185	Conrel Pods (2/plane)
9	Conrel fibers	Bio-Tac sticker	Cessna 185	Conrel Pods (2/plane)
10	Hercon PVC flakes	H_2O Unspecified glue	Cessna 180	Slung device (2/plane)
11	Hercon PVC flakes		Piper Pawnee	Custom designed pods (2/plane)
12	Hercon PVC flakes	H_2O Pherotech Polybutene sticker	Unspecified	Unspecified Pods
13	Hercon PVC flakes			
14	ICI microcaps	H_2O + dye	Cessna 188	Micronaire Au 4000 (4)
15	ICI microcaps	H_2O	Bell, Jet Ranger	Micronaire Au 4000 (4)
16	3M microcaps	H_2O	Cessna 188	Micronaire Au 4000
17	3M microcaps	H_2O	Cessna 188	Micronaire Au 4000
18	3M microcaps	H_2O	Cessna 188	Micronaire Au 4000
19	Hercon Disrupt Micro-Flakes (PVC)	H_2O, Gelva sticker Guar Gum	Cessna 188	Boom & Nozzle (open)
20	Hercon Disrupt Micro-Flakes (PVC)	H_2O, Gelva sticker	Cessna 188	Boom & Nozzle
21	Hercon Disrupt Micro-Flakes	Flakes alone (dry)	Helicopter	Bucket with rotating speeder

Specific details for the different experiments are provided in Table 1 and the Appendix (http://atl.cfs.nrcan.gc.ca/sprucebudworm).

Reference sources corresponding to different experiment numbers as listed in Table 1.

performed to allow identification of consistent patterns in the literature.

Logistics of mating disruption

A broad variety of formulations, specialized application material, and aircraft types have proven effective at disseminating a pheromone disruptant that interferes with the orientation of males toward pheromone sources. Two paths of formulation development (micro-encapsulated products [microcaps] and macro-carriers such as Conrel fibers and Hercon Micro-Flakes) have been explored. The flowable microcaps are dispersed in water with a standard spray system; the macro-carriers usually require specialized equipment to apply the particles coated with a sticker. Both types of release devices are broadly used in pest management programs and have proven effective at disseminating pheromone for mating disruption against numerous moth pests.

The amount of aerially applied pheromone in mating disruption studies is calibrated as a function of the concentration of pheromone in the sprayed solution, the speed and height of the airplane during application, and the flow rate of the application devices (atomizers or pods). Achieving a specific application rate of pheromone in terms of g AI/ha is a difficult task, and in many studies only a fraction of the target application was achieved (Miller 1979; Seabrook and Baskerville 1988; Kettela *et al.* 2006). In two extreme cases, the concentration of pheromone was considerably lower than the target value (60%, 148 *versus* 250 g AI/ha [Seabrook and Kipp 1986] and 5%, 5 *versus* 100 g AI/ha [Silk and Kettela 2001]).

Two methods have been used to sample the relative abundance of pheromone in treated plots: (1) counts of pheromone-impregnated flakes that adhere to the foliage or that deposit on horizontal surfaces such as glass slides or cloth screen and (2) concentration of residual pheromone over time in flakes, on the foliage, or in a volume of air. The relative abundance of pheromone is expressed in terms of quantity applied (g AI/ha), release rate of flakes (g AI/ha/h), or concentration of pheromone in the air (ng AI/m^3). Converting these values is difficult because any conversion factor is dependent on the half-life of pheromone-impregnated flakes, which varies between studies.

The efficacy of mating disruption increases with the level of pheromone between 14–100 g AI/ha (Seabrook 1989; Silk and Kettela 2002; Kettela and Silk 2005), 0.3–1.8 ng AI/m^3 (Seabrook and Kipp 1986), and 0.1–84 mg AI/ha/h (Miller 1979; Palaniswamy *et al.* 1982). The lower level of pheromone for which some level of mating disruption has been documented corresponds to 5–7 g AI/ha (Sanders 1979; Silk and Kettela 2001), 0.3 ng AI/m^3 of air (Seabrook and Kipp 1986), or 0.1 mg AI/ha/h (Miller 1979). Upper thresholds of pheromone above which the level of mating disruption remains stable are around 1.8 ng AI/m^3 of air (Seabrook and Kipp 1986) or 330 mg AI/ha/h (Schmidt and Seabrook 1979). Laboratory tests revealed that sensory fatigue occurred in spruce budworm at a threshold concentration of 20 ng/m^3 and that mating disruption is based on false-trail followings for lower concentrations (Sanders 1996).

Because methodology and local conditions vary between studies, it is difficult to infer an optimal dose of pheromone by comparing results from different studies. The use of portable electroantennogram systems in future studies may provide a tool to determine the threshold pheromone concentration for effective mating disruption, as has been documented in other insects (Milli *et al.* 1997). Based on a trial in which mating disruption reduced the mating success and oviposition of feral females, an application rate of at least 50 g AI/ha encapsulated in Hercon Micro-Flakes has been recommended for operational mating disruption trials (Kettela and Silk 2005).

Measuring the efficacy of mating disruption

The efficacy of pheromone-based disruption is evaluated using three parameters: (1) orientation of males toward females (captures of males in traps baited with synthetic pheromone or virgin females), (2) mating success of females (presence or absence of a spermatophore in the reproductive tract of tethered, caged, or feral females), and (3) reproduction of females (counts of eggs deposited on foliage or second instars).

Mating disruption interfered with the orientation of males toward pheromone sources in all 13 studies where this parameter was recorded, usually by more than 90% (Table 1) and, in one instance, captures of males in pheromone-treated plots was suppressed to zero (Kipp *et al.* 1990). Captures of males in traps baited with pheromone-impregnated flakes (Sanders and Silk 1981; Dimond *et al.* 1984) suggest that false-trail following by males is involved, at least to some extent, in mating disruption; this hypothesis is supported by numerous laboratory studies. The lack of apparent effect of pheromone treatment on captures of males in blank or light traps (Sanders 1976; Miller 1979; Sanders and Silk 1981; Seabrook 1989; but see Seabrook and Baskerville 1988) further suggests that mating disruption does not have a direct effect on the abundance of foraging males in treated or control plots, but rather on the orientation of males toward pheromone sources (Miller 1979). It is theoretically possible that a high pheromone dose could influence the abundance of males in treated areas, if for example the pheromone attracts males from surrounding populations or triggers emigration from treated areas.

Mating disruption reduced the probability of mating in caged or tethered females in 15 of 16 studies (Table 1) and the proportion of mated females was usually more than five times lower in treated plots than in control plots. The mating success of feral females was also evaluated by collecting females with sweep nets or vacuum devices, by treating trees with insecticide, or by collecting females that died from natural causes. Pheromone treatment has a limited effect on the mating success of feral females compared with that of caged or tethered females. In the majority of studies, most (>99%) feral females collected in treated plots were mated, despite considerable reduction in mating success among caged or tethered individuals (Miller 1979; Sanders and Silk 1981; Seabrook and Baskerville 1988; Kettela *et al.* 2006). In one study (Dimond *et al.* 1984), the proportion of virgin feral females was high (up to 55% in some plots) through the entire period of adult emergence, but no effect of pheromone treatment was detected. The high incidence of virgin females was not due to a shortage of males *per se* because the ratio of male to female exceeded 10:1 at most sites (Dimond *et al.* 1984). Only one study (Kettela and Silk 2005) reported a consistently lower proportion of mated females in treated plots than in control plots, but the reduction in mating success among feral females was only about one-fifth of that observed among caged females.

Those results suggest that females have either evolved behavioral adaptations (*i.e.*, calling periodicity or dispersal) to enhance mating in pheromone-treated environments (Palaniswamy and Seabrook 1978; Sanders 1987; see also Pearson *et al*. 2004; Rhainds 2010), or that they immigrate in large numbers into treated plots. In any event, assessments of pheromone treatment based on caged or tethered females tend to systematically overestimate the efficacy of mating disruption.

Male-biased sex ratio may result in a poor level of mating disruption (Schmidt and Seabrook 1979; Palaniswamy *et al*. 1982; Ponder *et al*. 1986). Interestingly, Kipp *et al*. (1987) reported that body size of females did not affect their mating success in control cages (wing length of mated and unmated females: 11.6 ± 1.1 and 11.5 ± 1.2 cm, respectively, $N = 517$, $P < 0.20$), whereas mated females were significantly larger than unmated females in cages treated with pheromone (wing length of mated and unmated females: 11.4 ± 1.1 and 11.1 ± 1.1 cm, respectively, $N = 448$, $P < 0.01$). Even though the difference in size was significant, the amplitude of variation was small and may have limited biological meaning. The link among body size, pheromone emission level, and attractiveness of females has not been explored to any extent in spruce budworm or any other moth species (Johannson and Jones 2007), thus the results reported above remain difficult to interpret. Only one study has evaluated the mating success of males (using the method developed by Bergh *et al*. 1988); no difference in the proportion of mated males was observed in control plots or pheromone-treated plots (Seabrook 1989).

Mating disruption has a limited, inconsistent effect on the level of reproduction by females. The reduction in density of egg masses in pheromone-treated compared with control plots at the end of the oviposition period is either nil (Sanders 1976; Miller 1979; Sanders and Silk 1981; Dimond *et al*. 1984; Seabrook and Baskerville 1988; Seabrook 1989) or small (<20%) (Sanders 1979) compared with the level of disruption inferred from female mating success. This apparent paradox has been attributed to the immigration of gravid females from outside treated plots, a hypothesis that was indirectly supported in a trial conducted in an isolated area in which a high (46%) reduction of egg deposition was observed (Kettela and Silk 2005).

Sampling constraints may complicate the interpretation of oviposition data because accurate estimates of low population density require a large number of samples (Régnière and Sanders 1983). For example, Kettela *et al.* (2006) observed a six-fold reduction in egg mass density in treated plots compared with control plots, but did not conclude that mating disruption was effective because densities were low (19 and 3 egg masses sampled on 90 branches in control and treated plots). Seabrook and Baskerville (1988) reported the number of egg masses per pupa to be three times higher in control plots than in treated plots, but data on the number of eggs in different plots were not reported and the ratio of eggs to pupa may have limited heuristic value due to sampling imprecision in the numerator and denominator parts of the equation. The proportion of infertile eggs in treated and control plots does not vary (Miller 1979; Dimond *et al.* 1984), indicating that the results reported above are not an artefact of unmated females laying infertile egg masses in pheromone-treated plots. Some studies reported a reduction in egg density early in the season but no overall cumulative effect late in the season (Sanders and Silk 1981; Seabrook and Baskerville 1988; Seabrook 1989), which can be explained by the low level of mating disruption among late-emerging females (see "Spatio-temporal constraints on mating disruption").

Spatio-temporal constraints on mating disruption

Pheromone was applied over 1 or 2 days in most experiments, with the exception of three trials in which pheromone was applied twice 13 days apart (Lonergan *et al.* 1997) or over an interval of 7 days (Miller 1979; Sanders 1979). The timing of pheromone application varied from the onset of adult emergence (Miller 1979; Sanders and Silk 1981; Dimond *et al.* 1984; Seabrook 1989) to the median date of emergence (Sanders 1976, 1979; Kettela and Silk 2005; Kettela *et al.* 2006).

The effect of mating disruption is most pronounced shortly after application due to a decline in pheromone concentration over time (Sanders 1976; Alford and Silk 1983; Dimond *et al.* 1984; Seabrook and Baskerville 1988; Lonergan *et al.* 1997; Silk and Kettela 2001; Kettela and Silk 2005). The decay of pheromone over time is related to the half-life of flake release devices, which varies from 5 to 13 days (Miller 1979; Sanders and Silk 1981; Lonergan *et al.* 1997; Silk and Kettela 2001, 2002; Kettela and Silk 2005; Kettela *et al.* 2006) and may occur earlier following heavy rainfall (Seabrook 1989; Seabrook and Baskerville 1988). The release rate of pheromone from flakes is temperature dependent and thus higher during daytime than at night, an opposite pattern to the primarily nocturnal release of pheromone by females (Sanders and Silk 1981; Seabrook and Baskerville 1988; Seabrook 1989). Traps baited with pheromone-impregnated flakes were more attractive to males than were traps baited with females, and the difference was consistent over time, although the magnitude of variation was smaller during the portion of the evening when females were actively calling (Sanders and Silk 1981). Broad-scale phenological models of adult emergence as a function of latitude or elevation (Régnière 1996; Régnière *et al.* 2012) will help schedule the timing of pheromone application in the context of operational mating disruption.

The efficacy of mating disruption depends upon adequate distribution of pheromone throughout the forest canopy. The greater level of mating disruption at the center of experimental plots than at the periphery (Sanders 1976) suggests that pheromone treatment is most effective in large forest stands with a low perimeter to area ratio. The distribution of aerially applied flakes varies between experiments from relatively uniform (Sanders 1976; Lonergan *et al.* 1997) to extremely clumped (Sanders 1979; Kettela and Silk 2005); the latter distribution may be most effective for mating disruption (Alford and Silk 1983; Silk and Kuenen, 1984). Similar results were observed in wind-tunnel experiments and interpreted as evidence for false-trail following as a mechanism underlying mating disruption (Sanders 1982). A lower concentration of pheromone in the upper canopy than on the ground likely results in a lower level of mating disruption on tree tops (Miller 1979; Sanders and Silk 1981; Seabrook and Kipp 1986; Seabrook and Baskerville 1988; Seabrook 1989; but see Silk and Kettela 2001).

Mating disruption and early intervention strategy

Current (2012) spruce budworm management programs seek to mitigate economic losses by protecting host trees from defoliation (Fournier *et al.* 2009). An early intervention strategy has been proposed to prevent defoliation but the success of this strategy ultimately depends on spruce budworm population dynamics (Régnière *et al.* 2001). Periodic outbreaks have occurred at intervals of 35 to 40 years since the middle of the 16th century (Royama 1984; Boulanger and Arsenault 2004) and the causality of recurrent outbreaks remains the subject of a longstanding debate among insect ecologists.

Early models assumed that population dynamics are mediated by internal processes such as bird predation or mortality of ballooning larvae within local populations (Morris 1963). Within that framework, the spread of outbreak conditions can be mediated by females dispersing from heavily infested locations. Such dispersal is density dependent and rarely occurs at low density, thus mating disruption may be used to prevent the spatial spread of spruce budworm infestations.

Subsequent models have assumed that synchronized outbreaks over large areas are due to climatic perturbations affecting natural enemies, *i.e.*, Moran effects (Royama 1977, 1984; Royama *et al.* 2005). Dispersal by adults is assumed to have a stabilizing effect on population dynamics by homogenizing spatial variation of population density. Because dispersal is assumed to be density independent, mating disruption will be ineffective unless applied over sufficiently large areas; otherwise, massive immigration by gravid females will obfuscate any effect of mating disruption (Miller and McDougall 1973; Greenbank *et al.* 1980). Thus the objective of early intervention through mating disruption will be limited to suppression of populations below a defoliation threshold that negatively affects tree growth (Régnière *et al.* 2001).

The debate on spruce budworm population dynamics is ongoing, and it remains difficult to forecast the spatio-temporal occurrence of outbreaks. This situation is due to a limited amount of empirical data on preoutbreak populations, as well as sampling constraints related to the difficulty of obtaining accurate low-density estimates (Régnière and Sanders 1983). An enhanced understanding of spruce budworm population dynamics at the early stage of an outbreak (in particular, the nature of female dispersal in relation to population density) is needed to assess the future role of mating disruption as a management tool.

Operational mating disruption will likely target low-density populations of spruce budworm. This is suggested by the declining efficacy of mating disruption with an increasing density of mating pairs in field cage trials (Miller 1979; Schmidt and Seabrook 1979; Palaniswamy *et al.* 1982), the lower mating success of females in low-density populations than in high-density populations (Sanders and Lucuik 1972; Outram 1973; Sanders 1979; Kipp *et al.* 1995), and the pest management objective to prevent extensive defoliation before populations of spruce budworms have reached high densities. As documented in other moth species (Miller *et al.* 2006b), the physiological mechanism of mating disruption in spruce budworm appears to involve competitive attraction between synthetic sources and calling females, which results in lower efficacy of mating disruption at higher population densities (Barclay and Judd 1995; Cardé and Minks 1995).

Conclusions

Aerial application trials have been carried out with products containing spruce budworm pheromone since the mid 1970s. A broad variety of test products, specialized application material, and aircraft types have proven effective at disseminating pheromone and interfering with the orientation of males toward pheromone sources. Macro-particle dispersal technology (Hercon Disrupt® II) has been extensively used over large areas in the "Slow the Spread Program" for North American populations of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) (Thorpe *et al.* 2007). Mating disruption may provide an effective tool for managing low-density populations of spruce budworm, but additional studies are needed before it can be implemented.

Following are suggestions of five research topics to guide future studies of spruce budworm mating disruption:

(1) The contextual use of mating disruption as an early intervention strategy remains to be defined, and requires a better understanding of population dynamics, in particular low-density populations before the onset of outbreaks.

(2) The cause and consequences of the consistently higher mating success of feral females than caged or tethered females in pheromone-treated plots need to be investigated. Future experiments *must* use feral females to assess the efficacy of mating disruption; sampling at low population density will likely require a network of light traps.

(3) Few studies on mating disruption have been replicated in a true statistical sense, and none has been conducted over more than 1 year at a given location because of the high cost of field trials, product availability, and lack of suitable sites. Multi-year studies are needed to evaluate the effect of mating disruption on the population dynamics of spruce budworm and the resulting defoliation.

(4) Empirical and experimental data on the dispersal behavior of females in relation to population density are urgently needed to assess the potential of mating disruption in relation to reinvasion of treated plots by migrating females.

(5) Spruce budworms exhibit life-history traits (univoltine cycle, relatively narrow period of adult emergence) that facilitate the implementation of mating disruption (Witzgall *et al.* 2010). Future studies are needed to evaluate the efficacy of mating disruption as a function of the timing of pheromone application relative to the period (and broad-scale temporal variation) of adult emergence.

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