Codling Moth Management and Chemical Ecology

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Annu. Rev. Entomol. 2008. 53:503–22

First published online as a Review in Advance on September 17, 2007

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev.ento.53.103106.093323

0066-4170/08/0107-0503$20.00

Key Words

pheromone, kairomone, sexual communication, integrated pest management

Abstract

Lepidopteran insects use sex pheromones to communicate for mating. Olfactory communication and mate-finding can be prevented by permeating the atmosphere with synthetic pheromone. Pheromone-mediated mating disruption has become a commercially viable pest management technique and is used to control the codling moth, *Cydia pomonella*, a key insect pest of apple, on 160,000 ha worldwide. The codling moth sex pheromone, codlemone, is species specific and nontoxic. Orchard treatments with up to 100 grams of synthetic codlemone per hectare effectively control codling moth populations over the entire growing season. Practical implementation of the mating disruption technique has been realized at an opportune time, as codling moth has become resistant to many insecticides. We review codling moth chemical ecology and factors underlying the behavioral mechanisms and practical implementation of mating disruption. Area-wide programs are the result of collaborative efforts between academic research institutions, extension, chemical industries, and grower organizations, and they demonstrate the environmental and economic relevance of pheromone research.

INTRODUCTION

Pheromone: chemical signal produced and released by an organism, eliciting a behavioral response when perceived by a member of the same species

Pheromone dispenser: device for controlled release of synthetic pheromone

Olfaction is the primal sense, because "smells are surer than sounds or sights" (Rudyard Kipling, "Lichtenberg"). Insects, like many other animals, rely on chemical signals to find food and mates. The discovery that moths depend on pheromones for mate-finding soon led to the idea that sexual communication could be disrupted by permeating the atmosphere with synthetic pheromone (122). Since then, research on pheromone chemistry and biology has made it possible to control insects through mating disruption, including the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), the key pest of apple.

The application of sex pheromones for pest control offers several advantages over conventional insecticides. Sex pheromones are nontoxic and species specific and they elicit behavioral reactions at minute amounts. Specificity and nontoxicity are also the Achilles' heel of pheromone-based methods, when immigration of mated females occurs and where crops are infested by several species (55, 86) (see sidebar, Practical Use of Pheromones and Other Semiochemicals in Insect Control). Successful codling moth mating disruption also requires low initial population densities (26).

In 1991, the first effective pheromone dispenser for codling moth mating disruption was registered in the United States. Since then, mating disruption has steadily gained acceptance and has become an integral part of codling moth management in several pome fruit production areas (**Table 1**) (103).

Why is the use of codling moth mating disruption widespread in some areas, whereas it is limited or nonexistent in other areas? Why is the technique used when its reliability is sometimes in doubt? We analyze its mode of action in view of codling moth chemical ecology. We describe the limitations and discuss the pros and cons to the adoption of codling moth mating disruption, leading to suggestions for continued development.

PRACTICAL USE OF PHEROMONES AND OTHER SEMIOCHEMICALS IN INSECT CONTROL

Hundreds of sex pheromones have been identified in moths and other insect orders. Long-range attraction is typically encoded by female signals. Practical applications of sex pheromones are based on two principal modes of action: air permeation, leading to communication and mating disruption, and attraction to point-source lures for population monitoring, and for control by mass trapping and attract-and-kill. The detection sensitivity and species selectivity of pheromone-baited traps make them ideal tools to detect the presence of insects and to monitor their flight period phenology. Attractant lures can also be used for population control, in combination with large-capacity traps or a contact insecticide. The efficacy of mass trapping and attract-and-kill is greatly enhanced when using lures that attract females. Female attractants are either male-produced pheromones or other semiochemicals, such as plant odors or fermentation by-products, that indicate oviposition sites or food sources. Mass trapping or attract-and-kill is used against moths, beetles, and fruit flies. To date, mating disruption has only seen widespread application with moths.

CODLING MOTH CHEMICAL ECOLOGY

Female Sex Pheromone

Codlemone, the main compound of codling moth sex pheromone, was first identified by gas chromatography (GC) and electroantennogram (EAG) recordings (88). Its structure and presence in the female pheromone gland were then confirmed by chemical analysis (19, 78). The development of more sophisticated analytical techniques later made it possible to identify a suite of additional, structurally related compounds. The females produce several saturated, monoenic and dienic straight-chain alcohols, including all four geometric isomers of codlemone, along with the analogous acetate and aldehyde (6, 41, 119). The key step of codlemone biosynthesis is an *E*9 desaturation of dodecanoic acid,

Table 1 Worldwide use of mating disruption[a]

Species	Main crop	Region	Area (ha)
Gypsy moth (*Lymantria dispar*)	Forest	United States	230,000
Codling moth (*Cydia pomonella*)[b]	Apple, pear	North America	77,000
		European Union	38,000
		South Africa	19,000
		Argentina, Chile, Australia, New Zealand, Israel	28,000
Grapevine moth (*Lobesia botrana*)	Grape	European Union	60,000
Oriental fruit moth (*Grapholita molesta*)	Peach, apple	United States, Australia, European Union, South America, Japan	50,000
Pink bollworm (*Pectinophora gossypiella*)	Cotton	United States, Israel, South America, European Union	50,000
Grapeberry moth (*Eupoecilia ambiguella*)	Grape	European Union	45,000
Leafroller moths, Tortricidae	Apple, pear, peach, tea	United States, Australia, European Union, Japan, New Zealand	25,000
Other species	Fruit, vegetables, rice	Australia, European Union, Japan, Mexico, New Zealand, United States	40,000
Total			662,000

[a]Data courtesy of Kinya Ogawa, Shin-Etsu Chemical Co., Tokyo.
[b]Annual estimated codlemone production in 2006 was 25,000 kg.

followed by transformation of the *E*9 double bond to the conjugated (*E*,*E*)-8,10-diene (73).

Male attraction to live calling females matches male attraction to gland extracts released at rate of 6 ng codlemone/h, which corresponds well with the average release rate of 6.5 ng codlemone/h from calling females (**Figure 1**) (10, 43). Synthetic codlemone elicits the entire sequence of male precopulatory behavior and attracts males over a wide dose range (30, 77). Olfactometer, wind tunnel, and field tests show, however, marked differences in male wing fanning and anemotactic flight to synthetic codlemone versus extracts of female pheromone glands (14, 43, 45). The idea that pheromone synergists would intensify the male response to codlemone and thus improve the efficacy of mating disruption formulations has encouraged further studies of the compounds produced in female pheromone glands.

Dodecanol and tetradecanol. Dodecan-1-ol (12OH) is the second-most abundant compound in female glands, and it enhances male attraction in the wind tunnel to low codlemone doses and restores the biological activity of codlemone at overdose amounts (6, 42). Thereafter, it was shown that addition of both 12OH and tetradecan-1-ol (14OH) was necessary to obtain a close-range response equivalent to that elicited by natural pheromone (15). The most widely used mating disruption dispenser formulation contains a blend of codlemone, 12OH, and 14OH (20, 59), although a behavioral effect of these two compounds has not been demonstrated for attraction in the field.

Codlemone isomers. Several other compounds modulate male attraction to codlemone. Females produce the geometric isomers of codlemone (6, 119), and codlemone isomerizes on the surface of dispensers used for monitoring or mating disruption (20). Small amounts of the codlemone isomers do not strongly decrease attraction, as evidenced by season-long attractiveness of codlemone-monitoring lures. Larger amounts of the isomers have an antagonistic

Codlemone: (*E*,*E*)-8,10-dodecadienol or *E*8,*E*10-12OH

Anemotactic flight: upwind-oriented flight

Synergist: chemical, often inactive by itself, that enhances the behavioral response to another chemical

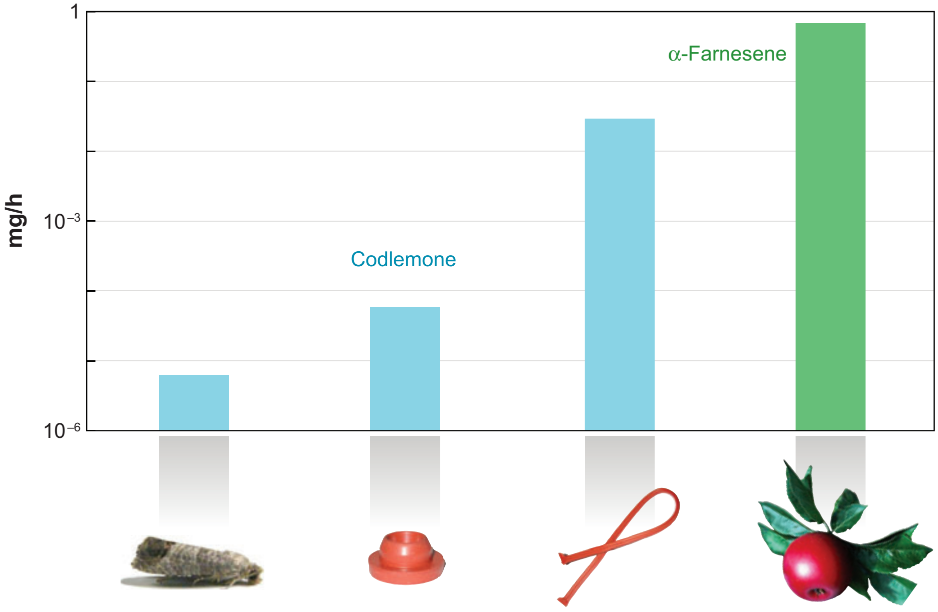

Figure 1

Calling codling moth females release codlemone at a rate of ∼6.5 ng/h. A fresh monitoring lure, baited with 100 μg codlemone, releases ∼10 times more codlemone. A 30-day-old field-aged polyethylene rope dispenser evaporates >1000 times more codlemone than a calling female; the release in an orchard is ∼50 mg/ha/h. The release of the main apple volatile α-farnesene from a semidwarf apple tree is estimated to be up to 1 mg/h and 2000 mg/ha/h in an orchard (10, 17, 20, 43, 59, 118).

effect, and an equilibrium isomer blend is only a weak male attractant. EZ [(*E*,*Z*)-8,10-dodecadienol] is behaviorally the most active isomer. It is a synergist when added to codlemone at 3%, but an antagonist when added at 20% or more (44, 77, 118, 119).

Codlemone acetate. Two types of pheromone receptor neurons, accounting for 46% and 6% of the antennal sensilla, are most abundant on codling moth male antennae. The first is tuned to codlemone and its isomers, as well as to codlemone acetate [(*E*,*E*)-8,10-dodecadienyl acetate or *E*8,*E*10-12Ac] and its geometric isomers. The second responds to the codlemone acetate isomers only and not to codlemone (9). This underscores the importance of codlemone acetate for pheromonal communication in codling moth.

The strong antagonistic effect of codlemone acetate on male attraction was discovered soon after codlemone. Large amounts inhibit male attraction when added to codlemone (50). Codling moth females produce trace amounts of codlemone acetate, which have a synergistic effect on male attraction to codlemone in the wind tunnel (119). Codlemone acetate is the sex pheromone of pear moth, *Cydia pyrivora*, the sibling species of the codling moth (74), and a 1:1 blend of codlemone and codlemone acetate is the sex pheromone of beech tortrix, *Cydia fagiglandana* (120).

Other compounds. The behavioral effect of other gland compounds, for example, the monounsaturated alcohols *E*8-12OH and *E*9–12OH, or codlemone aldehyde *E*8,*E*10-12Al, needs investigation. Addition of synergists to pheromone might improve the performance of mating disruption dispenser formulations. It is necessary to assess qualitative differences in male upwind flight or courtship behavior to identify further pheromone synergists, owing

Antagonist: chemical that decreases the attraction response to another chemical

Codlemone acetate: (*E*,*E*)-8,10-dodecadienyl acetate or *E*8,*E*10-12Ac to the strong attractant effect of codlemone alone.

Many other tortricid moths use multicomponent pheromone blends, including strongly synergistic minor components. Most species share pheromone components with other species and maintain species isolation by uniqueness of blend composition or blend ratio. In comparison, codling moth is the sole species whose main pheromone compound is codlemone. Selection pressure for a behavioral role of pheromone synergists is probably lower in codling moth than in most other tortricids. The individual variation in the blend released by calling females corroborates this hypothesis (10).

An investigation of codling moth pheromone should also take into account that calling females release pheromone into orchard air, which contains a host of plant odors. Some of these plant compounds directly affect codling moth behavior and some of them affect codling moth response to sex pheromone. For example, a behavioral effect of large amounts of 12OH added to codlemone in clean wind tunnel air, surpassing by far the female gland proportion (6), may reflect the synergism between sex pheromone and plant volatiles, because apple releases several alcohols, including 12OH (38).

Plant Volatiles

Host plant volatiles, in addition to sex pheromones, shape the reproductive behavior of insect herbivores. Plant volatiles mediate host finding and may synergize sexual communication (70, 93).

Female response to plant volatiles. Concurrent with the identification of codling moth sex pheromone (88), (*E*,*E*)-α-farnesene was shown to be a codling moth oviposition stimulant and larval attractant (100, 113). However, a breakthrough in the search for a codling moth kairomone was achieved 30 years later, when pear ester [(*E*,*Z*)-2,4-decadienoate] was discovered by Light and coworkers (71, 72). Pear ester, a major compound of the aroma of ripe Bartlett pears, attracts males and females and is being incorporated into orchard monitoring programs (64–66). The background odor in orchards interferes with female attraction to pear ester as with other kairomone lures (34, 67). Pear ester traps adjacent to apples capture most females, and attractiveness in apple orchards depends on the cultivar and season (65, 72), probably because maturing apples release volatiles that mask pear ester (17, 28, 107).

The principal hosts of codling moth are apple and pear, and a host race occurs on walnut (85, 117). Volatile signals attract gravid females for oviposition close to apples (52, 115, 124), and several apple volatiles elicit an antennal response in females (3, 17). However, the chemicals that allow codling moth females to discriminate between host and nonhost trees, or between different hosts, remain to be discovered.

Male response to plant volatiles. Codling moth mating occurs on or in close proximity to host plants, and males fly actively about host trees prior to the onset of female calling (29, 85, 118). Mechanisms to accelerate matefinding in short-lived insects are adaptive. In natural habitats with a patchy distribution of hosts, males improve reproductive success by locating rendezvous sites before females release pheromones. Even in orchard monocultures, male codling moth distribution is not uniform, as shown by the strong variation of male captures in pheromone traps. Because trees bearing the greatest fruit load receive the most eggs, it is conceivable that such trees are preferred mating sites (115, 118, 121).

Codling moth males likely use plant volatiles to find suitable host trees. Both sexes of codling moth respond to apple odors and possess olfactory receptor neurons tuned to these chemicals (3, 4, 9, 28, 36). Several compounds, including pear ester (*E*,*Z*)-2,4-decadienoate (64, 66, 72), (*E*)-β-farnesene, and (*E*,*E*)-farnesol (34), attract males, and the upwind flight behavior in

Kairomone: chemical signal eliciting a behavioral response in an interspecific receiving organism that benefits the receiver and disadvantages the emitter

Pear ester: (*E*,*Z*)-2,4-decadienoate response to pheromone and plant volatiles is similar.

As with pheromone components, there is a synergistic interaction between plant volatiles: Males are attracted to a blend of (*E*,*E*)-α-farnesene and (*E*)-β-farnesene, but not to the individual compounds (34). There is also a synergistic effect between sex pheromone and apple volatiles (125). The strong behavioral response of codling moth males to plant volatiles and their interaction with sex pheromone emphasize the role of plant odor in pheromone-mediated mating disruption, an area that has been neglected.

Larval Olfactory Response

Mate-finding in codling moth may also involve communication between larvae, and between larvae or pupae and adults. Codling moth females lay most of their eggs on leaves surrounding apples (115) and the larvae appear to possess the necessary sensory apparatus to detect fruit. First-instar larvae respond to α-farnesene and pear ester, both of which attract adults to host plants (63, 100). Infested apples become more attractive to both first-instar larvae and egg-laying females, presumably because of an increased volatile emission (51, 69).

Volatiles from cocoon-spinning larvae induce larval aggregation, and freshly eclosed adult males appear to respond to small amounts of codlemone emanating from mature female pupae (40, 58). It is unclear whether mating disruption can interfere with short-range sexual communication shortly after adult emergence.

MECHANISMS OF MATING DISRUPTION

Behavioral Mechanisms

The main behavioral mechanisms of mating disruption have been defined as sensory fatigue, competition between natural and synthetic sources, and camouflage (13, 24, 26, 80, 90). This coarse classification does not adequately describe the behavioral modifications leading to communication disruption. Male moth behavior under mating disruption treatment depends on many factors, including the pheromone blend, dispenser application and release rate, pheromone dispersal within the crop canopy, plant volatile composition and airborne concentration, moth population density, and attributes of the target species, such as male responsiveness to pheromone. Some of these factors are modulated by diel periodicity, seasonal changes, and climate. Attempts to decipher the behavioral mechanisms are set back by difficulties in collecting field data on the behavior of moths and pheromone dispersion, and in estimating the contribution of individual factors to efficacy.

Sensory fatigue. Codling moth males are sensitive to picogram amounts of pheromone released by calling females (**Figure 1**) during a short diel calling window. Treatment with synthetic pheromone continuously exposes males to elevated pheromone concentrations and may lead to desensitization of the olfactory apparatus through peripheral antennal adaptation, central nervous habituation, or both.

Pre-exposure to pheromone at concentrations of a milligram per cubic meter of air reduces male codling moth responsiveness (57, 96). Average aerial concentrations in pheromone-treated orchards are about six orders of magnitude lower than the concentrations required to induce peripheral adaptation (68), but attraction of males close to dispensers may sufficiently increase pheromone exposure to evoke adaptation or habituation (**Figure 1**) (27, 90, 98, 118). Wind tunnel experiments confirm that brief encounters with pheromone dispensers are sufficient to raise the response threshold of codling moth males (97). This effect is dose dependent, because codling moth males remain capable of orienting to higher amounts of pheromone. For example, high-dosage pheromone lures are used for monitoring males in mating disruption orchards that are otherwise unattractive (97, 110).

Exposure of cotton leafworm males (*Spodoptera littoralis*) to low concentrations of pheromone results in behavioral sensitization and this effect depends on the quality of the pheromone blend (2). The three-component blend of codlemone, 12OH, and 14OH may accordingly have a stronger effect on the male olfactory system than codlemone alone. The saturated alcohols enhance upwind flights and close-range behavior at high pheromone doses (6, 15). Plant volatiles may further contribute to the sensitization effect of pheromone exposure (99, 126).

Competitive attraction. Codling moths fly upwind toward disruption dispensers with a wide range of release rates (12, 46, 98, 118). Thus, competitive attraction contributes to orientation disruption, as in other species (27, 80, 90). If competitive attraction is crucial, densities of both moths and pheromone dispensers should be limiting factors of effective disruption. This is indeed the case (31, 46, 84, 111).

Camouflage. Another proposed mechanism suggests that the female plume is camouflaged by a background of synthetic pheromone. This concept is probably not relevant for codling moth. The pheromone permeation produced by reservoir dispensers is not uniform (68, 81) and males are still capable of flying upwind to pheromone sources (12, 46, 98, 118). A completely homogenous pheromone permeation would be difficult to achieve in orchards, irrespective of dispenser type. Moreover, male moths efficiently detect superimposed pheromone plumes against a uniform background (90, 92).

Upwind orientation flight. Mating disruption treatments, for example, with reservoir dispensers (**Figure 1**), disperse sufficient amounts of pheromone to evoke male upwind flight behavior throughout the orchard (118). The pheromone cloud has a turbulent structure, as shown by field-EAG measurements, which is crucial for maintaining the orientation flight response (68, 81, 82). Males fly upwind along tree rows, in the upper part of the tree canopy, and thus encounter plumes from trap lures, dispensers, or calling females. At least some of the males are still capable of responding to these pheromone sources, despite the pheromone treatment (57, 97, 118).

Males flying along the tree canopy are often seen to land on dark spots on leaves, confirming the role of visual cues in close range mate-finding behavior (30). Males may also smell calling females against the synthetic pheromone background because females release additional pheromone compounds (43, 119). The success of pheromone-enhanced search activity is also a function of population density. At a lower density, males are more likely to fly past females and along plumes of synthetic pheromone. Flight activity in the upper third of the tree canopy is typical for codling moth (87, 54, 12, 114) and may in part be due to microclimatic factors. After sunset, temperature drops more slowly above the canopy. Slightly higher wind speeds enhance turbulent diffusion and make it difficult to maintain high pheromone concentrations in the upper tree canopy (118).

The pheromone signal acts as a switch to activate orientation behavior, but it does not contain structural elements or a concentration gradient to reveal information about the location of the source. The males will continue to fly upwind even without source encounters (82, 90). Competitive attraction and camouflage can therefore be viewed as semantic extremes of a continuum.

Antagonists. Blends of sex pheromone and attraction antagonists can be effective mating disruptants (18), and both codlemone geometric isomers and codlemone acetate have been evaluated in codling moth (76, 118). However, orchard permeation with antagonist blends does not disrupt male upwind flight behavior along the tree canopy. This may be due to the males' inability to discriminate between contrasting pheromone and pheromone/antagonist signals while in flight (33, 118).

Population biology. Recent field studies suggest that codling moth control by mating disruption may be due largely to the effects of delayed female mating or a reduction in multiple matings, given that most females trapped with pear ester lures in pheromone-treated orchards have already been mated (60, 66, 109). This finding illustrates that a detailed demographic analysis of mating disruption is still lacking. Intuitively, delayed mating would sufficiently reduce populations only at low densities, when larval or adult mortality become relatively more important. The beneficial effect of mating disruption on natural enemy populations, due to reduced insecticide input, probably is a contributing factor (47).

The study by Knight (60) emphasizes that the mechanisms of mating disruption are not solely composed of effects on male orientation behavior. The detrimental effects of delayed mating on female reproductive output likely contribute to population control in cases in which mate-finding is not completely prevented.

Climatic factors. The effect of pheromone treatments is likely enhanced by suboptimal climatic conditions. A sharp temperature threshold has been observed for the onset and cessation of male mating flights. The time window for male response to pheromone is shorter on cold nights because of an earlier drop in temperature (118). Elevated temperatures may account for difficulties in achieving satisfactory control during the second seasonal flight period in the middle of summer (49, 89, 103).

Dispenser Technology

Practical applications of the mating disruption technique require efficient and economic dispenser materials that release sufficient amounts of pheromone over an extended period.

Reservoir dispensers. Rubber tubes impregnated with codlemone were successfully used during pioneering field trials in France and Switzerland (8, 31, 75). Hand-applied reservoir dispensers with an application rate of 500 to 1000 units per ha are still widely used.

A polyethylene rope dispenser with rather constant season-long release rates, containing a three-component blend of codlemone, 12OH, and 14OH as active ingredients, has become a standard. The main improvements since its first registration in the United States in 1991 are increased dispenser loading rate and stabilization of the active ingredient against isomerization and photochemical degradation (20, 59, 79, 83). A disadvantage is that pheromone released during daytime is lost, as buildup of airborne pheromone in orchard air is prevented by turbulent diffusion, adsorption on leaves, and photodegradation. In addition, pheromone release drops under lower evening temperatures at the onset of codling moth diel flight. Photosensitive polymers could provide a solution to this problem. Application cost is another drawback and necessitates a single application early in the season.

Given that reservoir dispensers exploit competitive attraction and sensory fatigue, a straightforward solution for improving efficacy is increasing dispenser density. For example, with a more economical application method, such as a mechanized applicator, the cost-effectiveness and efficacy of mating disruption might be improved. Furthermore, dispenser formulations may be improved by adding more pheromone compounds.

Female-equivalent dispensers. Excellent communication disruption was achieved in a pilot study in 1976 that used hollow fiber dispensers of lower loading and higher application rate, compared with rope dispensers (25). Commercial and experimental formulations are available, but dispenser life and mechanical application techniques need to be improved (46).

Sprayable microcapsules. Substantial effort has been invested in sprayable formulations. Main drawbacks are short longevity, loss by rain wash-off, photodegradation, and prohibitive cost. Season-long control of codling moth would require several applications of large amounts of codlemone. Low-volume sprays, leading to point sources of clumped microcapsules, produce better results than a homogenous distribution (62, 95).

Puffers. Spray machines are programmed to atomize pheromone from pressurized canisters at regular intervals during the diel flight period of codling moth. These puffers are spaced at 10- to 20-m intervals around the orchard perimeter. A release rate of 250 mg/ha/day provides instant aerial concentrations of up to 60 ng/m^3 (94). In comparison, rope dispensers are applied at a rate of approximately 100 g/ha/season and aerial concentrations do not exceed 1 ng/m^3 (68). However, aerial concentrations alone may not be a sufficient criterion for successful communication disruption. Both sprayable microcapsules and puffers are expected to be less suitable than reservoir dispensers, because it is difficult to camouflage female plumes in orchard environments.

Active ingredient. Significant progress has been made toward cost-efficient large-scale synthesis of the active ingredient (123). At least 25 tons of codlemone were produced in 2006 (**Table 1**). Adding synergists to codlemone may intensify the habituation effect of mating disruption treatments by increasing male attraction and by prolonging close-range behavior near dispensers. This issue has not been sufficiently investigated because methods to monitor or predict the effect of formulations are not available. Even the role of 12OH and 14OH is still unclear, and further compounds should be tested. Leafroller moths are important secondary pests in all apple-growing areas, and combined dispenser formulations contain (*Z*)-11-tetradecenyl acetate and/or (*Z*)-9-tetradecenyl acetate in addition to codlemone (56, 108).

Registration. The U.S. Environmental Protection Agency (EPA) has granted pheromones and other semiochemicals regulatory relief, motivated by a low-risk potential, low rate of application, low-exposure formulations, and high volatility minimizing the risk of residues (105). Straight-chain aliphatic (9–18 carbons) alcohols, aldehydes, and acetates with up to three double bonds are exempt from the requirement of tolerance at application rates below 365 g active ingredient/ha/year and do not require an experimental use permit for testing on areas of 100 ha or less. Other countries have adopted similar policies. Codlemone is now registered in 21 countries.

IMPLEMENTATION OF MATING DISRUPTION

Commercial codling moth mating disruption has greatly expanded over the past 15 years. Despite considerable research efforts during this time, insights into the behavioral mechanisms have not made a decisive contribution to the design of the industry's standard commercial product. Of the 160,000 ha currently treated with codling moth mating disruption (**Table 1**), 80% are treated with the pheromone formulation registered in 1991, demonstrating the significance of practical implementation work.

Limiting Factors

Population density is a most important restriction. If population density exceeds 1000 overwintering larvae per hectare, codling moth mating disruption is difficult to achieve owing to low damage tolerance. At higher

CAMP: Codling Moth Areawide Management Program

densities, mating disruption must be supplemented with applications of insecticide or granulovirus in early season (11, 31, 35, 48, 53, 61, 75, 89, 103).

Cost-competitiveness is a function of codling moth population density. Combining a half-rate pheromone dispenser application with a reduced insecticide program is efficient and economical, especially at high populations, when otherwise multiple insecticide sprays would be needed. The benefits of combining pheromones and insecticides include worker protection, reduced risk for outbreaks of secondary pests, and insecticide resistance management (49, 103). Recently, the economics of mating disruption has improved, as the less expensive organophosphate and carbamate insecticides have been replaced by more expensive and selective reduced-risk insecticides such as the neonicotinoids and insect growth regulators.

Orchards should be isolated to avoid immigration of mated females. Orchard borders are also vulnerable with respect to depletion of pheromone concentrations by wind (68). The best opportunity for codling moth control is in orchards where topographical conditions allow for uniform pheromone permeation: flat orchards with small trees, square rather than elongated in shape, and at least 1 ha large (31, 75, 103).

Codlemone is species specific and nontoxic. Monitoring tools therefore are vital for mating disruption implementation (31, 48, 103). Failure to capture moths in pheromone traps alone is an unreliable indicator, and the development of a kairomone attractant for female moths has been an important improvement (64–66). It is also advisable to accompany mating disruption applications with fruit infestation counts. In addition to codling moth, a large complex of other fruit pests requires continuous monitoring and remedial treatments. Multiple-species monitoring and the risk of fruit damage makes the pheromone treatment technically complex and costly (103, 116).

Area-Wide Programs

The breakthrough for codling moth mating disruption was the Codling Moth Areawide Management Program (CAMP) organized by the USDA and universities in California, Oregon, and Washington in 1993. The goal was to reduce broad-spectrum insecticide sprays and to enhance natural enemies for control of secondary pests by introducing mating disruption against codling moth. The Worker Protection Standard (1992) and Food Quality Protection Act (1996), which served to limit insecticide use, became an extra stimulus for the rapidly expanding project. The success of the area-wide program helped to expand the use of codling moth mating disruption. By 2006, mating disruption covered 48,000 ha or 66% of the apple-growing area in Washington State (22, 23, 48, 49, 102, 103). Area-wide programs in states such as Michigan and California, in Italy's South Tyrol, and in the Alto Valle of Argentine have been similarly successful (103, 112).

Because of its technical complexity, adoption of mating disruption relies on education. CAMP succeeded by bringing together growers, advisors, pheromone distributors, and industries. This joint effort mitigated the shortcomings and lifted the status of codling moth mating disruption to facilitate adoption by growers (22, 48, 103).

Treatment of large contiguous areas has the technical advantage of improving pheromone permeation and concentration, thus minimizing damage along the vulnerable orchard borders. The overall reduction of sprays enhances the impact of natural enemies (47). Future challenges include developing biological methods against other orchard insect pests and promoting ecological homeostasis within orchards through suitable ground covers and surrounding habitats.

Motivation

Drawbacks to insecticide use were a key incentive for the development of codling moth mating disruption during the 1990s (22, 47, 48, 112). The severely neurotoxic organophosphate azinphos-methyl was historically the most efficient insecticide against codling moth, but an increasing incidence of physiological resistance due to repeated and persistent use has mandated alternative control options (39). Multiple seasonal sprays of azinphos-methyl also induce outbreaks of phytophagous mites (101), which are difficult and costly to control. Replacing organophosphates with codling moth mating disruption makes miticide sprays unnecessary and thus offsets the cost of the mating disruption treatment (112).

Where codling moth is controlled by mating disruption, more selective and less toxic insecticides or biological tools can be used efficiently against other orchard insect pests. The result is more reliable insect control, a lower impact on the beneficial arthropod fauna, and a measurable reduction of insecticide use (37, 48, 103, 112) (**Figure 2**).

Neonicotinoid insecticides and spinosad (104, 106) have been proposed as possible alternatives to mating disruption. They are slightly less effective on codling moth than azinphos-methyl, but they are nonetheless harmful to beneficial arthropods (16, 21). Cross-resistance to these new chemicals also remains a problem (32, 39, 91). Currently, neither insecticides nor biological control techniques are available to replace mating disruption (1, 7, 16, 21, 32), which has become a cornerstone in orchard management programs.

Results from the Howard Flat site illustrate the success of CAMP by obtaining a high level of crop protection and advances in health and environmental issues (22) (**Figure 2**). Results from several growing areas confirm that mating disruption, as opposed to

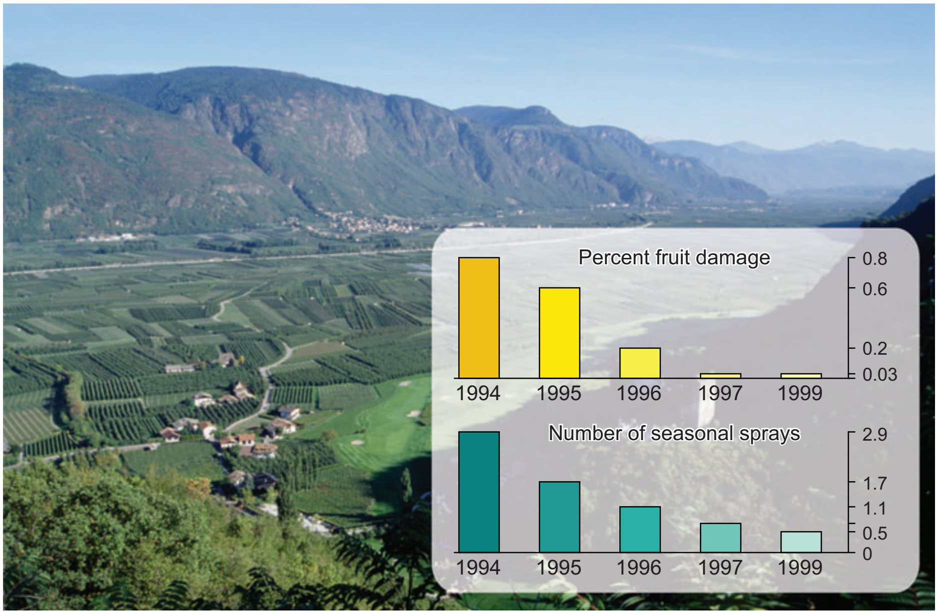

Figure 2

Codling moth damage (percent fruit damage) and number of seasonal sprays in mating disruption apple orchards at the Howard Flat CAMP site, 1994 to 1999 (22). Treatment of a contiguous orchard area improves pheromone permeation and concentration and prevents immigration of mated females from untreated orchards. The reduction of sprays over an entire fruit-growing area has a significant environmental impact. Photo of the Etschtal areawide site by Michael Unterthurner.

insecticides, achieves the best long-term reduction of populations (22, 103, 112, 118). An area-wide reduction in insecticide use is another remarkable achievement. Insecticide poisoning of farmworkers and groundwater contamination are urgent current problems in many fruit-growing areas.

The idea of controlling insect populations through species-specific manipulation of sexual communication, without adversely affecting other organisms, has been a driving force for pheromone research. This has been achieved and technological shortcomings have been overcome through a joint effort between researchers, industry, and growers. Adoption of pheromone-based pest management has increased in the face of dwindling conventional options, increased government regulations, and improved cost-competitiveness.

Pheromone-mediated codling moth management is an impressive demonstration of how the knowledge of powerful natural signals can be brought to practical application, and how an ecologically safe technology can lead to an industrial development with measurable environmental impact, as long as people are motivated to achieve such changes (5).

Continued use of pheromone-based control of codling moth and greater worldwide adoption will depend on development of more reliable and less expensive application technologies. Desired further improvements to disruption technology for codling moth are robust effectiveness at high population densities, season-long efficacy, machine application, and compatibility with other semiochemicals for multi-species control. Other rewarding topics for future research include the interaction of pheromones with plant volatiles and the manipulation of female behavior. In addition, there is a need for more data on the behavior of moths and molecules to describe more accurately the factors leading to population control.

SUMMARY POINTS

1. Pheromone-mediated mating disruption is used to control codling moth on 160,000 ha worldwide.
2. Codling moth mating disruption enables sustainable and reliable control at low population densities. In contrast to insecticides, the effectiveness of mating disruption increases with long-term use, resulting in a substantial reduction of populations.
3. Mating disruption is not effective at high population densities, and immigration of mated females must be avoided by treating adjacent orchards. Area-wide programs of 100 or more hectares promote the effectiveness of mating disruption.
4. Pheromone dispenser technology determines the efficacy and the economics of mating disruption.
5. Sensory fatigue and competitive attraction are contributing mechanisms of codling moth communication disruption.
6. Effective monitoring of codling moth and secondary pests is essential to the successful implementation of codling moth mating disruption technology.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their constructive criticism. This work was supported by the Linnaeus Grant IC-E3.

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Annual Review of Entomology

Volume 53, 2008

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