MATING DISRUPTION

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The following is an excerpt from a book chapter by Miller and Gut that is currently in review. The references have been removed to make it easier to read.

The concept of broadcasting sex attractant pheromones within a crop so as to disrupt reproduction of insect pests caught hold in the early 1970s. It helped birth the field of chemical ecology and remains prominent for several reasons. Firstly, sex pheromones are among the most potent stimuli known in terms of sensory reception and processing, as well as urgency and precision of the behavioral responses they elicit. And secondly, the prospect that use of these non-toxic natural products for pest control can reduce insecticide load in the environment continues to have justified broad appeal.

Mating disruption products have been developed for more that 20 insect species and are used on more than 750,000 hectares worldwide (Table 1). This amounts to a 75% increase in the commercial adoption of the approach in the past ten years. The first registration of a mating disruption product in the U.S.A. was for the pink bollworm (*Pectinophora gossypiella*) (Gelechiidae) in 1978. Additional registrations came slowly in the 1980's, but increased dramatically over the past two decades. Currently there are more than 120 disruption products registered with the U.S.A. EPA spread across 18 target species. Codling moth (*Cydia pomonella*) (Tortricidae) and Oriental fruit moth (*Grapholita molesta*) (Tortricidae) have garnered the most attention; 24 products have been registered for control of each.

Table 1. Growth in use of mating disruption products globally.

		Area treated (ha)		
Species	Principal crop	2002[a]	2012[b]	% Change
Lymantria dispar	Deciduous forests	60,000	200,000	233
Cydia pomonella	Pome fruit, Walnut	120,000	220,000	83
Grapholita molesta	Stone and pome fruit	50,000	60,000	20
Lobesia botrana	Grape	41,000	150,000	266
Eupoecilia ambiguella	Grape	32,000	60,000	88
Endopiza viteana	Grape	1,000	1,000	0
Chilo suppressalis	Rice	4,000	8,000	100
Leafrollers (Tortricidae)	Tea, pome fruit, peach, grape	24,000	15,000	-38
Synanthedon spp.	Peach, apricot, black current	5,000	6,000	20
Zeuzerina pyrina	Pear, olive	2,000	3,000	50
Plutella xylostella	Cabbage	2,000	2,000	0
Keiferia lycopersicella	Tomato	10,000	2,000	-80
Pectinophora gossypiella	Cotton	55,000	19,000	-66
Others	Vegetables, apple, peach, turf	27,000	10,000	-63
TOTAL		433,000	756,000	75

[a] Figures from Cardé (2007).
[b] Figures courtesy of Pacific Biocontrol and Shin-Etsu Corporation.

Disruption mechanisms: In practice, the success of mating disruption depends on the cost-effective delivery of an appropriate blend, amount, and spatial distribution of pheromone for an extended period of time. Once the pheromone is delivered though, how is the behavior of males impacted to achieve mating disruption? There are two general ways this might be achieved: 1) by competitive attraction where males are diverted from orienting to females due to competing attraction of nearby false trails emanating from pheromone dispensers, or 2) by a non-competitive means where exposure to synthetic pheromone subsequently reduces or blocks the male's ability to sense pheromone normally and this happens without attraction. The latter could be achieved by negating the male's ability to respond to pheromone or by camouflaging the location of a pheromone-emitting female.

Our findings over the past several years indicate that both mechanisms are operating, but that in by far the most cases competitive attraction is the key initial step. Three principal lines of evidence support the primary importance of competitive attraction. Extensive observations of male response to reservoir dispensers in the field reveal that male moths readily approach the dispensers, even in a fully pheromone treated orchard. Additionally, mating disruption appears to be highly dependent on moth density. This is consistent with a scenario whereby the capability of false pheromone sources in competing with females for searching males is easier if there are fewer individuals in the competition. If on the other hand the presence of pheromone in the orchard atmosphere impacted a male's ability to respond to pheromone, all males present in the pheromone-laden area should be affected regardless of how many are present. In other words non-competitive mating disruption would not depend on the pest's density. Finally, the effect of increasing numbers of point sources on mating disruption is predictable, with the first few dispensers have the greatest impact, but as more and more dispensers are added the effect of each diminishes. In other words, achieving 60% disruption takes only a few dispensers, bringing this up to 80% disruption requires a substantial number of additional dispensers, and levels of disruption above 90% require a huge bump in the number of point sources.

Types of formulations used in mating disruption: Mating disruption formulations have been engineered with the following criteria in mind: release of pheromone over an extended period of time, protection of the sensitive active ingredient from degradation, ease of application, affordability in the marketplace, and the extent to which male orientation is impeded. Two general types of formulations have been developed: densely distributed point sources and sparsely distributed point sources. Densely distributed technologies include those applied at densities ranging from as few as 300-1000 ha^{-1} (hand-applied reservoir dispensers) to several hundred million release devices ha^{-1} (sprayable microcapsules). Sparsely distributed technologies are applied at only a few units ha^{-1} (mega dispensers), or at about 50 devices ha^{-1} (meso-dispensers). The two approaches differ greatly in release rate per source and the homogeneity of pheromone distribution within the canopy. The higher the deployment density, the lower the emission of pheromone from individual point sources. For example, very high-density fiber formulations release nanograms of pheromone per hour, while low-density aerosol emitters release milligrams of pheromone hourly. Densely distributed formulations distribute pheromone via the application process itself, while sparsely distributed sources largely rely on the wind to distribute pheromone. The former is intended to provide an even distribution of pheromone in the canopy, while the latter relies on natural areal redistribution of pheromone to avoid gaps due to uneven deployment. Not surprisingly, the vast differences in application density, emission rate, and pheromone distribution among formulations have resulted in considerable differences in efficacy and likely means by which disruption is achieved.

Hand-applied reservoir dispensers: The greatest commercial successes of pheromone-based mating disruption have been achieved through the manual application of reservoir-type release devices. Pheromone is enclosed in plastic or dispersed in synthetic polymers and slowly diffuses from these reservoirs for up to 180 days. Some of these formulations are hand-applied at a rate of 500-1000 sources ha^{-1}; each dispenser releases up to several μg of pheromone h^{-1}. A major factor limiting greater adoption of reservoir formulations is the labor requirement and associated cost of applying a large number of point sources. This can be especially daunting in orchard crops where dispensers may need to be applied high in the canopies of 5-15 m tall trees.

Disruption using hand-applied reservoir formulations appears to rely primarily on competitive attraction. Males are initially attracted to the dispensers and subsequent physiological changes can prevent them from searching for females over an extended period. The process is largely a number game; disruption is strongest when competing sources vastly outnumber females. Not surprisingly, the efficacy of reservoir formulations is often greatly affected by point source and pest population density. Specifically, the highest levels of orientation disruption are achieved where dispenser density is high and pest population density is low. For some pest species, like Oriental fruit moth, reservoir dispensers may operate via a non-competitive mechanism and very high levels of disruption should be achievable regardless of pest density.

Manufacturers have made great strides in improving the release characteristics and ease of application of reservoir formulations over the past twenty years. Enhanced efficacy however, has been more elusive. Farmers continue to apply dispensers at rates of 300-1000 ha^{-1} and anticipate that supplemental insecticide treatments may be required to achieve control. Figure 4 provides powerful insights into the current use pattern for reservoir formulations and the lack of enhanced efficacy over the past twenty years. The most 'bang for the buck' is obtained at the lower application rates. There is little incentive to add hundreds of dispensers to achieve a small increase in disruption efficacy. The cost is prohibitive. Recognizing this, many producers have opted to use fewer dispensers and apply supplemental insecticides as needed. Perhaps the greatest opportunity for improvement may lie in reducing the amount of active ingredient per dispenser, and ultimately the cost to the grower.

Development of alternative means of dispensing pheromone has to a large extent been driven by the need to make application more cost-effective. The basic approaches have been either to develop densely distributed formulations that do not require hand application or sparsely distributed formulations that greatly reduce the requirements for manual application.

Sprayable dispensers: The most densely distributed formulations consist of pheromone encapsulated in microscopic polymer capsules (20 μm average size) that are sprayed on a crop at extremely high densities. Microencapsulated (MEC) formulations are typically applied as a hundred million or more capsules ha^{-1} that together deliver 20-100 g of pheromone and aim to release over a period of 3-4 wks. Sprayables offer the advantage of ease of application and the accompanying reduction in labor costs, thus it is not surprising that the development and testing of MEC formulations has been pursued for nearly four decades. Unfortunately, although they are highly desirable from a practical standpoint, efficacy has been inconsistent and short-lived in the field. The most effective disruption using sprayable MEC has been achieved for Oriental fruit moth. Across a range of other targeted pests, MEC formulations have consistently proved less effective than hand-applied formulations. Field studies have shown that MEC formulations initially provide substantial levels of disruption, but lose efficacy 3-4 wks after application. The decline in efficacy is an outcome of the inherent rapid decline in release rate from the microcapsules and the susceptibility of formulations to be washed off by rains. Thus, multiple sprays of substantial amounts of pheromone each are required to achieve season-long inhibition of mate location.

Improving the performance of MEC formulations has proven to be a challenge. Frequent application of low rates can provide better disruption than high rates applied at longer intervals. A low volume application method has improved efficacy of sprayable formulations for codling moth. However, the need for multiple applications to maintain efficacy remains problematic.

Recent field studies and flight tunnel assays support a non-competitive mechanism as the primary means by which high volume application of MEC formulations provide communication disruption. Initial release of high concentrations of pheromone precludes males from finding pheromone sources either by desensitization of males or camouflaging the female plume. The improved efficacy of the low-volume concentrated MEC application is likely related to the increased role of competition as the disruption mechanisms due to the clumping of capsules making them attractive point sources for searching males. Regardless of the mechanism, the effect diminishes or is lost as the amount of pheromone released from the capsules falls below some threshold level and this varies by species.

Machine-applied formulations: Machine-applied formulations, such as flakes, fibers or wax droplets, represent another option for automated delivery of pheromones. Such point sources are designed to release pheromone at about the same rate as calling females and thus are commonly referred to as female-equivalent formulations. Small-plot trials demonstrated that deployment of such formulations could provide high levels of disruption. For example, paraffin wax drops (0.1 ml) containing 5% pheromone and hand-deployed at 8,200 and 27,300 ha^{-1} completely disrupted mating of Oriental fruit moth under heavy population densities as measured by tethered female moths and disrupted orientation of feral males to optimally-baited traps above 99% relative to control plots. The most successful commercial adoption of machine-applied formulations has been achieved for the gypsy moth. Over 150,000 ha are treated annually with flakes or wax drops to slow the spread of this pest. The presumable advantages of these technologies are low cost and rapid deployment of many thousands of point sources ha^{-1}. Unfortunately, major factors limiting the commercialization of this technology for pests other than gypsy moth include the low efficiency of product adherence to crop foliage, short field life, and lack of rain-fastness following machine or aerial application.

In addition to ease of application, the thinking behind development of female equivalent formulations was that thousands of point source competing with calling females would improve efficacy relative to hand-applied devices that are deployed at lower densities. Competitive attraction appears to play a principal role in how mating disruption is achieved using these high-density technologies. However, formulations releasing ng of pheromone turn out to be weaker disruptors than dispensers releasing μg of pheromone. Although both types of densely distributed formulations are attractive to searching males, the complex formed between low-releasing dispenser and males is not as long-lived as that formed between higher-releasing dispensers and attracted males. Fiber, flakes and wax drops may only divert the attention of males away from calling females for minutes, while reservoir dispensers can tie up males for hours or an entire evening. The bottom line is that female-equivalent formulations allow males many more opportunities to search for actual females over the course of their lifespan than do reservoir dispensers, thus decreasing the odds of their preventing mating.

Meso dispensers: Meso dispensers are an attempt to retain the best qualities of reservoir dispensers, yet reduce application effort. These passive devices release substantially more pheromone than standard reservoir dispensers. The idea is that the higher release can allow for application of meso dispensers at much lower densities and thus greatly reduce the labor required for hand application. A novel controlled release system called the Metered Semiochemical Timed Release System, or MSTRS® was field-tested for communication disruption of the blackheaded fireworm. Significant reductions in male catch in pheromone-baited traps was achieved by deploying MSTRS plastic bags releasing high quantities of pheromone at a rate of 20 bags/ha. More recently, manufacturers of codling moth disruption formulations have tested mega dispensers that are essentially the equivalent of 10-20 standard dispensers. The approach, in part, has been validated by work where some success with codling moth control was achieved using clusters of 10-100 standard dispensers applied at reduced densities.

Given that high densities of distributed reservoir dispensers produce the best results, sparsely distributed mega-dispensers would not be expected to perform well if the mechanism of disruption was competitive attraction, unless the complex formed was substantially more long lasting. Alternatively, mega dispensers could operate by desensitization or by elevating male threshold. Recent studies with Oriental fruit moth disruption reveal that reservoir dispensers release at rates high enough to cause mating disruption via a non-competitive mechanism. In a sense, standard reservoir dispensers for Oriental fruit moth are already operating as mega dispensers. For other current targets of mating disruption, such as codling moth, the release rate needed to change the mechanism from competitive to non-competitive is unknown. Optimization of mega dispensers will be aided by determining this rate.

Mega dispensers: An ultra sparsely dispersed approach stores and releases the insect sex attractants via aerosol devices that dispense very large quantities of pheromone mechanically. Emitters are deployed at densities of only 2-5 ha^{-1}, but each unit releases mg quantities of pheromone every 15-30 min over a 6-12 h cycle. These extremely low-density devices provide a controlled constant release rate and a stable environment for the pheromone prior to its release. Aerosol emitters have been tested across a range of pests and commodities, but the only notable commercial adoption has been for disruption of codling moth in pome fruit and nut crops in the Western United States.

Sparsely distributed high-release pheromone dispensing strategies are a promising alternative to widely dispersed technologies. However, making meso- or mega-dispensing technologies mechanically robust or consistently effective has been a challenge. Improvements will arise through sorting out the mechanism by which disruption is achieved and determining the optimum deployment pattern. Recent experiments examining codling moth mating disruption using aerosol emitters show that male captures in pheromone traps are inhibited for considerable distances downwind of the unit. It has been argued that males within the expansive downwind plume are desensitized and unable to respond to pheromone. However, there is no direct evidence to support this supposition of a threshold elevation. An alternative explanation is that the males are drawn away from females and become aggregated near mega-dispensers, i.e. induced allopatry.

Regardless of the mechanism, the major risk in using mega-dispensers is that the low deployment density will leave areas of little on no pheromone coverage where mate finding can occur. Indeed, edges are known to be problematic in aerosol-treated crops and supplemental treatment of borders with reservoir dispensers is recommended. This technology is likely to benefit substantially from treatment of large contiguous blocks of crop and is less desirable for small and irregular fields.

The economics of mating disruption via sparsely distributed dispensers also is overdue for a careful evaluation. The use of mega dispensers is limited to deploying only one per acre because of the high cost of the unit and especially the pheromone. Is the extremely high amounts released by current technologies to achieve disruption needed? Current research on codling moth mating disruption suggests that lower rates of pheromone could be emitted from mega dispensers without compromising efficacy. Additionally, the cost of current technologies is quite high due to the sophisticated electronics used to control pheromone release. A passive mega-dispenser offers further opportunity for reducing cost. The control achieved using mega dispensers may be greatly improved if less costly units that release lower rates of pheromone were deployed at densities of 5-10 per acre.

Case Studies

Codling moth: At present an estimated 162,000 ha of fruit crops worldwide, including over 77,000 ha in North America, are treated with pheromone for CM management. The commercial development of CM mating disruption is one of the great success stories for chemical ecology. The widespread adoption of CM mating disruption has been driven by a strong foundation of laboratory and field research, along with the impetus for growers to adopt new technologies as insecticides failed to control CM due to resistance or became unavailable due to changing regulations. Largely by trial-and-error it was determined that two factors had the most impact on CM control in pheromone-treated orchards, the initial population level and the size of the treated area. The best control was recorded when starting population densities were low. Achieving control if CM densities were excessive (above 1% crop damage the previous season) required the use of supplemental insecticides to reduce pest pressure. The larger the area treated the better the control, likely due to mitigating the influx of mated females from adjacent untreated areas. Demonstrating the effectiveness of CM disruption in government-sponsored area-wide management programs played an especially important role in the commercial success of the approach.

A great deal of practical research has accompanied grower adoption of this novel control tactic. Codling moth mating disruption was found to work best when dispensers were placed high in the canopy and efficacy increased as dispenser density increased. Early on, growers found that monitoring CM to determine if and when companion insecticides needed to be applied was problematic. A pheromone trap baited with a standard CM lure containing 1 mg of codlemone was the monitoring tool of choice. The rationale was that not catching males should correspond with a failure of males to locate actual females. Unfortunately, trap shutdown was an unreliable indicator of successful disruption. Two important advances facilitated CM trapping in the presence of pheromone: i) the use of high-load lures and ii) the discovery and use of pear ester, a kairomone attractive to CM males and females. Most recently, a lure combining codlemone and the pear ester has proven especially effective for monitoring CM activity in disrupted orchards. Pheromone traps baited with these alternatives to standard lures are not shutdown in disrupted orchards, providing growers with an effective means of assessing the population density within the orchard and of timing insecticide sprays.

The observed efficacy and persistence of hand-applied pheromone technology for CM has resulted in many new products reaching the market place and increasing grower adoption worldwide (Table 1). Pheromone companies have developed dispensers that improve the ease of application relative to older technologies and build flexibility into labels to address point source density issues. Codling moth completes multiple generations per year, thus formulations must release sufficient quantities of pheromone for up to 180 d. Photochemical degradation of codlemone can decrease both product efficacy and longevity. Thus, various anti-oxidants and UV inhibitors are now commonly added to CM mating disruption formulations.

Although the majority of formulations registered over the past 20 years for CM mating disruption require hand-application, substantial efforts have been invested in other formulations to make application easier. Fibers and flakes have been evaluated; but they have provided levels of CM control inferior to the currently used hand-applied dispenser technology and have proved difficult to apply and to keep in the crop. Sprayables have faired only slightly better. A 20-30 fold increase in the rate of active ingredient (AI) per hectare failed to improve the disruption efficacy of CM MEC when both low and high rates were applied at equivalent frequencies per season. The best approaches for using a sprayable formulation to disrupt CM are a low-rate frequent application protocol or a low volume application method. From a practical standpoint, growers using CM MEC primarily make one or two applications at peak flight for the purpose of reducing pest density and improving the effectiveness of their insecticidal control program.

Aerosol emitters have turned out to be the most promising alternative to high-density hand-applied technology, recently gaining a substantial share of the CM mating disruption market. The ease of application and labor savings associated with deploying only a few devices per hectare has largely driven producer interest in the approach. In the Western U.S., high levels of orientational disruption of CM have been achieved with deployment of as few as 2 emitters ha^{-1} placed along the perimeter or in a grid pattern. Aerosol emitters are often supplemented with a border application of hand-applied pheromone dispensers and/or companion insecticides. Puffers did not perform as well in early Michigan field trials; less than 75 % disruption of male CM orientation to pheromone-baited traps was achieved in treated plots compared with untreated controls. More recent trials in Michigan have produced results similar to those reported from the Western U.S.

Although pheromone-based mating disruption has become a viable and accepted component of CM management programs, the majority of growers worldwide still rely on insecticides for control of this key pest. Several factors have impeded further adoption; however, chief among them is the high cost along with the economic ceiling this places on how the technology is used. Growers are not likely to deploy more than the maximum of 1000 hand-applied dispensers ha^{-1} at a cost of more than $300, even though it may improve efficacy. Indeed, many growers find that the most economical approach is to deploy dispensers at a moderate rate of 500 per hectare and they apply one or a few supplemental insecticides. Similarly, the current trend for aerosol emitters is to deploy only a few of the costly units ha^{-1} and rely on companion insecticides to keep CM densities low. Considering the primary importance of cost, it seems logical that the pheromone requirements for disrupting CM using reservoir dispensers or aerosol devices would have been well worked out. It turns out this is not the case.

Current formulations targeting codling moth are loaded with 50-120 mg of codlemone and release upwards of 5 μg of the active ingredient h^{-1}. The experimental basis for this high per dispenser emission rate was essentially a series of trial-and-error field studies conducted in the

1980's. The process entailed loading pheromone into rubber tubing, and later polyethylene dispensers, and measuring the level of trap shutdown and fruit protection provided. Good results led to additional studies using experimental dispensers loaded with less pheromone. Further tests at higher loading rates were conducted when the disruption outcome was inadequate. The aim was to balance the desire to achieve a commercially acceptable level of disruption for the entire adult codling moth flight of 120-180 days, yet keep the loading rate low enough so as not to be cost-prohibitive.

Recent studies examining the mechanism of codling moth mating disruption for reservoir dispensers suggest that release rates could be substantially reduced without compromising efficacy. Using a large-cage study system, the MSU research group was able to document for Isomate C Plus a competitive-attraction disruption profile and the scenario of disruption lasting for an evening. Field observations and wind-tunnel assays support the scenario that codling moth males first are attracted to the dispenser and once exposed are incapable of normal sexual response for the remainder of a diel cycle. Additional cage experiments revealed that Isomate C Plus was more effective at reducing capture of males in central monitoring traps than pheromone lures (Trécé L2) placed in traps without liners operating as dispensers. Isomate dispensers deployed at a density of 500 ha^{-1} provided over 70% disruption. Standard pheromone lures deployed as dispensers at 500/ha yielded a competitive disruption profile and provided nearly 50% disruption, despite their releasing 10-fold less pheromone than Isomate dispensers. It was deduced that high rates of pheromone released from the hand-applied dispensers (D_a = 0.17) eliminated further orientations by attracted males for the evening, while low-releasing point sources (D_a = 0.04) eliminated orientations for only a short period of time allowing multiple visits in the same evening.

The costs of current hand-applied formulations for CM are high, in part, because they release substantially more pheromone than is required to achieve disruption. A comparison of rubber septa and polyethylene dispensers deployed at densities of 500 ha^{-1}, but with release rates varying between 0.1-5.0 $\mu g\ h^{-1}$, revealed that the disruptive effects plateaued at a release rate of about 1.0 μg pheromone h^{-1}. Based on these findings, Shin-Etsu (Tokyo, Japan) produced experimental Isomate Flex® dispensers with 80%, 50% 25% or 10% of the standard load of codlemone giving average release rates of *ca.* 3.9, 2.4, 1.2 or 1.0 $\mu g\ ^{-1}$, respectively. The fully loaded Flex dispenser releases an average of *ca.* 4.8 $\mu g\ h^{-1}$. Field trials conducted in Washington and Michigan, U.S.A. revealed that all four of the experimental Flex dispensers provided very high levels of catch suppression in pheromone traps; no significant difference were found among the formulations. Shin-Etsu currently markets the 80% loading rate as Isomate CM Flex. The development of the Flex technology illustrates how optimizations can be achieved through an understanding of the underlying factors that determine the disruption efficacy of a particular technology.

Little is known about how aerosol emitters disrupt moth behavior and reduce mating, or the release rate and density of units required to achieve codling moth mating disruption. For example, dosage-response studies determining whether disruption operates competitively on non-competitively are yet to be done. Experiments examining the behavior of CM in orchards treated with aerosol emitters are also needed to help optimize the necessary number of devices required in a given area, the target release rate to effectively disrupt moth communication, and the period of nightly operation required to dispense the proper amount of pheromone. The current parameters established for using aerosol emitters include a loading rate *ca*. 70 gm of codlemone per unit and release of 7 mg of pheromone every 15 min over a 12 hr cycle (1700-

0500). The amount currently released per day was simply chosen to equate the release rate from one emitter to that of 1000 reservoir dispensers. The use of aerosol emitters is limited to deploying only a few ha^{-1} because of the high cost of the unit and the pheromone. Do we need the extremely high amounts released by current technologies to achieve satisfactory disruption? Is the emission of pheromone as an aerosol important or would a passive mega dispenser work just as well? Aerosol emitters once deployed dispense pheromone over a much longer period than the 3-4 hr activity window of CM and continue to emit even when conditions for moth flight are unfavorable. Moreover, the previously discussed work showing that a substantial reduction in rate of pheromone emission from reservoir dispensers did not reduce orientational disruption of CM provides impetus for examining the effectiveness of aerosol emitters releasing at 50, 25 or even 10% of the current dosage. This could be achieved by reducing the loading rate, the length of the emission cycle, or the spray interval. The control achieved using aerosol emitters may be greatly improved if less costly units that release lower rates of pheromone were deployed at densities of 10-15 ha^{-1}. This would likely also help mitigate the border problems encountered when using this low-density approach. Understanding what parameters are optimal could significantly reduce cost and improve efficacy, leading to more widespread adoption of mating disruption.

Oriental fruit moth: This fruit-infesting tortricid is abundant throughout the stone-fruit growing regions of Europe, Asia, America, Africa and Oceana. Although it is primarily a pest of peaches and nectarines, OFM recently has become a major pest of pears in Australia and apples in North America. The pheromone of OFM is principally a blend of Z8-12Ac, E8-12Ac and Z8-12OH in about a 93:6:1 ratio. Efforts to develop mating disruption for this tortricid began over four decades ago. Promising results using various release devices culminated in the development and commercialization of a polyethylene dispenser marketed as Isomate M (Shin-Etsu, Tokyo, Japan). There are currently 24 OFM mating disruption formulations registered in the U.S.A. and an estimated 58,000 hectares worldwide treated with these technologies.

Numerous field trials have demonstrated great success in managing this pest using various hand-applied technologies. A single application of 250-500 dispensers ha^{-1} alone, or with minimal insecticidal input, have consistently provided levels of fruit protection from OFM equivalent to those achieved using a full insecticide program. Control failures under mating disruption have typically only occurred on borders as a result of the migration of mated females from nearby untreated hosts. Area-wide adoption of mating disruption has proved to be a very effective means of overcoming this problem. Edge infestations of OFM in disrupted peach and nectarine orchards in Victoria, Australia were reduced or eliminated following the expansion of pheromone treatments to include not only all peach and nectarine orchards, but also all pear, apple, apricot and plum orchards. In addition to minimizing fruit damage, treating all stone and pome fruit orchards in this 1,100 ha production region nearly eliminated the need for insecticide sprays targeting OFM.

Even with the consistent success of reservoir dispensers, considerable effort has been devoted to the development of OFM disruption technologies that require less labor to apply. Multiple applications of sprayable pheromone have consistently provided a high level of trap shutdown and fruit protection. Monthly applications of MEC OFM in Australian peach and pear orchards reduced fruit infestation as well as hand-applied dispensers or multiple insecticide sprays. Large plot studies in apple revealed little difference in disruption among application rates of MEC ranging from 12.4-49.1 gm AI ha^{-1}. Efficacy did decline 3-4 wks after the application of only 2.4 gm AI ha^{-1}. A low-rate high-frequency protocol (nine applications per season) provided equivalent or greater reduction of male captures in traps compared with a protocol of three high-rate applications per season, despite using two-fold less total pheromone with the former treatment. Given the ease of application and proven efficacy, it is somewhat surprising that sprayable formulations comprise a very minor share of the OFM disruption market. The major factor limiting the use of this technology appears to be grower reluctance to make multiple applications given the reliable option of achieving season-long control with a single hanging of reservoir dispensers.

A recent tactic for dispensing pheromone based on refinement of a paraffin-wax formulation for dispensing pheromones aims to improve the ease of application. A low-viscosity wax formulation developed for commercial use, Confuse OFM (Gowan Co., Yuma, Arizona) effectively controlled OFM in field tests, however it proved difficult to apply and had an inefficient release profile. Release profiles and efficacy were improved by thickening the paraffin wax formulation resulting in the formation of wax dollops following application. A single application of 74 g AI (590 dollops) ha^{-1} as 3-ml dollops (2.5-g) provided season-long control equivalent to that of Isomate-M 100 tubes deployed at the recommended rate of 57 g AI (250 dispensers) ha^{-1}. Similarly, the level of mating disruption following deployment of thousands of small wax drops (0.1 ml) was superior to that with label-recommended applications of Isomate M-Rosso dispensers. ISCA Technologies, Inc. (Riverside, CA) licensed the wax emulsion patent and their Specialized Pheromone & Lure Application Technology (SPLAT) was granted a federal registration for *G. molesta* control by the U.S. Environmental Protection Agency in 2006. A tractor-mounted mechanized applicator capable of covering one ha in *ca.* 20-25 min was developed and tested on-farm. A field test with very high populations of OFM yielded 100 % disruption of tethered female mating and 99% disruption of pheromone traps with machine-applied wax drops during the spring generation of moth flight.

Aerosol emitters appear to be another viable option for pheromone-based control of OFM. Our research team conducted a two year study evaluating Puffer® aerosol dispensers (Suterra LLC, Bend, OR, USA) for mating disruption of OFM. The devices were deployed at the label-recommended rate of 2.5 ha^{-1} and released 5.0 mg of the 3-component OFM pheromone blend every 15 min during a 12-h cycle beginning each day at 15:00 h for the duration of the season. Up to 98% inhibition of male orientation to pheromone-baited traps and equivalent fruit protection was recorded in Puffer®-treated plots compared with control plots not receiving pheromone.

Control using pheromones has turned out to be much easier to achieve for OFM compared to CM. As discussed above, while the entire range of densely- to sparsely-distributed formulations can provide high levels of OFM disruption, MEC and female-equivalent formulations fail to provide adequate control of CM. And substantially less pheromone is required to disrupt OFM than CM. Hand-applied formulations targeting OFM are generally applied at a rate of 250-500 dispensers ha^{-1} so as to provide a total AI in the range of 60-120 g of pheromone. In contrast, the application rate for CM formulations is 500-1000 dispensers ha^{-1} for a total AI in the range of 120-240 g of codlemone. An OFM pheromone treatment typically results in nearly complete shutdown of male catch in pheromone traps, even if pest densities are high. The extent to which male catch is reduced in pheromone-treated compared to untreated control plots is quite variable for CM. If pest densities are high, levels of trap shutdown often do not exceed 70%. At lower pest densities a reduction in catch of 80-90% is typical; generally complete shutdown only occurs at extremely low pest densities. Disruption alone is often sufficient for OFM control, while one or more insecticide treatments usually are applied along with the pheromone treatment to keep CM populations in check.

Early recognition of the high sensitivity of OFM to pheromone treatments drew the attention of chemical ecologists seeking to understand the mechanisms of mating disruption. Flight tunnel and field studies revealed that pre-exposure to synthetic pheromone desensitized males, affecting subsequent orientation behavior. It was found that the effect was dependent on the intensity and duration of prior exposure and the recovery time that elapsed before assessing behavior. Pre-exposure to stimuli of low intensity and short duration had no effect. Levels of desensitization increased as the intensity and duration of exposure increased. Males regained responsiveness to the highest dose and exposure if the recovery time was extended. Furthermore they concluded that significant effects were only produced following exposures that were much more intense than those that could be expected in orchards under a disruption regime.

Most recently, our research group proved that disruption of OFM could occur via competitive or non-competitive mechanisms, depending on the pheromone release rate from each dispenser. Large field cage experiments were carried out to generate dosage response profiles for low-releasing (0.04 µg h^{-1}) and high releasing (60 µg h^{-1}) dispensers. Mathematical tools and graphical analyses revealed that low releasing dispensers disrupted OFM competitively. This confirmed the conclusion that OFM is disrupted competitively when exposed to low concentrations of pheromone. It also was consistent with the findings that exposure to low intensity stimuli does not desensitize OFM males. Under identical experimental conditions other than the dispenser-type, OFM disruption shifted to a non-competitive mechanism for high-releasing dispensers. This supports the tentative conclusion that 12 ml dollops of emulsified wax formulation releasing OFM pheromone at >40 µg h^{-1} in an open-field situation operated non-competitively. It was concluded that desensitization, not first requiring attraction, was the likely behavioral explanation for the non-competitive disruption of OFM. They went on to postulate that this and other easier to disrupt species might be so because of the ability to disrupt them by non-competitive means.