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**Journal of Chemical Ecology**

ISSN 0098-0331
Volume 42
Number 9

J Chem Ecol (2016) 42:896-907
DOI 10.1007/s10886-016-0769-9

Springer

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# Optimizing the Point-Source Emission Rates and Geometries of Pheromone Mating Disruption Mega-Dispensers

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Received: 12 August 2016 / Revised: 30 August 2016 / Accepted: 8 September 2016 / Published online: 15 October 2016

**Abstract** High-emission-rate "mega-dispensers" have come into increasing use for sex pheromone mating disruption of moth pests over the past two decades. These commercially available dispensers successfully suppress mating and reduce crop damage when they are deployed at very low to moderate densities, ranging from 1 to 5/ha to 100–1000/ha, depending on the dispenser types and their corresponding pheromone emission rates. Whereas traditionally the emission rates for successful commercial mating disruption formulations have been measured in terms of amounts (usually milligram) emitted by the disruptant application per acre or hectare per day, we suggest that emission rates should be measured on a per-dispenser per-minute basis. In addition we suggest, because of our knowledge concerning upwind flight of male moths being dependent on contact with pheromone plume strands, that more attention needs to be paid to optimizing the flux within plume strands that shear off of any mating disruption dispenser's surface. By measuring the emission rates on a per-minute basis and measuring the plume strand concentrations emanating from the dispensers, it may help improve the ability of the dispensers to initiate upwind flight from males and initiate their habituation to the pheromone farther downwind than can otherwise be achieved. In addition, by optimizing plume strand flux by paying attention to the geometries and compactness of mating disruption mega-dispensers may help reduce the cost of mega-dispenser disruption formulations by improving their behavioral efficacy while maintaining field longevity and using lower loading rates per dispenser.

**Keywords** Moth sex pheromones · Pheromone mating disruption · Pheromone emission rates · Pheromone dispenser geometry · Pheromone dispenser design · Metered aerosols · Polyethylene tubes · Pheromone plumes · Pheromone flux · European corn borer · Blackheaded fireworm · *Ostrinia nubilalis* · Rhopobota naevana

## Introduction

Dispensers for emitting sex pheromone for mating disruption have increasingly been engineered to be deployed as high-release-rate, widely spaced dispensers. Such "mega-dispensers" (Miller and Gut 2015) have been effective at producing satisfactory population control and reduced damage to agricultural crops (McGhee et al. 2014; Miller and Gut 2015; Witzgall et al. 2010). Whereas attention with regard to mating disruption success traditionally has been paid to achieving emission rates in terms of amounts emitted per acre or hectare per day, our laboratory has focused on the amounts emitted per dispenser per minute (Baker et al. 1997a, b; Fadamiro et al. 1998, 1999). The key reason for this focus is because we and others learned through long series of behavioral experiments in the 1980s and 1990s that upwind flight responses of moths to pheromone occurs via their upwind surges in response to individual pheromone strands in pheromone plumes and cross-wind casting flight in response to pockets of clean air between the strands (Baker and Haynes 1987; Kennedy 1983; Mafra-Neto and Cardé 1994; Vickers and Baker 1994). Sustained upwind flight toward the pheromone source in pheromone plumes is, therefore, due to reiterative upwind surges in response to strand after strand of

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pheromone as the male makes his way upwind. Because upwind flight is due to the intensity of molecular flux of individual strands, we focused on producing dispensers that would create the strongest possible strands downwind. Informed by this behavioral knowledge, in this paper we discuss the idea that in addition to optimizing emission rates, coupled with maximizing dispenser emission lifetimes for good field longevity of individual dispensers, the geometries of dispensers and their alignment with respect to the wind line might be another way to optimize dispensers' abilities to create strong plume strands and thus possibly use the pheromone in the dispensers more efficiently. Such dispenser designs might result in an increase in dispensers' field longevity while reducing the amount of expensive pheromone active ingredient that is used per dispenser.

Harry Shorey and his colleagues were the first to demonstrate the effectiveness of sex pheromone mating disruption of moths and write compellingly about the future promise of this new mating disruption technique for agriculture (Gaston et al. 1967; Shorey et al. 1967). Early-on they also paid attention to dispenser emission rates and dispenser deployment spacings in a large number of mating disruption field experiments (Gaston et al. 1971, 1977; Kaae et al. 1972, 1974; McLaughlin et al. 1972a, b; Shorey et al. 1972, 1974). In an unusually perceptive experiment, the Shorey group demonstrated that mating disruption dispensers need not be deployed in a closely spaced array of low-emission-rate point sources. Rather, their experiments showed that by accumulating into large bundles the same numbers of dispensers that had previously been distributed as small point sources over a wide area now could provide the same levels of mating disruption when the bundles were separated by 200 or even 400 m (Farkas et al. 1974). As the technologies for mating disruption have evolved over the ensuing decades from aerially applied micro-dispensers, to hand-applied "meso-dispensers" (Miller and Gut 2015), the more widely separated hand-applied mega-dispensers have been increasingly successful in IPM systems and sold for controlling moth pests on many crops (Miller and Gut 2015; Witzgall et al. 2010).

The lowest emission-rate mega-dispensers included sealed polyethylene tubes that emitted several hundred nanograms (0.2–0.3 μg) per minute (see below). Higher-emission-rate mega-dispensers included dispensers that emitted aerosol sprays of pheromone in timed, metered amounts onto surrounding foliage or onto pads that then emitted pheromone into and over the crop for mating disruption of various species (Baker et al. 1997a, b, 1998; Fadamiro et al. 1998, 1999; Fadamiro and Baker 2002; Mafra-Neto and Baker 1996; McGhee et al. 2012, 2014; Shorey and Gerber 1996a, b, c; Shorey et al. 1996; Welter et al. 2005). The aerosol dispenser idea for mating disruption stems from the work of Thomas et al. (1975) who experimented with ways to direct southern pine beetles to attack particular trees in order to control outbreaks. They used pressurized aerosol canisters on a timer system to spray southern pine beetle pheromone solution onto a piece of cheesecloth, with each canister system being affixed to the trunks of designated pine (*Pinus* spp.) trees.

Two decades later, metered aerosols of moth sex pheromones were experimented with and developed for use in mating disruption, by using pads similar to the cheesecloth of Thomas et al. (1975) to catch the emitted sprays that were usually emitted every 30 min over a period of several hours. The pads would then release pheromone passively between sprays (Mafra-Neto and Baker 1996; Shorey and Gerber 1996a, b, c; Shorey et al. 1996). Subsequently, some systems evolved to abandon the pads such that the aerosol mists were sprayed directly into the air to drift onto surrounding foliage (McGhee et al. 2012, 2014; Welter et al. 2005). Plumes from such mega-dispensing systems were shown to sometimes have a long downwind "reach" of ca. 300–400 m to successfully disrupt males' ability to locate pheromone sources in traps (Welter et al. 2005). Such a long disruption-zone reach occurred in cases in which the plumes and wind conditions were such that the pheromone could travel downwind between, and not across, the rows of trees in an orchard (Welter et al. 2005).

Such strong plumes were thought to perhaps cause sensory adaptation or central nervous system habituation with subsequent in-flight arrestment far downwind before a male could reach the dispenser (c.f., Baker et al. 1989; Hansson and Baker 1991). However, males of some moth species have been observed in the field to be attracted for some distance to mega-dispensers such as sealed polyethylene tubes (Cardé et al. 1998; Stelinski et al. 2004, 2005) or aerosol-pheromone–impregnated pads (Mafra-Neto and Baker 1996). In several of these studies, the males were observed to then leave the dispenser area and not return, apparently after becoming habituated. Aerosol mega-dispensers emitting their spray into the air and surrounding foliage also have been shown to induce some level of competitive attraction of males in causing disruption (McGhee et al. 2014).

Thus there are two mechanisms — one behavioral and the other neurophysiological — that need to be involved in achieving mating disruption by using mega-dispensers: 1) getting males to orient upwind in response to plume strands, and 2) achieving habituation of the sex pheromone olfactory systems of males as they expose themselves during their sustained upwind flight toward the source in these strong plumes. Males have evolved over millions of years to visually lock onto the wind (its direction and speed) and then using flow-field cues, steer up the wind whenever they are in contact with airborne pheromone plume strands (Kennedy 1983). In doing so they end up dosing themselves with strong amounts of pheromone in the plumes from mega-dispensers, and they eventually become desensitized to their own pheromone through their own preprogrammed behaviors. This means that the farther downwind that plume strands are engineered to be strong enough to evoke upwind flight from males, the greater is the ability of each dispenser to draw males in from greater distances and get them to dose and habituate themselves, by using their own highly evolved reaction to pheromone against them.

The concept of creating strong plume strands from dispensers to attract males from a longer distance is fairly simple, as we show herein. This concept is not entirely new; it was demonstrated, in part, in a largely overlooked paper by Lewis and Macaulay (1976). They showed in field experiments how the effectiveness of sex pheromone traps designed for the pea moth, *Cydia nigricana* (F.) deployed with identical *C. nigricana* pheromone lures in them, could be optimized by taking care to align the openings of the traps to be parallel to the wind line. The plumes issuing from the traps that captured the most moths were narrower and more concentrated than the plumes from the same traps that instead were positioned with their openings oriented more cross-wind (Lewis and Macaulay 1976).

Lewis and Macaulay (1976) focused on improving trap catch, not on mating disruption, and interpreted their results in terms of the importance of preserving the plumes' overall downwind pheromone concentration, not the molecular flux of pheromone strands within the plume. This is understandable because at that time the relationship of individual plume-strand concentrations to behavior was not known. Nevertheless, their results from using smoke plumes to demonstrate the traps' differential effectiveness at trapping the most moths are instructive for designing the best mating disruption dispensers with the greatest effect on getting males to fly upwind toward the dispensers from the greatest downwind distances.

Here, we discuss how measuring the emission rates from different mega-dispensers that are known to be behaviorally effective in successful mating disruption experiments can inform researchers how to further improve and economize on mating disruption pheromone use. We also show results of some experiments in which the orientations of some mega-dispensers with respect to the wind line can improve the flux intensity of pheromone strands that shear off from the dispenser surfaces.

## Methods and Materials

**Emission Rates from Entire Surfaces of Pheromone Dispensers by Using Glass Funnel Collection System** Three types of pheromone mating disruption mega-dispenser systems were used in these studies; two of them were developed and used by the Baker laboratory in field disruption experiments. The first was the metered aerosol spray system called MSTRS (metered semiochemical timed release system; Baker et al. 1997a, b) in which a timer coupled to a spray actuator depresses the nozzle on an aerosol-producing canister or bottle, and 50 μl of pheromone solution are atomized onto an absorbent cloth pad (Fig. 1). The typical pheromone solution in the non-pressurized pump-spray bottles used for blackheaded fireworm [*Rhopobota naevana* (Hübner)] and European corn borer [*Ostrinia nubilalis* (Hübner)] was 4 g of pheromone in 250 ml of ethanol. Thus, each 50-μl discharge from the bottles emitted 0.8 mg of pheromone onto the pads. The pads were formed by 0.5-cm-thick circular acrylic padding stretched across a 17.8-cm-diameter needlepoint hoop (Fig. 1).

The second type of pheromone mating disruption dispenser was the MSTRS "baggie" dispenser (Fig. 2) that replaced the MSTRS machines, and which has been used successfully against several moth pest species. A baggie consists of a sealed 8 × 10-cm sachet of thin acrylic plastic approximately the thickness of kitchen garbage bags that contains a piece of cardboard impregnated with 1 g of neat pheromone.

The third type was the Shin-Etsu "rope" dispensers that have been used worldwide in successful mating disruption programs targeting many different moth pests (Witzgall et al. 2010).

For the MSTRS pad sprayed from the machine's pump-spray bottle, the pheromones used were those of the blackheaded fireworm, for which we measured the release rate of the major component (*Z*)-11-tetradecenyl acetate (Z11–14:OAc) (Slessor et al. 1987). We also used the pheromone of the "Z" strain of the European corn borer for which we again measured the release rate of the major component, Z11–14:OAc (Klun et al. 1973). The MSTRS baggies were those containing the blackheaded fireworm pheromone, and for these measurements, the amounts of Z11–14:OAc found in airborne collections were measured. The Shin-Etsu rope dispensers used were the "Hamaki-con" sealed polyethylene tube dispensers that we had used successfully for disrupting mating of the European corn borer (Baker et al. 1997a, b; Fadamiro et al. 1999). These dispensers were manufactured by Shin-Etsu Corporation for commercial mating disruption of the smaller tea tortrix moth (*Adoxophyes honmai* (Yasuda)), and they contained 80 mg of a blend of 11-tetradecenyl acetates in the proportions 95 % Z11–14:OAc and 5 % (*E*)-11-tetradecenyl acetate (E11–14:OAc). The amounts of Z11–14:OAc released from the Shin-Etsu dispensers were quantified as detailed below.

We measured the release rates from MSTRS pads by using a large glass funnel with a diameter of 10 cm at its widest orifice. Ten-centimeter-diameter cutouts of the standard 17-cm-diameter MSTRS pads were affixed over the funnel's orifice, always with the sprayed side of the pad facing out from the funnel entrance. These pads had been taken from machines that had been deployed in the field over time and had received pheromone sprays for those time periods. Pheromone was collected from the pads by using a moderately packed 0.25 g plug of glass wool (Baker et al. 1981) at the end of the funnel's

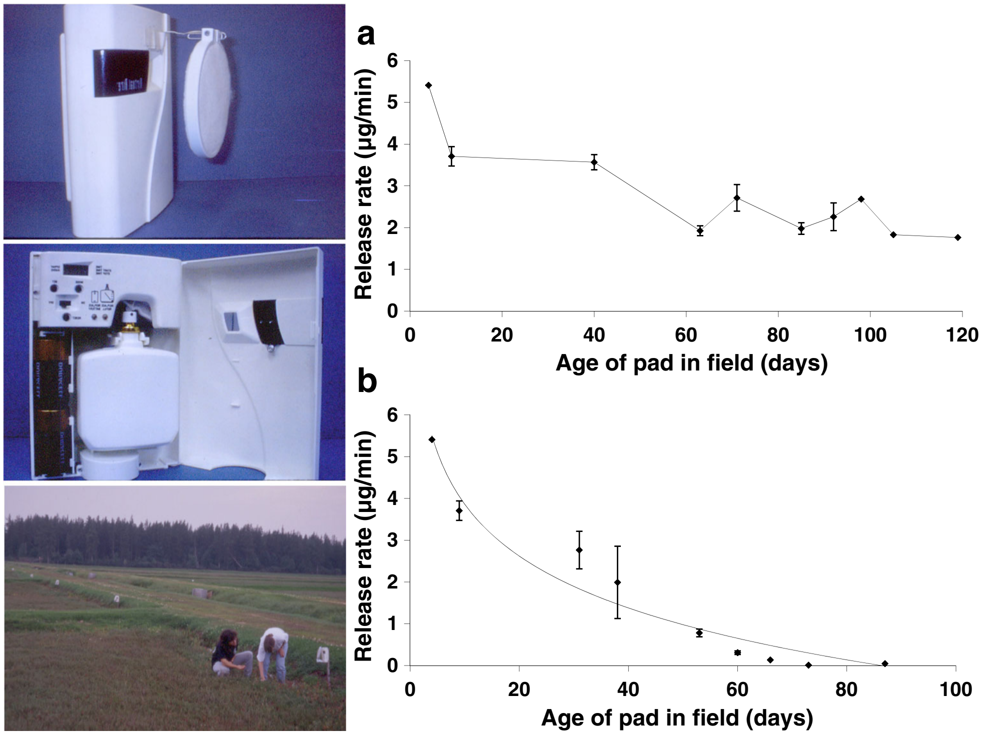

**Fig. 1** Emission rates of blackheaded fireworm pheromone from the pads of MSTRS mating disruption machines, sampled over the time they were deployed in Wisconsin cranberry marshes. Photos at left show: (*Top*) MSTRS machine with spray pad to catch pheromone aerosol; (*Middle)* Pump spray bottle housed in metered semiochemical timed release system (MSTRS) machine containing pheromone solution and spray actuator nozzle; (*Bottom*) MSTRS machines deployed around the perimeter of several cranberry beds in the Wisconsin cranberry marshes. Panels at right show the emission rates of Z11–14:OAc from the MSTRS pads that had been deployed in cranberry marshes and sprayed with blackheaded fireworm pheromone over many weeks. **a**. Mean ± SE emission rates (μg/min) of Z11–14:OAc from pads that had been primed with 0.5 g of pheromone on day 1 (at time of deployment) and then received daily sprays every 25 min for 12 h. **b**. Mean ± SE emission rates (μg/min) of pads deployed in the field that had been primed with 0.5 g of pheromone and received no further sprays thereafter. Standard errors in A for Days 98, 105, and 119 were ±0.19, 0.12, and 0.22 μg/min, respectively. Standard errors in B for Days 60, 66, 73, and 87 were ±0.04, 0.01, 0.01, and 0.02 μg/min, respectively. $N = 9$ pads' emission rates measured on each day that measurements were taken

stem, with airflow drawn through the pad affixed across the funnel's orifice, and then onto the funnel walls and the glass wool trap by means of a vacuum drawn on the stem of the funnel. The vacuum created an airflow of 8 l/min with a linear flow of 1.73 cm/s through the pad. By affixing a second identical glass wool plug at the end of the collecting plug, we determined that there was no trace of Z11–14:OAc breakthrough after 15 min of collection on the first, upstream, glass wool plug. Collections lasted 15 min, whereupon the pad was removed from the funnel and 100 μg of an internal standard, (*Z*)-11-tridecenyl acetate, was added to the glass wool trap. The funnel walls then were washed with 3 ml of hexane such that the solution flowed onto and through the glass wool trap into a 2-dram collection vial. One microliter of this solution was injected onto a Hewlett-Packard 5890 gas chromatograph (GC) with a flame ionization detector (FID), and the amount of Z11–14:OAc emitted per minute was determined by analyzing the FID peak area of Z11–14:OAc relative to the FID peak area of the internal standard.

The same funnel collection system and airflow were used to measure the emission rates from the entire surfaces of individual MSTRS baggies and Shin-Etsu rope dispensers. These two types of dispensers each were suspended singly ca. 2 cm from the funnel entrance using two pieces of fishing line so that they could not rotate within the funnel. Again, a 15-min collection period with a flow of 8 l/min was used with the same 100 μg of internal standard added to the glass wool trap. The funnel walls and trap were rinsed with 3 ml of hexane as describe above for the MSTRS pads. One microliter of extract was analyzed via gas chromatography, and then the FID peak area of Z11–14:OAc was compared to that of the internal standard to calculate the amount of Z11–14:OAc emitted per minute.

**Experiments to Mimic Insect Antenna's Exposure to Pheromone Plume Flux from Mating Disruption Dispensers** Extruded solid phase microextraction (SPME) fibers (PDMS type; Supelco, Bellefonte, PA, USA) have a length (9.63 ± 0.15 mm) and diam (≈ 0.3 mm) that are in the range of the dimensions of antennae of many species of crambid and tortricid moth pests such as European corn borer and blackheaded fireworm, for which mating disruption

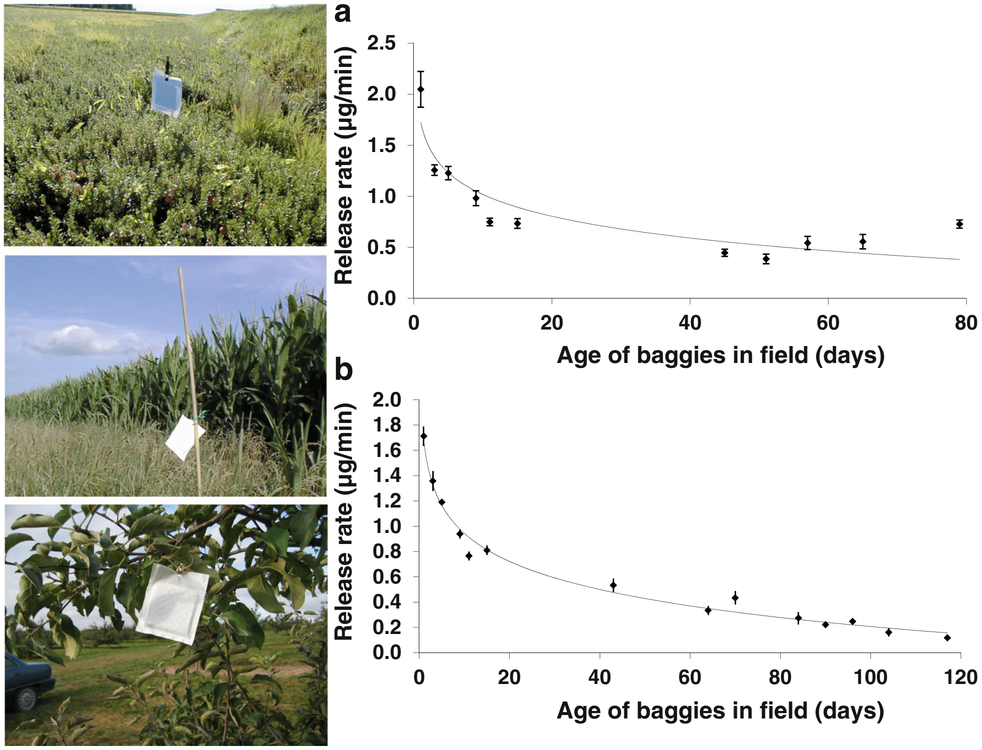

**Fig. 2** Emission rates of pheromone from metered semiochemical timed release system (MSTRS) "baggie" mega-dispensers, sampled over the time they were deployed in Wisconsin cranberry marshes. Photos at left show: (*Top*) MSTRS blackheaded fireworm baggie as deployed around the perimeter of a cranberry bed; (Middle) MSTRS European corn borer baggie deployed in a grassy corn borer aggregation and mating area bordering a corn field in Iowa; (*Bottom*) MSTRS oriental fruit moth baggie as deployed in a New York apple (*Malus* spp.) orchard. Panels at right: **a**. Mean ± SE emission rates (μg/min) of Z11–14:OAc from MSTRS blackheaded fireworm baggies that had been deployed in cranberry marshes over a period of many weeks. **b**. Mean ± SE emission rates (μg/min) of (*E*)-11-tetradecenyl acetate (E11–14:OAc) from Sparganothis fruitworm baggies in Wisconsin cranberry marshes. *N* = 3 baggies' emission rates measured on each day measurements were taken

already has been shown to be effective in reducing mating (Baker et al. 1997a; b; Baker et al. 1998; Fadamiro et al. 1999). We measured the possible differences in the amount of pheromone plume strand flux that the SPME—and therefore a male tortricid or crambid moth antenna—would encounter when these dispensers were oriented in different positions relative to the wind line. We used MSTRS blackheaded fireworm baggies that had been in the field for 40 days as well as Shin-Etsu Hamaki-con ropes that had been removed from their sealed packets for 1 day. For generating wind, we used our wind tunnel with a laminar flow of 30 cm/s. The same MSTRS blackheaded fireworm baggies or the Shin-Etsu rope dispensers used in the glass funnel collections described above were fixed, by using paper clip stands glued to the floor, in different wind-line orientations such that the SPME fiber could be held 10 cm downwind of them well above the paper clips that might otherwise disturb the laminar flow shearing pheromone off the downwind ends of the dispensers.

The SPME fibers for adsorbing pheromone were placed in different fixed orientations relative to these sources. We wanted to collect the initial plume strands shearing off these sources before micro-turbulence could possibly have shredded the initial strands into much smaller strands perhaps just tens of centimeters farther downwind. For the baggie dispensers oriented perpendicular to the wind, the SPME fibers were held vertically 10 cm downwind of the center of the baggie for 2 min, as well as vertically for 2 min, only 2 cm from the right-hand edge of the baggie (Fig. 3c, d). The SPME fibers were held for 2 min either perpendicular or parallel to the downwind edge of either the baggie (Fig. 3a, b) or rope dispensers (Fig. 4a, b), when these dispensers were aligned along the wind line, to measure the amount of pheromone we could collect on the SPME fibers. The amount adsorbed to the fiber would approximate the amount of pheromone that might contact a moth antenna that resulted from pheromone plume flux shearing from the dispenser.

The SPME fibers were desorbed in the injector port (250 °C) of a Hewlett-Packard 5890 GC, and eluted through a 30 m DB-1 capillary GC column. FID peak areas of Z11–14:OAc were measured and compared with the known amount (100 ng) of (*Z*)-11-tridecenyl acetate (Z11–13:OAc) injected as an external standard between the same SPME GC runs on a particular day. Thus, the amounts of pheromone (FID peak area) desorbed from the SPME were quantified relative to the FID peak area of the standard.

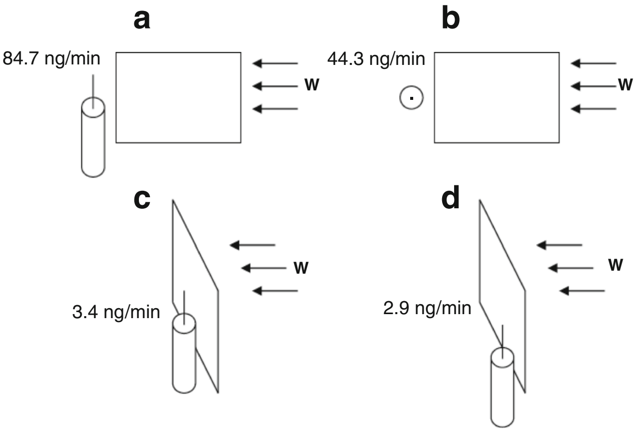

**Fig. 3** Different orientations of 40-d-old baggie dispensers with respect to the wind line in a 30-cm/s wind generated in our laboratory wind tunnel, and the orientations of a solid phase microextraction (SPME) fiber for collecting pheromone in the baggie's plume. The fiber was stationed 10 cm downwind of the baggie and oriented either parallel to (**a**) or perpendicular to (**b**) the downwind edge of the baggie when the baggie was aligned parallel to (along) the wind line (**a, b**). When the baggie was oriented 90° cross-wind, the SPME fiber was stationed 10 cm downwind either at the center of the baggie (**c**) or 2 cm from the baggie's right-hand edge (**d**). The pheromone plume flux issuing from the baggie and adsorbing to the moth-antenna–sized SPME fiber was higher when the baggies were aligned along the wind line (A and B) than when the baggie was oriented cross-wind (C and D). Arrows and "W" indicate wind direction. Standard errors for the means in A, B, C, and D are ±4.9, 2.1, 0.7, and 0.4, respectively. $N = 3$ trials of 2 min of SPME fiber-exposure for each position in A–D

## Results

**Measuring the Behaviorally Effective Emission Rates of Point-Source Mega-Dispensers** MSTRS pads sprayed with pheromone every 25 min over a 6-h period daily from time-programmed spray machines for 6–8 wk. had been shown to produce effective mating disruption and lower spermatophore numbers in female moths of two target species, the European corn borer and the blackheaded fireworm (Baker et al. 1997a, b, 1998; Fadamiro et al. 1998, 1999). The number of MSTRS dispensers needed for mating disruption of the corn borer was one dispenser per acre of corn (*Zea mays* L.). For successful disruption of the blackheaded fireworm mating, two or three MSTRS machines per acre were needed, depending on the geometry of the cranberry (*Vaccinium* spp.) marshes.

For the European corn borer, by measuring the release rates of the pads collected from the field after increasing numbers of days of field exposure had elapsed, we first measured the degree to which these release rates were maintained at normal machine-operating pad spray-rates over several weeks. Sprays were issued onto the pads from the MSTRS pressurized aerosol canisters every 25 min during a 12-h period (Baker et al. 1997a, b; Fadamiro et al. 1999). The emission rates of the pads were >5 μg/min for the 4 wk. of field exposure that we measured (Table 1). The Hamaki-con ropes emitted pheromone at above 0.2 μg/min for approximately the same 4 wk. of field exposure (Table 1).

Before the corn borer experiment, we had discovered that it took ≈5 days after the machines were first activated and deployed for the pads to reach their maximum release rates; they needed to receive daily machine-activated dosing from day 1 to day 5 to reach this saturation point. We had determined that to get the pads to be effective emission sources beginning on day 1, each pad would need to be "primed" with 0.5 g of pheromone on the initial day of deployment before being set out in the field. Thus, for the blackheaded fireworm experiments in cranberry marshes, we again first primed all the pads with 0.5 g of pheromone with hand-delivered sprays from the MSTRS bottles. After that, with a daily regimen consisting of timed sprays every 25 min over 12 h, the pads maintained an

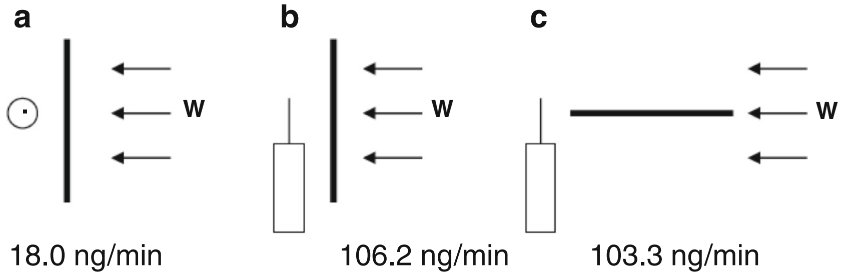

**Fig. 4** Different orientations of 1-d-old Shin-Etsu Hamaki-con rope dispensers (thick black line) with respect to the wind line in a 30-cm/s wind generated in our laboratory wind tunnel, along with the orientations of a solid phase microextraction (SPME) fiber for collecting pheromone in the rope dispenser's plume. The SPME fiber was stationed 10 cm downwind of the rope dispenser and oriented either perpendicular to (**a**) or parallel to (**b**) the downwind edge of the rope when the rope was aligned vertically and 90° cross-wind (A, B). When the rope was oriented parallel to the wind line and horizontal to the ground (**c**) the SPME fiber was stationed vertically, 10 cm downwind of the rope (**c**). The pheromone plume flux issuing from the rope and adsorbing to the moth-antenna–sized SPME fiber was higher when the rope was aligned parallel to (along) the wind line (C) than when it was oriented 90° cross-wind (**a**). The same small size of SPME exposure to the plume from the rope occurred in A and C, making this direct comparison of amount collected valid, but in B, the entire length of SPME fiber was exposed to the rope's plume. In this case, a similar amount of pheromone was collected as was collected in C. Arrows and "W" indicate wind direction. Standard errors for the means in A, B, and C are ±0.1, 12.3, and 1.3, respectively. $N = 3$ trials of 2 min of SPME fiber-exposure for each position in A–C

**Table 1** Mean (±SE) emission rates ($N$ = 3) from metered semiochemical timed release system (MSTRS) pads and Shin-Etsu Hamaki-Con pheromone "rope" dispensers when deployed against the European corn borer

| Days in field | Emission rate of Z11–14:OAc (μg/min) | |
|---|---|---|
| | MSTRS Pads | Shin-Etsu Rope |
| 1 | 5.29 ± 0.68 | 0.26 ± 0.01 |
| 7 | 6.09 ± 1.07 | 0.23 ± 0.02 |
| 26 | — | 0.22 ± 0.01 |
| 28 | 3.08 ± 0.35 | — |

average emission rate of between 2 and 3 μg/min for >100 days (Fig. 1a). We then decided to measure the degree to which the emission rate of pads that had received only one priming dose of pheromone on day 1 would diminish during the subsequent days in the field. It turned out that such pads maintained emission rates >1 μg/min for >40 days (Fig. 1b).

We concluded that despite the mating disruption success of the MSTRS timed release system on pads, we might have been wasting pheromone each day after the pads had reached their emission rate limit. Thus, it seemed that our initial thinking was erroneous, i.e., that daily timed emissions from the MSTRS pads could more efficiently use pheromone by emitting only atomized pheromone from the bottles during the daily periods of sexual activity of target moth species. In fact, there seemed to be little advantage to this timed emission, because a pad that had been primed to its behaviorally effective and maximal emission rate on day 1 served as an effective, passively emitting, disruptant dispenser for >40 days without receiving further daily sprays. This realization obviated all the programming and deployment of vast numbers of expensive machines to achieve disruption. We had essentially been developing and using a passive-releasing pheromone mega-dispenser that would need only a few extra rejuvenating sprays from day 40 onward.

We began working with ChemTica Internacional (San José, Costa Rica) and developed a polyethylene "baggie" dispenser (Fig. 2) that we used successfully for blackheaded fireworm mating disruption (Mahr and Baker 2001). We started with the knowledge from the success of the MSTRS machine-pads that the emission rates from baggie dispensers should begin in the range of 2–3 μg/min and stay at >0.5 μg/min for ≥40 days. The emission rates that we measured from the baggie dispensers for blackheaded fireworm in Wisconsin cranberry marshes had emission characteristics that were >0.5 μg/min for >80 days (Fig. 2a). For successful disruption of another cranberry pest, the Sparganothis fruit worm [*Sparganothis sulfureana* (Clemens)] the amount of pheromone used economically per baggie, and the resultant emission rates, were lower than for the blackheaded fireworm (Fig. 2b).

The baggie mega-dispensers have since been proven to be effective in successfully disrupting mating of several other moth pest species, including: the oriental fruit moth [*Grapholita molesta* (Busck)] in New York (Agnello and Reissig 2006), Pennsylvania (Joshi et al. 2008), and Brazil (Monteiro et al. 2013) where they are being used commercially; the almond moth [*Ephestia cautella* (Walker)] in Sweden (Ryne et al. 2006); and the Indian meal moth [*Plodia interpunctella* (Hübner)] and Mediterranean flour moth [*Ephestia kuehniella* (Zeller)] in Sweden and Denmark (Ryne et al. 2007) as well as in Poland (Sieminska et al. 2009). These baggie dispensers now are sold commercially by BASF under the name "Allure MD", and continue to be successfully used for mating disruption against these and other stored product moth pests in grain storage facilities and warehouses in North America.

Interestingly, baggie dispensers also are being used successfully against bark beetles, harkening back to the first mega-dispenser of Thomas et al. (1975) on southern pine beetle. Currently, baggie mega-dispensers that emit an antiaggregation (deterrent) pheromone have been shown to successfully reduce attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Perkins et al. 2015). Baggies that emit verbenone are now being used by the U.S. Forest Service to protect sensitive areas (ski resorts, campgrounds) where they do not want to spray carbaryl on trees near people (C. Oehlschlager, personal communication).

**Improving Plume Strand Flux by Orienting Dispensers along the Wind Line** For experiments that measure the amount of pheromone shearing off a MSTRS baggie dispenser and adsorbed onto a surface approximating the dimensions of a moth antenna, the positions of the baggie relative to the wind line and the position and orientation of the SPME fiber relative to the baggie are illustrated in Fig. 3. The main differences between these positions were whether the baggie was oriented parallel versus perpendicular to the wind line (cf. Fig. 3a, b with c, d), and also whether the SPME fiber was oriented parallel (in line with), or perpendicular to, the downwind edge of a baggie when the baggie was oriented parallel to (along) the wind line (cf. Fig. 3a with b).

We found that the SPME experienced higher pheromone flux from a plume sheared from the MSTRS baggie when the baggie was oriented parallel to the wind line (Figs. 3a, b). At this parallel-to-the-wind-line position, the plume sheared from the baggies showed more than a 20-fold higher pheromone flux over the "antenna" (Fig. 3a) than when they were oriented cross-wind (Figs. 3c, d). The parallel-to-the-wind-line orientation of the baggies produce a much stronger plume strand sheared from the dispenser than the more diffused plume milieu produced when the baggies are oriented across the wind line. It is likely that a parallel-to-the-wind orientation should preserve pheromone plume strand flux over a moth's antenna much farther downwind than the cross-wind baggie orientation.

When the emission rates of the baggies over their entire surfaces were measured in the glass funnel system, the cross-wind or parallel-to-wind positions produced emission rates that were not significantly different from each other. The overall pheromone emission rate from the cross-wind–oriented baggie's entire surface was 0.56 μg/min (± 0.09 SE; $N = 3$), and the emission rate from the parallel-to-wind–oriented baggie was 0.40 μg/min (± 0.06 SE; $N = 3$) This result shows the importance of using SPME as an antenna mimic to measure differences in plume-strand flux of the baggies in their different wind orientations. These differences would have been missed by merely capturing the emissions from the entire dispenser and ignoring the plume-strand concentrations in each case.

For the Shin-Etsu ropes, the main differences were first whether the SPME fiber was oriented in line with, or perpendicular to, the downwind leading edge of a narrow ribbon of pheromone that would be emitted by the rope when it was oriented vertically (Figs. 4a, b). The next position was with the rope's long axis oriented longitudinally along the wind line, parallel to the ground, such that the SPME fiber would be collecting a narrow plume-strand of pheromone that would shear off at a diameter approximating that of the diameter of the downwind end of the fiber (Fig. 4c).

The ropes, which in their original linear configuration as packaged in their shipping packets, already have a narrow plane of plume shearing. In the field, they are routinely twisted to become affixed around branches or twigs, and the tube is twisted around itself to tighten it to the branch. However, in this linear configuration, which should produce a narrow ribbon of pheromone regardless of its wind-related attitude, there was still an advantage in optimizing the narrowness of the plume by orienting the rope's long axis along the wind line and parallel to the ground (Fig. 4c). This orientation allowed the plume flux over the SPME antenna-fiber to be >5 times higher than when the rope was oriented cross-wind and the SPME was oriented perpendicular to the plane of the rope's sheared plume (cf. Fig. 4a, c). This 5-fold increase in plume-strand flux was as high as when the long axis of the rope was oriented cross-wind and the SPME-antenna-mimic was oriented parallel to the plane of the rope's sheared plume strand (Fig. 4b). Both of these orientations produced a 5-fold higher pheromone flux contacting the SPME "antenna" than when the SPME was oriented 90° across the downwind end of the crosswind-oriented rope (Fig. 4a).

One advantage of the rope's long axis being oriented along the wind line and parallel to the ground is that the downwind strand would be as strong as possible in contacting a moth's antenna no matter what relative orientation the antenna would have relative to the strand. The strand starts out as a narrow point off the downwind end of the rope. In addition, our measurements likely underestimate the flux from this small-point plume strand compared to that of the cross-wind–oriented rope's, because a much smaller part of SPME fiber is exposed to the pheromone plume in its position in Fig. 4c, in contrast to the rope's position in position in Fig. 4b in which the entire length of SPME is exposed to the length of the linear pheromone strand sheared from the rope. That there were no differences in the pheromone flux we measured between the positions in Fig. 4b and c in the rope experiment indicates that pheromone plume flux will be >5 times higher with the rope positioned as shown in Fig. 4c than in Fig. 4a or b.

When the Shin-Etsu ropes were placed parallel to (as in Fig. 4c) or perpendicular to airflow (as in Fig. 4a) in the glass funnel collector and their release rates from their entire surfaces were measured, the rates were not significantly different between the two positions. In the perpendicular position, the emission rate of the rope was 0.33 μg/min (±0.03 SE; $N = 3$) and in the parallel-to-flow position it was 0.34 μg/min (± 0.01 SE; $N = 3$). This result shows again the value of measuring plume-strand concentration via SPME compared with measuring the overall emission rate from the entire dispenser, in this case a Shin-Etsu rope dispenser.

## Discussion

The first step in understanding how a mating disruption dispenser type is behaviorally effective is to measure its emission rates over time to reconcile these week- and month-long rates with the dispensers' ability to successfully disrupt mating when deployed at a particular dispenser density or spacing in the field. For metered aerosol dispensing systems, merely knowing the amount released onto a surface, especially systems in which the spray is released into the atmosphere to drift onto surrounding foliage, will not inform researchers as to the behavioral strength of a plume that travels downwind and contacts a moth antenna. This uncertainty is especially true when the same amount of pheromone per atomized spray discharge drifts onto a very large surface area of foliage compared to being adsorbed to a much smaller surface area such as the small circular MSTRS pads. The larger surface area that is emitting the same total amount of pheromone per unit time will produce weaker plume-strand flux of the size of a moth's antenna than the same emission rate coming from a smaller surface area.

A male's antenna receives pheromone only from its antennal length and surface area. Therefore, the creation of higher emission rates by increasing the surface area of the emitter gives the false impression of having a stronger disruption dispenser. Such a dispenser will not improve what reaches the moth antenna, because as seen in Fig. 5, a higher release-rate dispenser that is formed by making a larger dispenser out of the same material with the same per-square-centimeter release

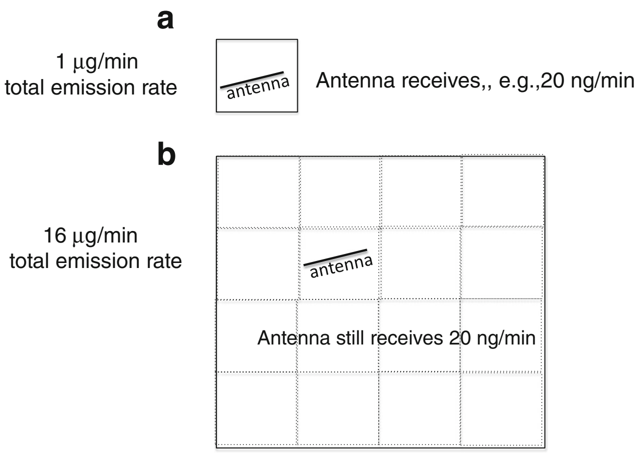

**Fig. 5** Depiction comparing the emission rates of two mega-dispensers: (**a**) dispenser releasing pheromone at 1 µg/min and having a surface area of 1 cm$^2$; (**b**) what seems to be a more powerful 16-cm$^2$ dispenser constructed by merely adding together the surface areas of 16 of the 1-cm$^2$ dispensers emitting 1 µg/min. The larger dispenser with the 16× higher overall release rate would seem to be able to better affect male moth behavior, but despite its large size and greater overall emission rate from its larger surface area, a moth's antenna downwind of this dispenser will still only be exposed to the same amount of pheromone as the smaller 1-cm$^2$ dispenser releasing 1 µg/min. The moth's antenna is the relevant measurer of the behavioral pheromone power of the two dispensers

rate does not change what is encountered by a male moth antenna. Although the dispenser seems to be more powerful—having a greater overall emission rate— the molecular pheromone flux remains the same from the perspective of the male's antenna (Fig. 5).

Corresponding to this, and almost counter-intuitively, maintaining the same high release rate while compacting the size of the dispenser to make a very small point source (Fig. 6) will increase the molecular flux within individual plume-strands that will stay stronger farther downwind to initiate upwind flight from farther downwind. Such a compacted high-release-rate mega-dispenser should be better than the greater-surface-area dispenser at gathering in a larger number of males per point source and habituating them as they dose themselves with these high-release-rate strands. This seems to be the strategy that has been selected for over evolutionary time in moth sex pheromone communication systems. Rather than emit pheromone from over their entire body surfaces, females have concentrated their pheromone-emitting surface into a tiny point source of glandular tissue near the tips of their abdomens, and they need to emit only vanishingly small amounts of pheromone that attract males from far downwind.

The concept of creating strong plume strands by engineering optimal geometries and wind alignments for mating disruption dispensers may be new for mating disruption researchers and commercial manufacturers, but the concept of improving downwind pheromone plume concentrations and male moth captures in pheromone monitoring traps already had been demonstrated in the paper by Lewis and Macaulay (1976). They showed how the effectiveness of different types of pheromone traps was correlated with the narrowness and apparent higher concentrations within their pheromone plumes. They showed, by using smoke, that plumes issuing from various types of traps captured fewer males when the test plumes of smoke issuing from them were more diffuse due to turbulent mixing, and captured more males when the plumes were narrower and more concentrated (Fig. 7; Lewis and Macaulay 1976). Importantly, trap captures and approaches to one kind of trap that was positioned either more crosswind or along the wind line were greatest when the trap was aligned along the wind line (Fig. 7). There were twice as many approaches to within 2 cm of this trap-type when it was oriented along the wind line compared to when it was oriented crosswind, thus indicating that the narrower and more concentrated plumes farther downwind contributed to the greater captures in the wind-aligned trap. At the time of this publication, the authors interpreted their results with regard to a greater preservation of the plumes' overall downwind pheromone concentration, rather than to the flux within the plumes' individual strands. During the 1970s, the importance of individual strand-strengths to behavior was not yet known. Nevertheless, their diagrams and

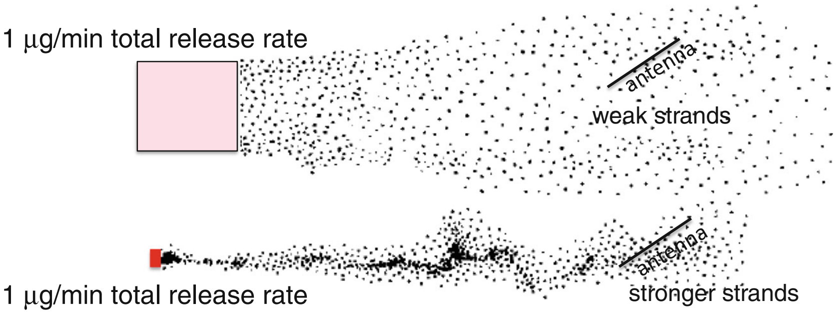

**Fig. 6** Depiction of how two dispensers, one large and one very compact but having the same overall emission rates, will differ in their ability to generate strong plume strands downwind. The more compact dispenser in (**b**) will create stronger plume-strand flux farther downwind than the dispenser in (**a**), even though their overall emission rates are identical. The stronger plume strands from the dispenser in (**b**) are better able to contact a male's antennae at above-threshold levels farther downwind and get the male to begin upwind flight toward the dispenser and become habituated

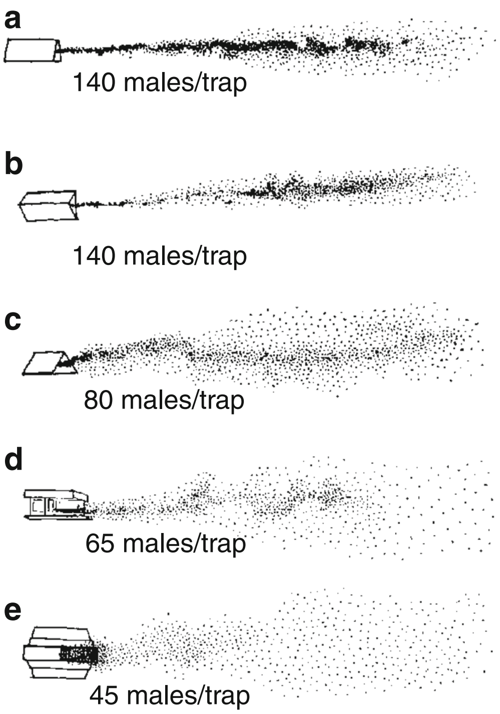

**Fig. 7** Examples from the field experiments of Lewis and Macaulay (1976) on pheromone trapping of the pea moth, *Cydia nigricana*. Smoke plumes emanating from different types of pheromone traps (cf.**a**–**c** with. **d** and **e**) or the same trap type oriented along (**a** and **b**), vs. 45° across (**c**), the wind line. When the different traps or the same trap oriented differently with respect to the wind were emitting pheromone of the pea moth from identical dispensers, they captured different numbers of moths, corrected for the different ensnarement surface areas of the traps. Traps oriented along the windline so that they generated narrow, well-defined plumes (**a** and **b**) captured more males than a trap angled more across the wind line (**c**) and generating a more diffuse plume or other trap types generating diffuse plumes (**d**, **e**). Adapted from Lewis and Macaulay (1976)

results are instructive now for how to design the best mating disruption mega-dispensers that can be used at the lowest per-area densities.

The two mechanisms of behavioral attraction and olfactory pathway habituation that seem to be dominant in achieving successful mating disruption Cardé (2007); Cardé and Minks 1995) recently have been partitioned into two mathematically defined mechanisms: competitive and non-competitive disruption effects (Miller et al. 2006a, 2006b). We feel that rather that by structuring discussions about mechanisms in this dichotomous way, there is a continuum of attraction and habituation, i.e., competitive and non-competitive mechanisms, evoked by mating disruption dispensers that emit a full, optimally attractive blend ratio of pheromone components. Of course, partial blends that do not attract males—and can cause only olfactory pathway habituation in males that are resting or flying in the environment— will not make use of the attraction mechanism that gets males to expose themselves to ups and downs in pheromone plume-strand flux as they approach mating disruption dispensers. Alternatively, when optimally attractive dispensers are used that emit a species' natural blend of components at proper ratios, there will always be some form of "competitive" effect, i.e., the attraction of males from some distance downwind of the source—even very great distances—and locking themselves onto the wind while in the plume. Moreover, with the optimally attractive blend, there will be "non-competitive" habituation effects when the males dose themselves to initiate habituation while flying upwind in disruption mega-dispensers' plumes, even if the males do not orient all the way to the dispenser. Habituation then reaches its peak when the males become arrested in-flight somewhere downwind due to the high flux in the plume strands.

Experimental evidence for this dual system of attraction-habituation working in tandem for mating disruption (e.g., a blending of the originally delineated competitive vs. non-competitive mechanisms; Miller et al. 2006a, 2006b) comes from laboratory experiments and field behavioral observations of Stelinski et al. (2004, 2005, 2006) with the codling moth and several other tortricid moths. The authors have shown that tortricid males in the field will approach and often land within a few cm of rope mega-dispensers, and then after a few tens of seconds, fly away (Stelinski et al. 2004, 2005). Further laboratory experiments focusing on the codling moth (Stelinski et al. 2006) have shown that even such short exposures to the plumes from rope mega-dispensers can significantly habituate the moths' pheromone olfactory pathways and reduce subsequent attraction to the dispensers or by inference, females.

By engineering and deploying mating disruption dispensers so that they stay aligned along the wind line, such as affixing them to rods so that the dispensers swing like wind vanes with any changes in wind direction, may have an extra effect in turbulent, gusting winds. When there is a sudden gust from behind the dispenser, i.e., an acceleration in wind speed across the dispenser from back to front, the first strand that issues from the dispenser that represents the new "front" of the accelerated wind should have a buildup of concentration of molecules and have a stronger flux than the previous strands that were sheared under constant wind velocity. The wind gust would add the molecular headspaces to each other from just above the release surface until the final headspace concentration at the downwind end of the dispenser would be achieved at the moment the strand leaves the downwind edge. This effect would be above and beyond the effect of narrowing sheared plume strands from a wind-aligned dispenser under constant wind velocity, or the advantage to wind alignment for pheromone trap capture that was demonstrated by Lewis and Macaulay (1976). This extra-strong single plume strand, a single burst that would occur at every acceleration in wind speed, would be able to reach males at behaviorally above-threshold levels farther downwind than strands sheared under constant wind velocities.

Thus, in summary, we suggest that when using the strategy of deploying widely spaced mega-dispensers for mating disruption, the dispensers should be designed to produce the strongest possible plume strands that manipulate the males' behavior and get them to be attracted from far downwind to dose themselves with large amounts of pheromone during the upwind-flight process. Such dispensers will result in the greatest habituation of olfactory neuronal pathways from the greatest distances downwind. Because we know that it is the plume strands in pheromone plumes that are important in producing male upwind flight, further advances in mating disruption mega-dispenser design might be made if dispensers' strands can be engineered to be made as concentrated as possible. We suggest that one way to do this is to reduce the surface area of mega-dispensers while retaining their emission rates. For dispensers having a linear configuration, a second way would be to improve the dispensers' ability to align themselves with respect to the wind line. Improvements such as these might not only help optimize the mating disruptive power (attraction and habituation power) of each dispenser but also help use the pheromone in each dispenser more judiciously, resulting in more efficient and cost-effective mating disruption formulations.

## References

Agnello A, Reissig H (2006) Management programs for internal Lepidoptera in apples using pheromone mating disruption and in-season fruit inspection. Cornell University, Ithaca, New York http://web.entomology.cornell.edu/agnello/assets/Int_Lep_MD_final_report.pdf

Baker TC, Haynes KF (1987) Manoeuvres used by flying male oriental fruit moths to relocate a sex pheromone plume in an experimentally shifted wind-field. Physiol Entomol 12:263–279

Baker TC, Gaston LK, Mistrot Pope M, Kuenen LPS, Vetter RS (1981) A high-efficiencly collection device for quantifying sex pheromone volatilized from female glands and synthetic sources. J Chem Ecol 7:961–968

Baker TC, Hansson BS, Löfstedt C, Löfqvist J (1989) Adaptation of male moth antennal neurons in a pheromone plume is associated with cessation of pheromone-mediated flight. Chem Senses 14:439–448

Baker TC, Dittl T, Mafra-Neto A (1997a) Disruption of sex pheromone communication in the blackheaded fireworm in Wisconsin cranberry marshes by using MSTRS™ devices. J Agric Entomol 14:449–457

Baker TC, Mafra-Neto A, Dittl T, Rice ME (1997b) A novel controlled-release device for disrupting sex pheromone communication in moths. In: Witzgall P, Minks AK (eds) Technology transfer in mating disruption IOBC wprs Bull, vol 20, pp. 141–149

Baker TC, Fadamiro HY, Cossé AA (1998) Widely-spaced, high-emission-rate pheromone sources suppress mating of European corn borer females. In: Zalucki MP, Drew RAI, White GG (eds) Pest management, future challenges Proceedings of the Sixth Australasian Applied Entomological Research Conference. University of Queensland Printery, Australia, pp. 279–288

Cardé RT (2007) Using pheromones to disrupt mating of moth pests. In: Kogan M, Jebson P (eds) Perspectives in ecological theory and integrated pest management. Cambridge University Press, New York, pp. 122–169

Cardé RT, Minks AK (1995) Control of moth pests by mating disruption: successes and constraints. Annu Rev Entomol 40:559–585

Cardé RT, Staten RT, Mafra-Neto A (1998) Behaviour of pink bollworm males near high-dose, point sources of pheromone in field wind tunnels: insights into mechanisms of mating disruption. Entomol Exp Appl 89:35–46

Fadamiro HY, Baker TC (2002) Pheromone puffs suppress mating by *Plodia interpunctella* and *Sitotroga cerealella* in an infested corn store. Entomol Exp Appl 102:239–251

Fadamiro HY, Cossé AA, Dittl T, Baker TC (1998) Suppression of mating by blackheaded fireworm (Lepidoptera: Tortricidae) in Wisconsin cranberry marshes by using MSTRS™ devices. J Agric Entomol 15:377–386

Fadamiro HY, Cossé AA, Baker TC (1999) Disruption of mating of European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae) by using two types of sex pheromone dispensers deployed in grassy aggregation sites in Iowa cornfields. J Asia Pac Entomol 2:121–132

Farkas SR, Shorey HH, Gaston LK (1974) Sex pheromones of Lepidoptera. The use of widely separated evaporators of looplure for the disruption of pheromone communication in *Trichoplusia ni*. Environ Entomol 3:876–877

Gaston LK, Shorey HH, Saario CA (1967) Insect population control by the use of sex pheromones to inhibit orientation between the sexes. Nature 213

Gaston LK, Shorey HH, Saario CA (1971) Sex pheromones of noctuid moths. XVIII. Rate of evaporation of a model compound of *Trichoplusia ni* Sex pheromone from different substrates at various temperatures and its application to insect orientation. Ann Entomol Soc Am 64:381–384

Gaston LK, Kaae RS, Shorey HH, Sellers D (1977) Controlling the pink bollworm by disrupting sex pheromone communication between adult moths. Science 196:904–905

Hansson BS, Baker TC (1991) Differential adaptation rates in a male moth's sex pheromone receptor neurons. Naturwissenschaften 78:517–520

Joshi NK, Hul LA, Krawczyk G, Rajotte EG (2008) Field results of mating disruption technologies for the control of codling moth, *Cydia pomonella* (L.), and oriental fruit moth, *Grapholita molesta* (Busck), in Pennsylvania apple orchards. Asp Appl Biol 84:153–161

Kaae RS, McLaughlin JR, Shorey HH, Gaston LK (1972) Sex pheromones of Lepidoptera. XXXII. Disruption of intra-specific pheromone communication in various species of Lepidoptera by permeation of the air with looplure or hexalure. Environ Entomol 1:651–653

Kaae RS, Shorey HH, Gaston LK, Hummel HE (1974) Sex pheromones of Lepidoptera: disruption of pheromone communication in *Trichoplusia ni* and *Pectinophora gossypiella* by permeation of the air with nonpheromone chemicals. Environ Entomol 3:87–89

Kennedy JS (1983) Zigzagging and casting as a programmed response to wind-borne odour: a review. Physiol Entomol 8:109–120

Klun JA, Chapman OL, Mattes JC, Wojtkowski PW, Beroza M, Sonnett PE (1973) Insect sex pheromones: minor amount of opposite geometrical isomer critical to attraction. Science 181:661–663

Lewis T, Macaulay EDM (1976) Design and elevation of sex-attractant traps for the pea moth, *Cydia nigricana* (Steph.), and the effect of plume shape on catches. Ecol Entomol 1:175–187

Mafra-Neto A, Baker TC (1996) Timed, metered sprays of pheromone disrupt mating of *Cadra cautella* (Lepidoptera: Pyralidae. J Agric Entomol 13:149–168

Mafra-Neto A, Cardé RT (1994) Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. Nature 369: 142–144

Mahr D, Baker TC (2001) Mating disruption for insect control: Where are we? In: Proceedings of the 2001 Wisconsin Cranberry School. University Wisconsin, Madison, pp. 1–4

McGhee P, Gut L, Thomson D, Jenkins J (2012) Field evaluation of Isomate CM Mist pheromone mating disruption. In: Proceedings of the 86th Annual Orchard Pest and Disease Management Conference, 17.

McGhee PS, Gut LJ, Miller JR (2014) Aerosol emitters disrupt codling moth, *Cydia pomonella*, competitively. Pest Manag Sci 70:1859–1862

McLaughlin JR, Shorey HH, Gaston LK, Kaae RS, Stewart FD (1972a) Sex pheromones of Lepidoptera. XXXI. Disruption of sex pheromone communication in *Pectinophora gossypiella* with hexalure. Environ Entomol 1:645–650

McLaughlin JR, Gaston LK, Shorey HH, Hummel HE, Stewart FD (1972b) Sex pheromones of Lepidoptera XXXIII. Evaluation of the disruptive effect of tetradecyl acetate on sex pheromone communication in *Pectinophora gossypiella*. Environ Entomol 1:1592–1593

Miller JR, Gut LJ (2015) Mating disruption for the twenty-first century: matching technology with mechanism. Environ Entomol 44:427–453

Miller JR, Gut LJ, de Lamé FM, Stelinski LL (2006a) Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone (part 1): theory. J Chem Ecol 32:2089–2114

Miller JR, Gut LJ, de Lamé FM, Stelinski LL (2006b) Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone (part 2): case studies. J Chem Ecol 32:2015–2143

Monteiro LB, Souza A, Argenton J (2013) Mating disruption with low density diffusers for the management of oriental fruit moths (Lepidoptera: Tortricidae) in apple orchards under subtropical climate in southern Brazil. Rev Bras Frutic Jaboticabal-SP 35:1007–1016

Perkins DL, Jorgensen CL, Rinella MJ (2015) Verbenone decreases whitebark pine mortality throughout a mountain pine beetle outbreak. For Sci 61:747–752

Ryne C, Ekeberg M, Jonzén N, Oehlschlager C, Löfstedt C, Anderbrant O (2006) Reduction in an almond moth *Ephestia cautella* (Lepidoptera: Pyralidae) population by means of mating disruption. Pest Manag Sci 62:912–918.

Ryne C, Svensson GP, Anderbrant O, Löfstedt C (2007) Evaluation of long-term mating disruption of *Ephestia kuhniella* and *Plodia interpunctella* (Lepidoptera: Pyralidae) in indoor storage facilities by pheromone traps and monitoring of relative aerial concentrations of pheromone. J Econ Entomol 100:1017–1025

Shorey HH, Gerber RG (1996a) Use of puffers for disruption of sex pheromone communication of codling moths (Lepidoptera: Tortricidae) in walnut orchards. Environ Entomol 25:1398–1400

Shorey HH, Gerber RG (1996b) Disruption of pheromone communication through the use of puffers for control of beet armyworm (Lepidoptera: Noctuidae) in tomatoes. Environ Entomol 25:1401–1405

Shorey HH, Gerber RG (1996c) Use of puffers for disruption of sex pheromone communication among navel orangeworm moths (Lepidoptera: Pyralidae) in almonds, pistachios, and walnuts. Environ Entomol 25:1154–1157

Shorey HH, Gaston LK, Saario CA (1967) Sex pheromones of noctuid moths. XIV. Feasibility of behavioral control by disrupting pheromone communication in cabbage loopers. J Econ Entomol 60:1541–1545

Shorey HH, Kaae RS, Gaston LK, McLaughlin JR (1972) Sex pheromones of Lepidoptera. XXX. Disruption of sex pheromone communication in *Trichoplusia ni* as a possible means of mating control. Environ Entomol 1:641–645

Shorey HH, Kaae RS, Gaston LK (1974) Sex pheromones of Lepidoptera. Development of a method for pheromonal control of *Pectinophora gossypiella* in cotton. J Econ Entomol 67:347–350

Shorey HH, Sisk CB, Gerber RG (1996) Widely separated pheromone release sites for disruption of sex pheromone communication in two species of Lepidoptera. Environ Entomol 25:446–451

Sieminska E, Ryne C, Löfstedt C, Anderbrant O (2009) Long-term pheromone-mediated mating disruption of the Mediterranean flour moth, *Ephestia kuehniella*, in a flourmill. Entomol Exp Appl 131:294–299

Slessor KN, Raine J, King GGS, Clements SJ, Allan SA (1987) Sex pheromone of the blackheaded fireworm, *Rhopobota naevana* (Lepidoptera: Tortricidae), a pest of cranberry. J Chem Ecol 13: 1163–1170

Stelinski LL, Gut LJ, Pierzchala AV, Miller JR (2004) Field observations quantifying attraction of four tortricid moth species to high-dosage pheromone rope dispensers in untreated and pheromone-treated apple orchards. Entomol Exp Appl 113:187–196

Stelinski LL, Gut LJ, Epstein D, Miller JR (2005) Attraction of four tortricid moth species to high dosage pheromone rope dispensers: observations implicating false plume following as an important factor in mating disruption. IOBC/WPRS Bull 28:313–317

Stelinski LL, Gut LJ, Miller JR (2006) Orientational behaviors and EAG responses of male codling moth after exposure to synthetic sex pheromone from various dispensers. J Chem Ecol 32:1527–1538

Thomas HA, White JD, Speers CF, Conrad H (1975) Dispensing pressurized aerosols of southern pine beetle pheromone under field conditions. J Ga. Enterp Soc 10:265–271

Vickers NJ, Baker TC (1994) Reiterative responses to single strands of odor promote sustained upwind flight and odor source location by moths. Proc Natl Acad Sci U S A 91:5756–5760

Welter SC, Pickel C, Millar JG, Cave F, Van Steenwyk RA, Dunley J (2005) Pheromone mating disruption offers selective management options for key pests. Calif Agric 59:16–22

Witzgall P, Kirsch P, Cork A (2010) Sex pheromones and their impact on pest management. J Chem Ecol 36:80–100