Chapter 11
Behavior-Modifying Strategies in IPM: Theory and Practice

Cesar R. Rodriguez-Saona and Lukasz L. Stelinski

Abstract The possibilities of using strategies to manipulate insect behavior in agricultural systems have increased due to strict regulations imposed on the use of insecticides worldwide. Here we discuss the potential of semiochemicals, specifically sex pheromones and host-plant volatiles, as tools to manipulate insect behaviors in integrated pest management (IPM) programs. Sex pheromones are widely used in agriculture for monitoring abundance and distribution of insect pest populations and predicting timing of insecticide applications. They have also been used, to a lesser extent, in insect pest control. One of the most promising concepts is the deployment of synthetic sex pheromones into a crop to disrupt insect mating. Three mechanisms of mating disruption: sensory desensitization, competitive attraction, and non-competitive mechanisms, are described. In addition to mating disruption, sex pheromones can be employed in mass trapping and attract-and-kill approaches for pest control. An area of increased interest among entomologists and chemical ecologists is the use of host-plant volatiles to manipulate insect behavior. Host-plant volatiles can be a source of attractants and repellents, and can be implemented into monitoring and pest management practices. These volatiles can be used alone or in combination with other stimuli in control strategies such as mass trapping, attract-and-kill, push-pull, and disruption of host finding. Plant volatiles in most cases synergize with sex pheromones and biological control. To be adopted by farmers, strategies to modify insect behavior will need to be comparable to newer insecticides in efficacy and costs. Increased adoption will also require extensive educational programs for farmers.

Keywords Semiochemicals · Sex pheromones · Mating disruption · Host-plant volatiles · Behavioral manipulation · Crop protection

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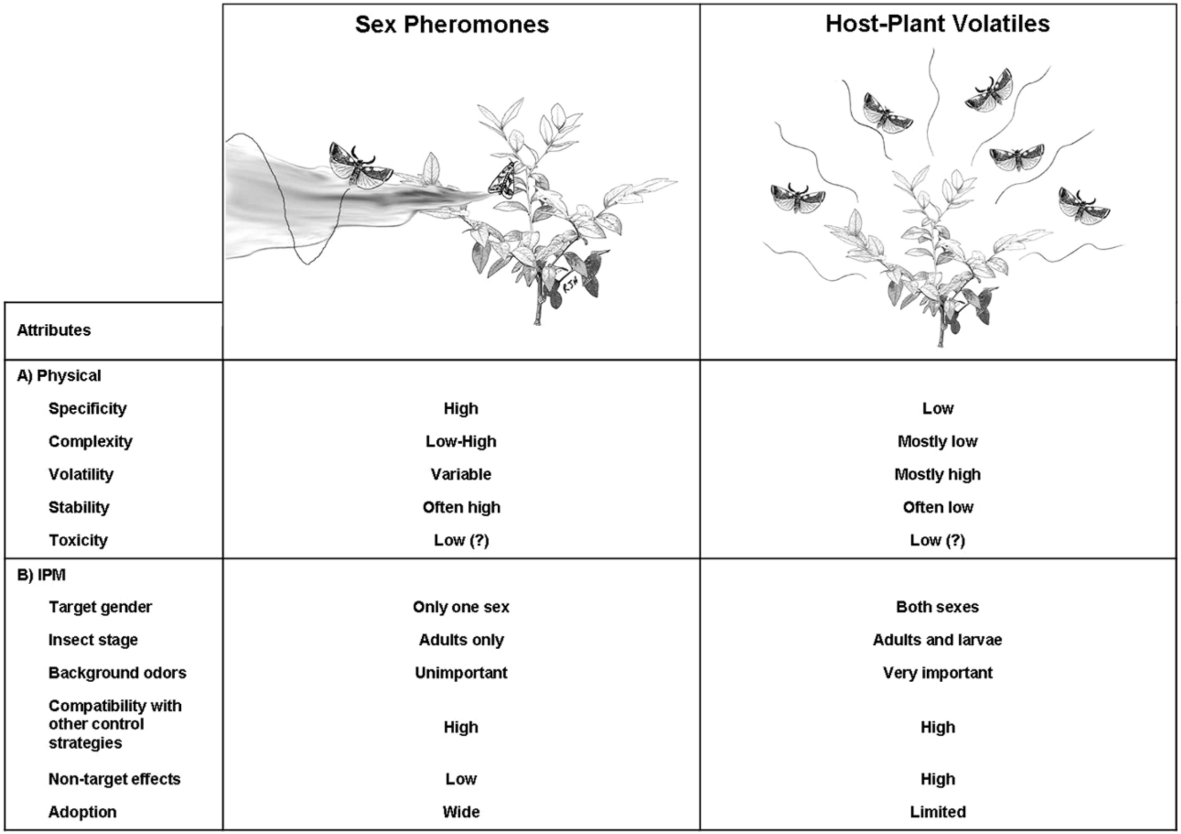
11.1 Introduction

Most control strategies against insect pests involve some sort of change to their behavior (Gould, 1991; Foster and Harris, 1997), whether it is through chemical (i.e., volatiles and non-volatile compounds, feeding deterrents), visual, or auditory signals. The concept of manipulating pest behavior for insect control has been known for centuries through the practice of trap cropping (Hokkanen, 1991). Food lures and baits treated with a poison have also been used for more than a century to control household pests (Pedigo, 1996). Historically, however, the adoption of technologies to manipulate insect behavior in agricultural systems has been slow largely due to the arrival of cheaper chemical controls with broad insecticidal activity. This situation is likely to change with the increasing public awareness of the negative effects of broad-spectrum insecticides on humans and non-target organisms. More stringent regulations have been imposed on the use of insecticides worldwide. In the United States, the Environmental Protection Agency (EPA) implemented the Food Protection Act (FQPA) in 1996 (U.S.E.P.A., 2008). Since then, several broad-spectrum insecticides have been either banned, scheduled for elimination, or their use has been restricted in several agricultural crops. These regulatory restrictions are expected to help the adoption of alternative pest management practices, including manipulation of pest behavior, and promote a transition from insecticide-based to more ecologically, integrated pest management (IPM)-based programs.

Manipulation of pest behavior is defined as “the use of stimuli that either stimulate or inhibit a behavior and thereby change its expression” (Foster and Harris, 1997). Manipulation of insect behavior involves detection of signal chemicals known as semiochemicals (Nordlund and Lewis, 1976), also referred to as infochemicals (Dicke and Sabelis, 1988). Pheromones are semiochemicals used in intraspecific communication, and can be classified according to their function, such as sexual attraction, aggregation, alarm, marking, etc. Allelochemicals are semiochemicals that facilitate interspecific communication. Allelochemicals include a greater number of chemicals than pheromones, and can be grouped into: allomones that benefit the emitter and are detrimental to the receiver; kairomones that benefit the receiver and are detrimental to the emitted; and synomones that benefit both the emitter and the receiver. Although other groups of allelochemicals have been added to this list (e.g., Dicke and Sabelis, 1988), they will not be discussed in this chapter and thus were omitted. Depending on the context, plant volatiles are allomones if they repel herbivores, kairomones if they attract herbivores, or synomones if they attract the herbivores’ natural enemies. In many instances, a single plant chemical has more than one function which may in turn limit their application for pest management, as will be discussed in this chapter.

Our main intent here is to provide a basic synopsis of our current knowledge of insect sex-attractant pheromones and host-plant volatiles (Fig. 11.1), including their chemistry, activity on insect pests and their natural enemies, applications to manipulate insect behavior in agricultural systems, and adoption. Although manipulation of insect behavior can be achieved through changes in chemical, visual, and/or auditory



Attributes	Sex Pheromones	Host-Plant Volatiles
A) Physical		
Specificity	High	Low
Complexity	Low-High	Mostly low
Volatility	Variable	Mostly high
Stability	Often high	Often low
Toxicity	Low (?)	Low (?)
B) IPM		
Target gender	Only one sex	Both sexes
Insect stage	Adults only	Adults and larvae
Background odors	Unimportant	Very important
Compatibility with other control strategies	High	High
Non-target effects	Low	High
Adoption	Wide	Limited

Fig. 11.1 Differences and similarities between sex pheromones and host-plant volatiles used for behavioral manipulation of insect pests. Graphic designed by Robert Holdcraft

stimuli, this review will focus only on the manipulation of chemical stimuli for insect pest management. Furthermore, we will only discuss volatile chemicals used by insects as long-range cues, as opposed to non-volatile compounds that only function as contact chemicals. This review will focus on examples where the chemicals that elicit a change in the insect's behavior have been isolated, identified, and used for pest management purposes. First, we will discuss general aspects of insect sex pheromones focusing mainly on mating disruption. We will discuss the proposed mechanisms underlying mating disruption, and provide two case studies in apples and blueberries from our own research. The second part of this review will focus on the responses of insects to host-plant volatiles and their potential for pest management. The final section provides an overview of farmer attitudes towards these technologies and the needs for increasing their adoption.

Although insect pheromones have been, and most likely will continue to be, the basis of insect behavior manipulation, the extent to which plant volatiles influence host-plant location in insects and their potential use in crop protection has become increasingly apparent in light of recent findings. This is most evident from the increasing numbers of studies on the chemistry, activity, and application of host-plant volatiles over the last five years (Table 11.1).

Table 11.1 Numbers of publications in selected journals that investigated sex phermones or plant volatiles as tools for insect control[1]

	Sex Phermones[2]		Plant Volatiles[3]	
	1994–2002	2003–2008	1994–2002	2003–2008
Journal of Economic Entomology	88 (9.8)	83 (16.6)	21 (2.3)	16 (3.20)
Environmental Entomology	57 (6.3)	26 (5.2)	25 (2.8)	23 (4.5)
Journal of Chemical Ecology	100 (11.1)	33 (6.6)	68 (7.6)	27 (5.4)
Chemoecology[4]	3 (3.0)	4 (0.8)	2 (2.0)	5 (1.0)
Entomologia Experimentalis et Applicata	45 (5.0)	25 (5.0)	26 (2.8)	23 (4.6)
Totals	122 (13.5)	171 (34.2)	40 (5.3)	94 (18.8)

[1] Based on records from Web of Science. In parenthesis are average numbers of records per year
[2] Keywords = Sex pheromones AND insect AND pest AND management
[3] Keywords = Plant volatiles AND insect AND pest AND management
[4] Records starting in 2002

11.2 Sex Pheromones and IPM

Insect sex-attractant pheromones are chemical signals emitted into air by one of the sexes and guide the opposite sex to the source of the resultant aerial plume for mating. In most insect species, especially in moth pests, it is the females that emit the sex pheromone to attract males. In many cases, stationary females can call responsive males from distances of 40 m or more, depending upon the degree to which vegetation breaks up and dilutes the pheromone plume. When in close proximity, both sexes may emit and receive short-range signals (chemical, visual, and acoustical) that reciprocally elicit the courtship sequence leading to copulation. One successful mating of a female moth, for example, can yield 100 or more fertilized eggs. The first chemical identifications and syntheses of sex-attractant pheromones of moths were published over 40 years ago (Butenandt et al., 1959; Berger, 1966). Realization that normal long-distance mate finding is elicited by minute quantities of sex pheromones gave rise to several decades of applied research toward development of insect control tactics with synthetic pheromones. One promising idea was that deployment of synthetic pheromone into the crop could confuse males encountering it such that they fail to find authentic calling females (Wright, 1965). The desired end-result is reduction in fertilized eggs and resultant damaging larvae because females failed to mate. Today, mating disruption, as the technique is commonly referred to, is practiced worldwide for control of moth pests in fruits, vegetables, and forestry (Cardé, 2007). Mating disruption reduces the need for chemical insecticide applications, and in some cases it is practiced as a stand-alone tactic. In addition, the use of pheromones for pest monitoring and as a tool for accurately timing insecticide sprays has become a cornerstone feature of many prominent IPM programs. Finally, other applications of pheromone-based technologies for direct pest control such as mass trapping and attract-and-kill have shown promise in specific instances.

11.2.1 Applications

11.2.1.1 Monitoring

The identification and synthesis of thousands of insect sex pheromones (El-Sayed, 2007) has allowed widespread and reliable use of synthetic attractants for pest monitoring. These synthetic copies of insect attractants are formulated in controlled-release devices and deployed in association with a wide variety of trapping surfaces (Cardé and Elkinton, 1984; Wall, 1989; Jones, 1998). Traps are often characterized by a sticky surface or liquid mote for capturing attracted insects. Synthetic semiochemicals attached to such traps are typically released from rubber septa, sleeves, or reservoirs made of polyethylene or polyvinyl chloride. Traps baited with pheromones or plant-derived kairomones are simple and inexpensive tools for detecting pest presence. Semiochemical-baited traps are effective means of monitoring for introductions of exotic pests, maintaining quarantine guidelines such as the “fruit fly free zone” in Florida citrus production (Simpson, 1993), and for determining the effectiveness of pest management techniques such as mating disruption. Furthermore, degree-day models have been developed using synthetic attractants; these models effectively predict insect egg hatch allowing for targeted applications of insecticides rather than prophylactic calendar-based sprays (Welch et al., 1981; Riedl et al., 1986; Knight and Croft, 1991). In certain cases, good correlations between adult insect captures in monitoring traps and larval damage has led to the development of predictive models for effective timing of management sprays (Van Steenwyk et al., 1983; McBrien et al., 1994; Bradley et al., 1998; Morewood et al., 2000). For example, severe outbreaks of the eastern spruce budworm, *Choristoneura fumiferana* (Clemens), can be predicted years in advance based on annual trapping data of adult moths (Sanders, 1988). One example where this has been effectively implemented is the apple maggot fly, *Rhagoletis pomonella* (Walsh), in North America (Stanley et al., 1987; Agnello et al., 1990). Using sticky traps baited with a potent apple maggot kairomone, an action threshold of 8 flies per trap was developed, which reduced annual sprays by 70% while maintaining acceptable levels of control. Similarly, treatment thresholds for tortricid pest of tree fruit have been developed using pheromone traps as the predictive tool (Riedl et al., 1986; Wall, 1989).

11.2.1.2 Mass Trapping

Mass trapping is the application of semiochemical-baited traps for capturing a sufficient proportion of a pest population prior to mating, oviposition or feeding so as to prevent crop damage. The utility of mass trapping as a practical application in IPM programs has been very limited given that the technique is density dependent (Knipling, 1979). Mass trapping is only viable at low pest densities, since male attractant traps are competing directly with females. In those cases where only males are targeted, they must be removed from the population prior to mating to impact population growth. Given that most male insects mate more than once, nearly 99% male removal is required to prevent sufficient female mating for effective crop protection (Roelofs et al., 1970). The effectiveness of the technique is likely greater in those rare instances in which a mating system is characterized by a male-produced sex attractant. Under such circumstances, the reproductive females would be trapped out and the impact on population growth would be much larger with fewer traps than in the typical case where a mating system is characterized by a female-produced sex attractant. Other drawbacks exist including the need for frequent trap maintenance given that traps can quickly become saturated with insects. The efficacy of mass trapping is also dependent on the development of highly effective lure and trap combinations that can attract insect from large distances and efficiently capture the majority of attracted individuals. Ultimately, the cost of deploying a sufficient number of attractive traps to effectively compete with typically high insect population densities renders the technique impractical. In situations where the tolerance for crop damage is relatively high or the pest population extremely low, the technique may prove effective (Zhang et al., 2002). However, attempts to control insects such as the Japanese beetle, which typically occur at high population densities, have generally failed (Klein, 1981; Gordon, and Potter, 1985, 1986).

One of the most prominent examples of success with mass trapping is with certain species of forest bark beetles, given their use of aggregation pheromones for mass colonization of host resources. Trapping out the conifer bark beetle, *Ips typographus* (L.), with a synthetic aggregation pheromone has proven highly effective in reducing populations and preventing damage (Dimitri et al., 1992). Also, mass trapping has proven highly effective for controlling ambrosia beetles in timber processing facilities (Borden, 1990). Furthermore, combining the use of both anti-aggregation and aggregation pheromones to manipulate bark beetle behavior has proven effective in mass trapping protocols (Lingren and Borden, 1993; Borden, 1997).

11.2.1.3 Attract-and-Kill

This approach is also known as “attract-annihilate” (Foster and Harris, 1997). In principal, attract-and-kill and mass trapping are variations of the same tactic and like mass trapping, the efficacy of attract-and-kill systems is highly dependent on pest density. The major difference between the two tactics is that in attract-and-kill a semiochemical-based lure is combined with a toxic substrate rather than a sticky surface or liquid receptacle. This difference can overcome the logistic constraint of trap saturation reducing the cost of trap maintenance.

Tephritid fruit fly pests have been the target of several attempts to develop effective attract-and-kill tactics. For example, protein or pheromone (1,7 dioxaspiro)-based bait sprays laced with either malathion or dimethoate have proven highly effective in controlling the olive fly, *Bactrocera oleae* (Gmelin) (Howse et al., 1998). In addition, biodegradable or wooden spheres with a low dose of imidacloprid have shown promise for control of *R. pomonella* in apple and *R. mendax* in blueberry (Hu et al., 1998; Liburd et al., 1999; Ayyappath et al., 2000; Prokopy et al., 2000; Stelinski et al., 2001, Stelinski and Liburd, 2001). Such devices have been termed “pesticide-treated spheres” and rely on both visual and olfactory attractants to lure the target pest as well as a surface-borne feeding stimulant that causes the insect to ingest the toxicant present on the surface of the device. Deploying such devices on perimeter trees or bushes of commercial apple or blueberry blocks, respectively, resulted in control of apple maggot (Prokopy et al., 2000) and blueberry maggot flies (Stelinski and Liburd, 2001) equivalent to that achieved with conventional insecticides.

11.2.1.4 Mating Disruption

One of the most successful applications of insect sex pheromones for direct pest control has been mating disruption. Table 11.2 provides a list of successful cases of mating disruption for insect pest management. Mating disruption is a biorational method of controlling insect pests by saturating the environment with synthetic copies of natural insect pheromones to interfere with normal mating behavior. Currently, hand-applied, Isomate-style dispensers (Fig. 11.2A) deployed at ca. 1–4 per tree are the dominant method of dispensing pheromone for mating disruption of moth pests in orchards (Nagata, 1989; Agnello et al., 1996; Knight et al., 1998; Knight and Turner, 1999). The exposure concentration of moths treated with this technology can vary widely. Male moths may be exposed: to a ‘cloud’ of pheromone resulting from a coalescence of plumes emanating from many dispensers; a localized plume down-wind of a single dispenser; or, at the highest level of exposure, a moth could directly contact a dispenser following attraction. Use of low-density, high-release dispensers like puffers (Shorey and Gerber, 1996) or Microsprayers

Table 11.2 Successful cases of mating disruption in IPM

Insect pest	Crop	Sex pheromone	Reference
Codling Moth (*Cydia pomonella*)	Pome fruit	(*E,E*)-8, 10-dodecadien-1-ol (major component)	Charmillot (1990) Brunner et al. (2002) Knight (2004) Stelinski et al. (2005d)
Oriental Fruit Moth (*Grapholita molesta*)	Pome fruit Stone fruit	(*Z*)-8-dodecenyl acetate and (*E*)-8-dodecenyl acetate (95:5 ratio), and (Z)-8-dodecen-1-ol	Charlton and Cardé (1981) Rice and Kirsch (1990) Il'lchev et al. (2006) Stelinski et al. (2007c)
Leafrollers (various species)	Pome fruit	Δ11-tetradecenyl acetate Δ11-tetradecenyl alcohol (common components)	Pfeiffer et al. (1993) Stelinski et al. (2007b)
Grapevine Moth (*Lobesia botrana*)	Grape	(*E,Z*)-7,9-dodecadienyl acetate	Schmitz et al. (1997)
		(*E,Z*)-7,9,-dodecadienol (*Z*)-9- dodecanyl acetate	Torres-Villa et al. (2002)
Pink Bollworm (*Pectinophora gossypiella*)	Cotton	(*Z,Z*)- and (*Z,E*)-7,11-hexadecadienyl acetate (1:1 ratio)	Doane et al. (1983) Flint and Merkle (1984) Cardé et al. (1998)
Tomato Pinworm (*Kaiferia lycopersicella*)	Tomoto	(*E*)-4-tridecenyl acetate	Trumble and Alvarado-Rodriguez (1993)

(Isaacs et al., 1999) likely increases the probability of exposure to extraordinarily high concentrations of pheromone. Pheromone solution sprayed from these dispensers adheres onto foliage and droplets of pure pheromone accumulate over time on the source tree. This may result in large and highly concentrated plumes that should waft great distances downwind of the source trees. Although the average airborne concentration of pheromone achieved in orchards treated with pheromone dispensers is unlikely to desensitize males flying or resting meters away from the source of emanating pheromone, anemotactic orientation of attracted male moths to within close proximity of dispensers likely does induce habituation (Stelinski et al., 2006a). Moths may be capable of making these close (within 1 m) approaches to high-dosage dispensers by orienting along the edge of the pheromone plume, modulating their exposure dosage (Kennedy et al., 1981; Stelinski et al., 2005b). Thus, the combination of initial orientation by tortricid male moths along plumes of synthetic pheromone followed by habituation due to over-exposure, likely explains disruption by Isomate dispensers and related technologies. This potential explanation for mating disruption of moths, in general, was proposed almost a decade ago (Cardé et al., 1998), and current evidence is consistent with this hypothesis.

Pheromone baited traps are often used to monitor the effectiveness of a mating disruption treatment (Fig. 11.2B). Acting as a female-proxy, if male catch in such traps is reduced by the mating disruption treatment, it is inferred that the

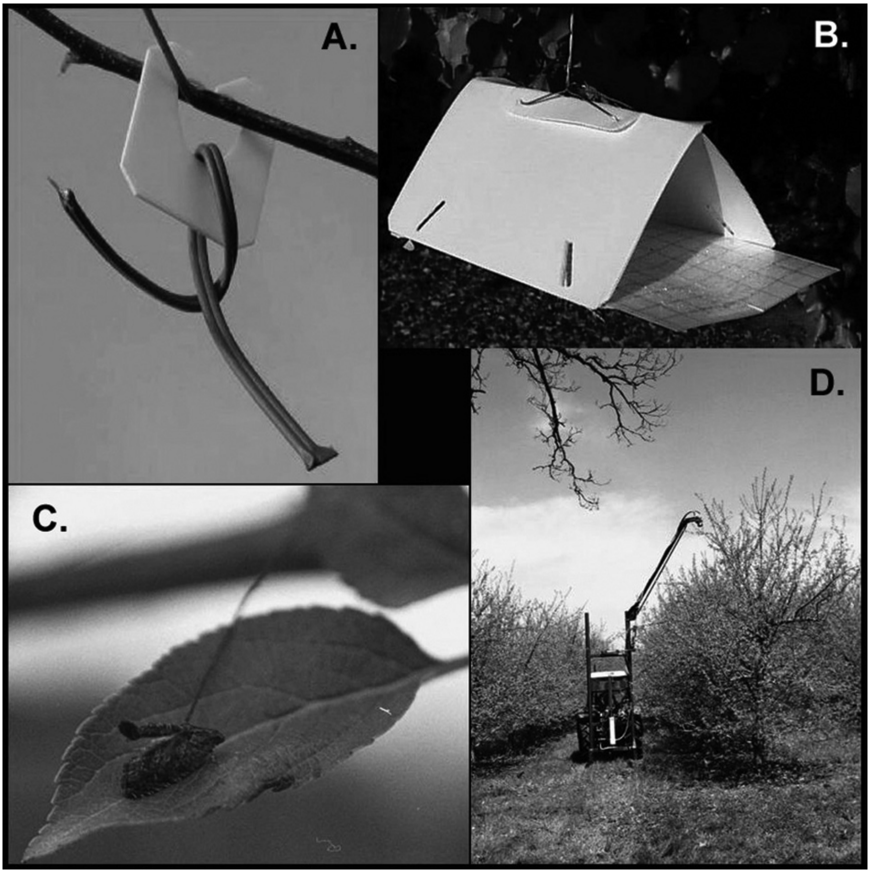


Fig. 11.2 Isomate (Shin-Etsu Chemical Co. Ltd.) polyethylene-tube dispenser of pheromone; this is the most commonly used dispenser type for releasing tortricid moth pheromones in tree fruit; depending on moth species and formulation type, each dispenser is typically loaded with 80–200 mg of pheromone and the treatment is deployed at 500–1000 units per hectare (**A**). Plastic delta trap with removable sticky insert card used for monitoring Lepidoptera with pheromone or kairomone lures placed inside (**B**). Tethered virgin female oriental fruit moth (*Grapholita molesta*) used to assess the effectiveness of mating disruption treatments; females are deployed for 24–48 h periods in pheromone treated and companion untreated control blocks; subsequently, females are harvested and dissected to determine mating status and thus effectiveness of the pheromone disruption treatment (**C**). Custom mechanized applicator (Proptec) for deployment of female-equivalent point source dispensers of pheromone (**D**). Photo Credit for A and B: Peter McGhee, Michigan State University

males' capability of finding authentic females was also impeded. A good correlation between disruption of male capture in traps, commonly referred to as "trap shut-down", and reduction of mating of tethered virgin females (Fig. 11.2C) has been observed (Stelinski et al., 2007a). However, there have been recorded cases in which a high level of trap shut-down due to the pheromone treatment have not correlated with adequate crop protection (Ridgeway et al., 1990; Rice and

Kirsch, 1990; Atanassov et al., 2002) or suppression of mating of females (Suckling and Shaw, 1992). In order to monitor for the presence of male moths under mating disruption, higher dosage lures have been developed and shown to be effective in catching moths in disrupted crops, particularly for *C. pomonella* (Charmillot, 1990; Barrett, 1995).

Mechanisms

Several hypotheses have been proposed to explain how sexual communication of insects is disrupted by deploying formulations of synthetic pheromones to prevent mating. These "mechanisms of disruption" have been formally defined in reviews by Bartell (1982) and Cardé (1990). A recent series of articles re-analyzed these mechanisms (Miller et al., 2006a,b) using mathematical models to "deconstruct the results of mating disruption trials with the goal of determining which possible mechanisms of mating disruption were operative" (Millar, 2006). Of these hypotheses, perhaps the most commonly cited mechanisms are: false-plume following, camouflage, desensitization, and sensory imbalance. False-plume following, also called competitive attraction, is the decrease in visitation rate of calling females by available males due to preoccupation with false plumes sent out by competing synthetic pheromone sources. For camouflage, it is believed that the boundaries of a calling female's plume are obscured by a background concentration of synthetic pheromone; this mechanism assumes that the male's sensitivity to pheromone is unaffected by continual exposure to high concentrations of background pheromone. Desensitization is defined as decreased sensitivity to pheromone due to continuous exposure to high background concentrations of pheromone. This mechanism is comprised of two possible sensory changes: (1) adaptation is defined as decreased sensitivity of the peripheral nervous system, while (2) habituation is defined as decreased sensitivity of the central nervous system. Finally, for sensory imbalance, it is believed that the natural pheromone component ratio released by females and required by males for normal orientation is adulterated by dispensing large amounts of one or more synthetic components of the pheromone into the atmosphere. Elevating the background concentration with a partial blend of synthetic pheromone component(s) may alter this required balanced ratio of sensory input perceived by males and thus disrupt the oriented response.

Sensory Desensitization

Investigations of the mechanisms of mating disruption were initiated over three decades ago. Attempts have been made, both in laboratory and in the field, to determine the dosage of pheromone required for disrupting normal behavioral responses and mating. In early laboratory studies, moths were caged in static or moving air with dosages of pheromone known to attract males to sticky traps in the field. Caging males and females in static-air 1.2 L containers with 1.0 mg of (*E*,*E*)-8,10-dodecadien-1-ol (codlemone) resulted in a 65% reduction of mating for the codling moth, *Cydia pomonella* (L.) (Fluri et al., 1974). Exposing caged males and females to air moving over 1 or 3 rubber septa loaded with 1.0 mg of codlemone resulted in a maximum of only 38% mating reduction (Charmillot et al., 1976). These initial studies with codling moth established that high-dosage exposure to pheromone in small cages reduced but did not eliminate mating. Pioneering laboratory studies with other tortricid species produced similar results in that exposure of males to high dosages of pheromone reduced subsequent behavioral responses for prolonged intervals (Bartell and Roelofs, 1973; Bartell and Lawrence, 1976; Bartell, 1977a,b). Although these early laboratory investigations showed that pheromone exposure affects mating behavior, they did not definitively establish the operative mechanism(s) (desensitization versus camouflage, for example) or the airborne concentration of pheromone mediating the effects.

A recent investigation of codling moth disruption quantified the airborne concentration of codlemone required for both adapting male antennal sensitivity and reducing subsequent behavioral response (Judd et al., 2005). Exposure to ca. 35 μg of codlemone / L of air in static-air chambers for 10–30 min reduced electroantennogram (EAG) responses and nearly eliminated subsequent male orientation in a flight tunnel. The effect was reversible and behavioral responses were subnormal for a much longer interval (ca. 4 h) than antennal sensitivity (ca. 1 h). This result suggested that habituation rather than adaptation was the more important and longer-lasting component of desensitization mediating disruption following high-dosage exposure to pheromone in the codling moth. Stelinski et al. (2005a) confirmed that the duration of peripheral adaptation in male codling moth following prolonged exposure at μg/L dosages of airborne pheromone lasts ca. 1 h. The duration of peripheral adaptation in codling moth males is substantially longer than that recorded for several other tortricids [*Choristoneura rosaceana* (Harris), *Argyrotaenia velutinana* (Walker), *Grapholita molesta* (Busck), and *Pandemis pyrusana* (Kearfott)] after exposure to their pheromone components at the same dosages; these durations of reduced antennal sensitivity range between < 1 min and ca. 15 min (Stelinski et al., 2003, 2005a). Regarding the extraordinary duration of adaptation in codling moth males, Judd et al. (2005) postulated that the codlemone diene alcohol might adsorb into the insect's waxy cuticle to a greater degree than the acetate and aldehyde pheromones of the other above-mentioned tortricids in which antennal adaptation has been investigated.

Despite the presence of a 60–75 min long duration of peripheral adaptation in male codling moth following exposure to pheromone, Stelinski et al. (2005a) questioned its potential importance as a contributor to mating disruption. Caging male codling moths for 30–34 h in an orchard treated with 1,000 Isomate C dispensers/ha did not impact the males' capability of subsequently orienting to pheromone sources in a flight tunnel (Judd et al., 2005). Thus, male sensitivity to pheromone was not affected under the standard Isomate dispenser pheromone treatment, which is known to disrupt male orientation to traps and virgin females and reduce crop damage (Gut et al., 2004; Epstein et al., 2006). The findings of Judd et al. (2005) for codling moth were similar to those reported by Schmitz et al. (1997) and Rumbo and Vickers (1997) for the European grape moth, *Lobesia botrana* (Denis and Schiffermüller) and the oriental fruit moth, *G. molesta*, respectively. For *L. botrana*, males were captured in attractive sticky traps in the field directly after 8 h of exposure in vineyards treated with polyethylene-tube dispensers (1 dispenser/5 m^2; each dispenser contained 500 mg of *E*7,*Z*9-dodecadienyl acetate; Schmitz et al., 1997). Reduction in male moth response to traps in the field occurred only after males were exposed in the laboratory at an airborne pheromone concentration of 4 μg/L of air. For *G. molesta*, reduction of male captures in attractive sticky traps occurred only after one hr of laboratory exposure to pheromone at 65 $\mu g/m^3$ (3,200 female equivalents) (Rumbo and Vickers, 1997). Collectively, current data suggest that desensitization of tortricid moth species is not induced after field exposures at rates of synthetic pheromone dispensers per area of crop known to result in effective disruption.

In addition, studies quantifying the airborne concentrations of pheromone achieved in the field by mating disruption dispensers suggest that laboratory experiments investigating desensitization have exposed moths to dosages of pheromone far greater than what is actually achievable in the field. Specifically, the average airborne concentration of pheromone achieved in crop treated with mating disruption dispensers has been quantified as ca. 1-2 ng/m^3 (Koch et al., 1997; Koch et al., 2002). Thus, the airborne concentrations of pheromone shown to desensitize moths in most laboratory investigations to date far exceed (by ca. 1,000-fold) the actual concentration of pheromone achieved in the field by application of commercially available dispensers such as Isomate polyethylene tubes.

Judd et al., (2005) postulated that desensitization of male codling moths might occur following prolonged or repeated visits in close proximity to Isomate C Plus dispensers. For example, moths exposed minutes-long might receive a sufficiently high dose of pheromone exposure to reduce behavioral responses as seen in laboratory experiments. However, in cases where male codling moth behavior has been directly observed in orchards treated with polyethylene-tube dispensers, including Isomate C Plus, males rarely directly contacted dispensers following oriented approach (Witzgall et al., 1997,1999; Stelinski et al., 2004a,b). Furthermore, the majority of approaching males remained visible in the vicinity of dispensers for approximately 10–120 s. This duration of exposure was likely insufficient to induce peripheral adaptation in the field (Judd et al., 2005; Stelinski et al., 2005a); however, subsequent behavioral response could have been affected due to habituation. Stelinski et al. (2006a) investigated the effect of brief exposure to Isomate C Plus dispensers and rubber septa loaded with codlemone at dosages ranging from 0.1 to 10 mg on subsequent behavioral responses of male codling moth in the wind tunnel and associated antennal changes as measured by EAGs. This series of experiments was designed to mimic the types of exposures males were observed receiving in the field while orienting within plumes emanating from Isomate C Plus dispensers (Stelinski et al., 2004a, 2004b). Specifically, males were allowed to dose themselves while orienting in or flying through plumes generated by the pheromone dispenser placed ca. 2 m upwind. Exposure durations were brief, lasting ca. 35 s on average (range 3–180 s) and male moth response was assayed 15 min or 24 h after exposure. These brief exposure treatments to Isomate C Plus dispensers nearly eliminated subsequent male moth responses to otherwise highly-attractive codlemone or 3-component (codlemone:14OH:12OH) lures in the flight tunnel.

This effect was much more drastic than that observed for *C. rosaceana*, *A. velutinana* (Stelinski et al., 2004a), and *G. molesta* (Stelinski et al., 2005b) in similar investigations. Also, it was dosage-dependent given that identical exposure to 0.1 mg lures with codlemone only or a 3-component blend mimicking that found in C Plus did not reduce behavioral responses of males to the same degree. Concurrent antennal (EAG) recordings revealed that the behavioral effect was likely explained by habituation, given that antennal sensitivity to codlemone was not different in pheromone-exposed moths compared with air-exposed controls. Given that long-lasting adaptation was not recorded in this investigation (Stelinski et al., 2006a), the exposure dosage was likely below the $\approx 355\ \mu\text{g} \times \text{min/L}$ of air required to induce the effect (Judd et al., 2005). The observed habituation was also consistent with an elevation in response threshold (Mafra-Neto and Baker, 1996). Specifically, more pre-exposed males oriented to elevated and normally unattractive dosages of codlemone (1.0 and 10 mg) than did air-exposed control moths (Stelinski et al., 2006a). In contrast, Isomate-exposed males did not orient to normally attractive dosages of codlemone (0.1 mg). The results of this study suggested that brief but high-dosage exposure to pheromone while orienting in plumes generated by Isomate C Plus dispensers raises the response threshold of codling moth males. This result is consistent with greater captures of males in traps baited with 10 mg codlemone lures in pheromone-treated orchards, which elicit little or no moth catch in traps when placed in untreated orchards (Vickers and Rothschild, 1991). Finally, as in Judd et al.'s (2005) report, the effect of brief exposure to Isomate C Plus was reversible; normal behavioral responsiveness was resumed after 24 h of recovery in clean air. Nevertheless, the results of this study suggested that habituation of male response following brief oriented flight to reservoir dispensers may be an important contributing mechanism to mating disruption of codling moth.

Competitive Attraction

Field observations have revealed that male codling moth orient to and approach mating disruption dispensers such as Isomate C Plus and "female equivalent" paraffin-wax dispensers (Barrett, 1995; Witzgall et al., 1999; Stelinski et al., 2004b; Epstein et al., 2006). Similar results have been observed with several other tortricid species (Stelinski et al., 2004a, 2005c). Far more males may actually orient to these dispensers than what has been actually observed given that oriented progress is likely terminated downwind at a certain distance at which the pheromone concentration is above the upper threshold for response (Cardé et al., 1975; Baker and Roelofs, 1981). These results suggest that competitive attraction between calling females and synthetic point sources of pheromone may be an important contributing mechanism to mating disruption.

If competitive attraction is an important contributor to mating disruption, then efficacy should be highly dependent on moth population density and the density of synthetic point sources that are deployed (Knipling, 1979; Miller et al., 2006a,b). One contested issue among investigators has been whether efficacy of mating disruption can be maintained while decreasing point source density per ha of crop and proportionally increasing the amount of pheromone released per point source. Some researchers (Shorey and Gerber, 1996; Knight, 2004) have suggested that this is indeed possible, postulating an economic advantage by deploying fewer dispensers of higher potency rather than many evenly distributed dispensers of lower potency throughout the crop. In fact, Shorey and Gerber (1996) demonstrated 95–98% disruption of codling moth in walnuts by deploying only 2.3 pheromone puffers/ha (each puffer releasing ca. 240 mg of pheromone/day). However, this was under comparatively low moth population densities (mean of 20 and 10 males/trap/week for lures and virgin females, respectively).

There is mounting corroborating evidence that disruption of various moth species is superior via higher rather than lower densities of pheromone release sites (Charlton and Cardé 1981; Palaniswamy et al., 1982; Suckling et al., 1994; Stelinski et al., 2005c; Miller et al., 2006a,b). This has also been recently confirmed by Epstein et al. (2006) for codling moth. In that recent study, the investigators varied Isomate C Plus density from 0 to 1,000 dispensers / ha. Male moth abundance in pheromone-baited traps decreased as a function of increasing dispenser density. Correspondingly, fruit injury decreased as the density of Isomate dispensers was increased and was lowest in plots treated with 1,000 evenly-distributed dispensers/ha. In a companion study, the density of 0.1 ml paraffin-wax drops containing 5% codlemone was manipulated. Disruption likewise increased with increasing density of wax drops deployed. In addition, the data with wax drops were analyzed according to recently proposed mathematical models developed to differentiate between competitive versus non-competitive mechanisms of disruption (Miller et al., 2006a). Under the scenario of competitive attraction, plotting 1/male visitation rate to a given attractant source on the y-axis against dispenser density on the x-axis yields a straight line with positive slope. Furthermore, plotting "male visitation rate" to a given attractant source on the y-axis against "dispenser density x visitation rate" on the x-axis yields a straight line with negative slope; disruption by a non-competitive mechanism was found not to share this set of properties (Miller et al., 2006a). The resultant analyses were consistent with the hypothesis that competitive attraction mediated disruption of codling moth with high densities of 0.1 ml wax drops (Miller et al., 2006b). Finally, the most compelling evidence in favor of competitive attraction was that male moths of several tortricid species were observed readily orienting to pheromone-releasing wax drops in the field (Stelinski et al., 2004a; Epstein et al., 2006). Collectively, these results suggest that false-plume following by male moths to dispensers contributes to disruption and that point source density and distribution may be critically important factors to achieving effective disruption, particularly under high moth densities.

Non-Competitive Mechanisms

Unfortunately, there are few manipulative studies on the impacts of non-competitive mating disruption mechanisms of moths. In fact, there is a paucity of studies investigating sensory imbalance in general, as a potential contributor to mating disruption (reviewed in Bartell, 1982; see also Flint and Merkle, 1984). Codling moth is a unique species in that the full repertoire of male sexual behaviors is elicited by the major pheromone component alone, codlemone, despite evidence of additive contribution of certain minor components (Einhorn et al., 1984; Arn et al., 1985; El-Sayed et al., 1999). Given that a complex multi-component and ratio-specific blend is not required for male orientation in this species, sensory imbalance may not be an important factor contributing to disruption of this species. However, in cases where antagonists are added to the blend (e.g. El-Sayed et al., 1999), there may be a greater impact of this mechanism. More research on sensory imbalance is needed to determine how it may contribute to disruption of codling moth. However, in most moth species, the pheromone is a blend of several chemicals released in a specific blend ratio. In these cases, the contribution of sensory imbalance to disruption is more likely.

The role of camouflage in mating disruption has also not been directly investigated, although this mechanism is often implicated in published studies on mating disruption. Indirectly, the role of camouflage has been falsified in a number of studies reporting male attraction to pheromone dispensers, including polyethylene reservoirs, in treated plots of various sizes (Barrett, 1995; Witzgall et al., 1996a, 1999; Stelinski et al., 2004b; Epstein et al., 2006). By definition, if plumes of attractant and/or female-equivalent pheromone sources were obscured by a sufficiently high background concentration of pheromone in treated plots, males should not be capable of orienting to point sources of synthetic pheromone in these plots. However, males have been directly observed orienting along plumes from pheromone dispensers or captured in sticky traps baited with these dispensers in pheromone-treated plots where disruption of lures or females was recorded (references above in this paragraph). This suggests that boundaries of discrete plumes are not camouflaged by background pheromone in plots treated with current commercial formulations of synthetic pheromone point sources.

Completeness of Pheromone Blend and Antagonists

The importance of pheromone blend components as well as antagonists and their impact on moth disruption has received considerable attention. The codling moth is an interesting example for which the importance of pheromone blend for disruption has received considerable attention. A total of thirteen minor compounds have been identified in addition to codlemone from the sex pheromone gland of female codling moths (Witzgall et al., 2001); dodecanol (12OH) and tetradecanol (14OH) were quantitatively most significant, enhancing behavioral responses of males to codlemone (Einhorn et al., 1984; Arn et al., 1985). Also, addition of the *Z*,*E* isomer to codlemone slightly increases male orientation in the wind tunnel, but does not increase capture of males in traps (El-Sayed et al., 1999). Conversely, *E*,*Z* isomer antagonizes male response to codlemone both in the wind tunnel and in the field (El-Sayed et al., 1999). In addition to the *E*,*Z* isomer of codlemone, *E*8,*E*10-12Ac (codlemone acetate) inhibits male attraction to codlemone in the field (Hathaway et al., 1974) and in the wind tunnel (El-Sayed, 2004). Given that attractiveness of synthetic codlemone is not greatly improved by the addition of synthetic minor components compared with codlemone alone, competitive attraction will likely not be enhanced by the addition of minor components to pheromone dispensers. Furthermore, exposure of male codling moths to a 3-component blend of codlemone, 12OH, and 14OH does not habituate males more than exposure to codlemone alone (Stelinski et al., 2006a). Thus, there is no published evidence that formulating dispensers with additional minor components such as 12OH and 14OH, as in the industry standard Isomate C Plus, should improve disruption over that achieved with codlemone alone. More laboratory and field research is warranted to determine whether any of the other behaviorally-active minor components may contribute to improved disruption over codlemone alone. However, addition of codlemone antagonists has shown some promise for improving disruption of codling moth. Witzgall et al. (1996b) investigated the potential of releasing a combination of codlemone and codlemone acetate from polyethylene-tube reservoir dispensers for improved disruption compared with treating plots with dispensers releasing codlemone alone. In 300 m^2 plots, disruption with codlemone dispensers alone was superior to that in plots treated with both codlemone and codlemone acetate dispensers; field observations confirmed that competitive attraction was the operating mechanism for the former treatment (Witzgall et al., 1996b). In smaller 100 m^2 plots, disruption of traps was highest in plots treated with a combination of codlemone and codlemone acetate. In a related follow-up study, Witzgall et al. (1999) conducted further observations in plots treated with codlemone dispensers with and without additional codlemone acetate dispensers (4.2 ha orchard) versus a 0.4 ha untreated control orchard. The dispensers used were either resin-treated cellulose flakes or polyethylene-tubes, similar to Isomate C Plus, containing codlemone, codlemone acetate or a blend of these two components. The investigators observed more male codling moths flying within codlemone-treated plots compared with untreated controls, implying that males were attracted into these plots. Also, male codling moths approached dispensers releasing codlemone and those releasing both codlemone and codlemone acetate in approximately equal frequencies. However, the major difference between attractant and attractant + antagonist treatments was that fewer males were observed taking long-range flights from nearby untreated orchards into those treated with codlemone and codlemone acetate compared with those treated with codlemone alone. The authors of that study postulated that deploying a combination of attractive codlemone dispensers with antagonistic codlemone acetate dispensers may improve disruption because long-range attraction into treated orchards may be reduced while close-range plume following and desensitization may be enhanced. Follow-up studies in large-scale replicated plots are warranted to fully test this hypothesis.

11.2.1.5 Case Studies

Mating Disruption of Tortricid Moths in Tree Fruit

Isomate polyethylene-tube reservoir dispensers have been the industry standard for mating disruption of tortricid moths for over a decade and have remained largely unchanged during this time; therefore, this section will discuss this technology in more detail. Disruption with this technology is practiced with success in many locations, especially under low population densities and with the application of companion insecticides to keep potential population outbreaks in check (Witzgall et al., 2008). With our current understanding of mating disruption, a greater emphasis has been placed on the importance of competitive attraction (Miller et al., 2006a,b) and the requirement for high-density pheromone point sources per area of crop, particularly under high population densities (Epstein et al., 2006). The idea of a "threshold concentration" for achieving effective disruption of tortricid moths (Vickers et al., 1985; Vickers and Rothschild, 1991) should be de-emphasized. Operating under the assumption that disruption is mediated mainly by a non-competitive mechanism, this hypothesis suggested that a minimum threshold concentration of pheromone release per hour exists for various moth species, above which mating disruption is completely effective. If this were true of current mating disruption technologies, then mating disruption should be density independent. Of course, this is not the case.

The Isomate polyethylene tube formulation and deployment protocol has remained unchanged as the industry leader for a decade because it effectively exploits the key combination of false-plume following and habituation. This is the case probably by happenstance rather than by intentional design given that the dispenser was not developed with these mechanisms in mind. Moths orient to such dispensers in the field, and such orientations habituate subsequent response, rendering males less capable of further oriented flight. The disruptive effects of competitive attraction and habituation are likely compounded in this case by other factors such as diminished fecundity with age (Knight, 1997; Jones and Aihara-Sasaki, 2001; Torres-Villa et al., 2002). At low to moderate population densities (1–2 moths per tree) and with the application of companion insecticides to keep these densities low, 1,000 Isomate dispensers/ha is likely an effective deployment rate to fully exploit the combination of these mechanisms. If Isomate C Plus functioned purely by competitive attraction without associated habituation, it is unlikely that only 1,000 units/ha would effectively disrupt even low population densities of codling moth. However, under high population densities, even as many as ca. 5,000 dispensers/ha fail to disrupt male codling moth orientation to traps (Stelinski et al., 2006a). This suggests that the desensitizing effect of this technology does not fully compensate for the density dependence of mating disruption. This is because a "threshold for disruption" does not exist with current mating disruption formulations and false-plume following to the dispenser is a prerequisite of habituation. Thus, at moderate to high moth densities, 1,000 dispenser/ha is insufficient. Simple mathematical modeling suggested that for densities of 2, 20, and 200 moths per tree, 1.3, 12.5, and 125 dispensers per tree are required for 98% disruption, if that disruption functions by pure competitive attraction (Miller et al., 2006a). The need for such high densities of dispensers per tree is likely realistically moderated by the beneficial impact of habituation. The density dependent nature of tortricid moth disruption by Isomate dispensers is highly consistent with the hypothesis that competitive attraction is an important contributing mechanism (Miller et al.,, 2006a,b).

Development of an ideal pheromone formulation or tactic for disrupting mating of moth pests will likely be governed more by economics and environmental considerations than by an understanding of the underlying biological mechanisms of disruption. Perhaps the most effective disruption formulation would be one that exploited a non-competitive mechanism such as camouflage or desensitization (without false-plume following). If this type of formulation could fully exploit the "threshold for disruption" hypothesis with 100% efficiency, mating disruption would be rendered density independent and perfect control could be achieved without the need of companion insecticides. However, this would likely require deploying an astonishingly high and economically (and perhaps environmentally) prohibitive amount of pheromone per area of crop. Remaining within the boundaries of economics, the second most effective direction is likely the exploitation of false-plume following to an attractive point source resulting in sufficient pheromone exposure so as to habituate males. As mentioned above, the Isomate hand applied formulation exploits this combination of mechanisms at low population densities. However, considerable improvement is needed given that habituation is likely a prerequisite of plume following and the degree of elicited plume following is a key component to achieving efficacy. Pheromones are susceptible to chemical degradation in the field (Millar, 1995), which affects their attractiveness. The breakdown products accumulating on the surface of certain Isomate formulations, commonly seen as a white film, likely decrease the attractiveness of these dispensers (El-Sayed el al., 1998). Thus, one area that to this day requires improvement is increasing the chemical stability of pheromones in release devices. This challenge is technological and thus economical in nature rather than biological. For example, the chemicals that stabilize codlemone and impede isomerization identified by Millar (1995) add to the cost of an already expensive pheromonal active ingredient. Identifying more effective and less expensive means of stabilizing codlemone from both isomerization and free radical formation will likely improve the efficacy of codling moth disruption.

A second component that requires improvement over today's commercial standard is increasing point source density per area of crop. A density of 500–1,000 units/ha has become the standard protocol based on economic limitations and not based on efficacy requirements. A reservoir dispenser that is applied by hand requires labor investment and this is why a single application of dispensers that stay effective season-long has remained an attractive idea among the applied pheromone industry. A single early-season application limits the total number of units that can be deployed per ha given the cost of materials and active ingredients. In order to improve upon this and develop a technology that deploys more than 1,000 point sources/ha, less active ingredient must be loaded per unit. This necessitates the development of a mechanized applicator to economically deploy many thousands of sources per ha of crop and it requires multiple (likely 2–4) applications per season given that dispensers with lower pheromone loading would likely not last season-long. Such technologies and pheromone formulations do exist, but are still ineffective due to technological flaws. These include Hercon Disrupt CM flakes (Hercon, Emigsville, PA) and Scentry NoMate CM Fibers (Scentry, Billings, MT)

(Swenson and Weatherston, 1989; Stelinski et al., 2008), and mechanically applied wax drops (Fig. 11.2D; Stelinski et al., 2006b). The first problem with these current so-called "high-density" or "female-equivalent" formulations is insufficient adherence of deployed material onto trees resulting in a waste of more than half of deployed dispensers, which do not contribute to disruption from the orchard floor (Stelinski et al., 2008). Second, in cases where the disruption formulations are phytotoxic, fruit can be damaged at mid-season applications (LLS, personal observation). In addition to chemical instability, a second challenge to overcome is the phytotoxicity of certain pheromone active ingredients (Giroux and Miller, 2001). Given that high-density formulations will likely require multiple applications per season onto fruit-bearing trees, these dispensers will need to be formulated so as to prevent pheromone from damaging fruit. This may be impossible to achieve and thus a single early-season application of a dispensers before fruit set remains a potential necessity.

One potential simple solution to the problem of developing a high-density reservoir formulation that is applied only once per season is decreasing the loading rate of active ingredients and their release rate per hour while proportionally increasing the deployment density of dispensers. For example, a reservoir dispenser that contains 1/3rd of the loading of Isomate polyethylene tube dispenser and that releases the pheromone at 1/3rd of the rate, but is applied at 3,000 units/ha will likely exploit competitive attraction better than Isomate C Plus while still inducing habituation in attracted males. This type of dispenser should be more effective than Isomate at higher moth densities. Such a formulation could be mechanically-applied (as a wax-based matrix for example, Stelinski et al., 2006b, 2007a) prior to fruit set, thus preventing the possibility of fruit damage due to phytotoxicity. The remaining technological challenge to overcome is that a high proportion of such mechanically-deployed dispensers would need to successfully adhere to tree foliage and hold out season-long.

The pursuit of sprayable microencapsulated formulations of pheromone (Knight and Larsen, 2004; Knight et al., 2004; Stelinski et al., 2007b) is likely not a productive direction for effective and economical disruption of tortricid moths because these formulations do not exploit the main operating mechanisms at dosages of pheromone that can be feasibly maintained in the field. This likely explains why such formulations have been either completely ineffective (Knight and Larsen, 2004; Stelinski et al., 2007b) or slightly effective for brief periods following application (Stelinski et al., 2007b). The concentration of airborne pheromone achieved by such formulations might affect disruption by a non-competitive mechanism for a brief period soon after application; but in the long run, pheromone is over-dispersed and lack of discrete point sources does not produce plume-following or habituation. Searching behavior of males and calling behavior of females (Weissling and Knight, 1995) may be affected by microcapsules adhering to foliage, but this requires further investigation. Knight and Larsen (2004) were able to improve the effectiveness of a sprayable microencapsulated formulation by modifying the deployment procedure. By applying microcapsules in a highly-concentrated, 'ultra-low volume', method using approximately 10 times less water in the spray tank as compared with standard formulations, efficacy was improved. The authors of that study found clumps of microcapsules adhering to leaves that were attractive to males and perhaps contributed to disruption as point sources. Stelinski et al. (2005d) confirmed that such clumps of microcapsules are highly competitive with optimally-attractive lures and likely attract males in the field disrupting moths by false plume-following. Also, Stelinski et al. (2007b) improved efficacy of sprayable pheromones by deploying lower rates of AI more frequently (ca. 10 times per season) than previous standard applications of more AI per application, but applied fewer (3–4) times per season. Excluding these cases where the application protocol has been manipulated to improve efficacy, microencapsulated formulations has shown limited effectiveness. The technological challenges that must be further improved, despite past progress (Knight and Larsen, 2004; Knight et al., 2004), remain protection of pheromone from degradation and rainfastness (Waldstein and Gut, 2004; Stelinski et al., 2007b). Rather than spending considerable effort toward modifying this technology and its associated application protocols to exploit the operating mechanisms of mating disruption, it might be more efficient to pursue other technologies that, by their existing design, exploit these key mechanisms.

Additional research with low-density dispensers such as puffers is also warranted. Given the savings associated with reduced labor cost compared with applying many hundreds of reservoir dispensers per ha, this technology is desired by the commercial industry and growers. Shorey and Gerber (1996) demonstrated a high degree of disruption efficacy (95–98%) with puffers (2.3/ha) when deployed over large acreages of walnut with low codling moth population densities. However, in Michigan apple orchards with moderate to high codling moth population densities, disruption efficacy using puffers has been very poor (50–80%) (Stelinski et al., 2007c). Shorey and Gerber (1996) estimated that their puffer treatment achieved an airborne concentration of pheromone of approximately 6.3 ng/m^3 air. This is below the concentration required to desensitize male codling moth antennal response (Judd et al., 2005; Stelinski et al., 2005a). Other interesting research questions regarding disruption of tortricid moths in tree-fruit are: by what mechanism(s) do low-density aerosol devices, such as puffers, affect disruption? Are moths attracted to the large plumes generated by these devices and the buildup of pheromone adhering to nearby tree surfaces? If so, following anemotactic orientations of males along these giant plumes is their behavior desensitized to a greater degree than that achieved by other commercial formulations? Or, do puffers disrupt males by a non-competitive mechanism such as camouflage? Answering these questions could potentially improve this tactic and make it more effective in higher moth density orchards. One potential avenue to explore is an intermediate device between puffers and reservoir devices such as Isomate C Plus (Stelinski et al., 2007c). Such devices could potentially better exploit competitive attraction under higher moth densities than the 2–3 currently designed puffers per ha, if plume-following is a mechanism of disruption by these devices. Such dispenser formulations would still reduce the total application cost relative to those requiring application of many hundreds of units per ha. Investigating whether fewer more-potent dispensers or more less-potent dispensers per area of crop achieve better disruption (Byers, 2007) will likely remain a productive area of research among investigators of mating disruption in the future. Although the balance will likely shift towards higher density point-source treatments under elevated moth densities given what we understand about competitive attraction. A compromise between the two density extremes will likely remain the leader of commercial market share given the need to balance economics and efficacy.

Oriental Beetle Mating Disruption in Blueberries

Almost all examples of successful tests for pheromone-based mating disruption involve moth pests (Cardé, 2007). One exception is the use of the sex pheromone to disrupt mating in the oriental beetle, *Anomala orientalis* (Waterhouse) (Coleoptera: Scarabaeidae). The oriental beetle became a problematic pest in the Northeast USA after its introduction sometime before 1920 (Vittum et al., 1999), and it is currently considered one of the most important turfgrass, ornamental, and blueberry insect pest in New Jersey, southeastern New York, Connecticut, and Rhode Island (Polavarapu, 1996; Alm et al., 1999). In blueberries, the root feeding damage caused by grubs can result in complete destruction of the root system and the death of host plants, especially when larval populations are high. Infested blueberry bushes show reduced vigor and support fewer berries compared to non-infested bushes.

Even though few options are currently available for management of oriental beetle in blueberries, the development of mating disruption for its control has been a very slow process. Currently, the neonicotinoid insecticide imidaclopid is the only treatment option available for grub control. Having a single control method not only raises the potential for resistance development, but also magnifies other constraints of using this active ingredient: imidaclopid is expensive, requires precise timing of application, it has limited efficacy against late-instar grubs (Koppenhöfer et al., 2002), is highly leachable (González-Pradas et al., 2002), and may disrupt pollination and biological control (Rogers, and Potter, 2003). Insecticides do not target the adults because they cause limited damage, the emergence period is long and coincides with harvest, and they are difficult to target with insecticide applications due to their cryptic behavior. The limited options available for oriental beetle control in blueberries makes the development of new environmentally safe alternatives, such as mating disruption, necessary for implementing in IPM programs.

The sex pheromone of the oriental beetle consists of (*Z*)-7-tetradecen-2-one and (*E*)-7- tetradecen-2-one (9:1 blend) (Zhang et al., 1994; Facundo et al., 1994). Previous field studies by Polavarapu et al. (2002) evaluated microencapsulated sprayable formulations of (*Z*)- and (*E*)-7-tetradecen-2-one for oriental beetle mating disruption. Adult male trap captures in blueberry plots treated with the pheromone formulation were reduced by over 90% compared to untreated controls. Mating rates were also lower in treated plots compared to untreated plots. However, the use of sprayable microencapsulated formulations is not feasible in fruit crops, such as blueberries, because the oriental beetle pheromone is a ketone. According to current EPA regulations, ketones do not qualify for tolerance exemptions allowed

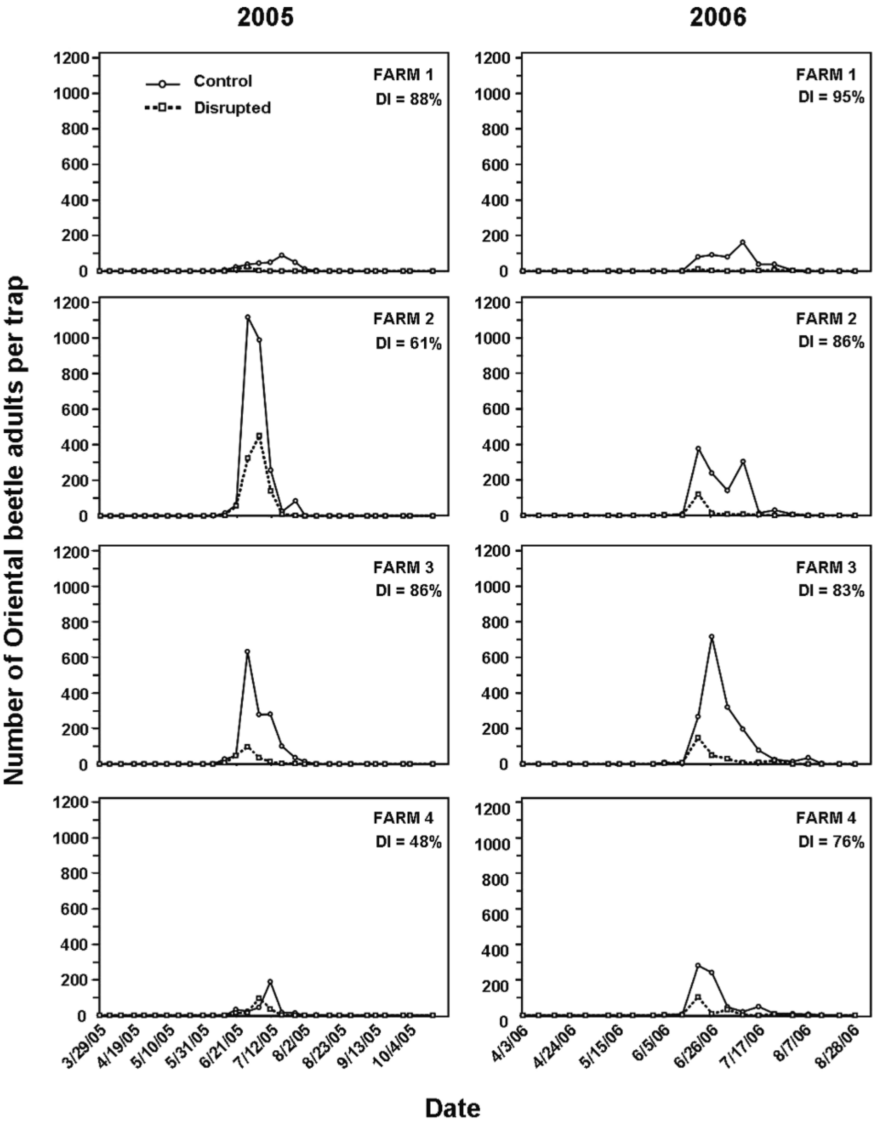


Fig. 11.3 Mating disruption for oriental beetle (*Anomala orientalis*) in blueberries: a field demonstration. The data are season-total male oriental beetle catches in pheromone-baited traps in control plots (control) and plots treated with 50 per ha dispensers loaded with 1 g of the sex pheromone (disrupted). Each plot was 1.6–2.0 ha. The study was conducted in four New Jersey (USA) blueberry farms in 2005 and 2006. DI = disruptive index

for alcohols, acetates, or aldehydes; this has been a key obstacle for the development of mating disruption in oriental beetle. An alternative formulation is the use of point-source dispensers, which are exempt from tolerance restrictions (Weatherston and Minks, 1995). Sciarappa et al. (2005) evaluated mating disruption for oriental beetle with 50–75 dispensers/ha with (*Z*)-7-tetradecen-2-one at 1 g active ingredient (AI) per dispenser. Pheromone treatment reduced beetle captures in traps, mating rates, and grub densities compared with those found in untreated control plots. Mating disruption for oriental beetle has also been used successfully in ornamentals (Polavarapu et al., 2002), turf (Koppenhöfer et al., 2005), and cranberries (Wenninger and Averill, 2006).

In a 2-year experiment (2005–2006), we evaluated the potential of mating disruption for oriental beetle in commercial highbush blueberry fields in New Jersey (USA). The experiment was conducted at four farms, each with two 1.6–2.0 ha experimental plots. One of the plots received 50 dispensers per ha at 1 g AI per dispenser (total of 50 g AI/ha; disrupted plots), while the other plot received no pheromone (control plots). One Japanese beetle trap baited with 300 mg of oriental beetle sex pheromone was placed in the interior of each plot and monitored weekly to determine adult male abundance. Successful mating disruption of oriental beetle is inferred by trap shut-down in disrupted plots, i.e., a decrease in number of male beetles captured in traps in treated plots compared with paired untreated controls. In both years, the disrupted plots had lower numbers of male beetles in traps compared to control plots (Fig. 11.3). The disruptive index ($(C - T)/C \times 100$ where $C =$ average beetle captures per trap in control plots and $T =$ average beetle captures per trap in disrupted plots), varied between 48–95%. These results indicate that oriental beetle mating disruption was effective in some farms but not in others. One of the potential reasons for this variability is the potential difference in oriental beetle pressure among farms. Mating disruption for oriental beetle might work best under low-to-medium population pressure. Similar to that observed with the codling moth, it is also likely that more point sources are required in areas of high oriental beetle populations (see Miller et al., 2006a,b). The size of fields might also limit efficacy of mating disruption because it often works best when used in larger areas (Cardé, 2007). Ongoing work is underway to address these and other factors, including obtaining a commercial product for oriental beetle mating disruption so that it can be tested on a large scale (i.e., an entire blueberry farm), testing new pheromone formulations that can be applied as multiple point sources, evaluating long-term effects of mating disruption on oriental beetle populations, and reducing pheromone rates to make the technology more cost effective.

11.3 Host-Plant Volatiles and IPM

Host-plant volatiles play a critical role in the life of insects (Miller and Strickler, 1984; Visser, 1986; Bernays and Chapman, 1994). Herbivorous insects may use host-plant volatiles to locate food, mates, and/or oviposition and hibernation sites

(Visser, 1986). Plant volatiles may also aid insects to remain in a suitable habitat (e.g. Eigenbrode et al., 2002), avoid a dangerous habitat (e.g. Choh and Takabayashi, 2007), and aggregate (e.g. Loughrin et al., 1996a; Dickens, 2006). The behavioral response of insects to plant volatiles may have important implications related to crop injury. Adult females need to locate suitable hosts for the successful development of their offspring (Thompson, 1988). Host-plant volatiles may play an important role in decision-making by females and thus affect the success and distribution of their offspring within a habitat (Courtney and Kibota, 1989; Mayhew, 1997). For mobile pests, such as alate aphids and thrips, plant volatiles may attract and arrest them in certain areas (e.g. Eigenbrode et al., 2002). This can be a disadvantage to farmers if aphids and thrips transmit viruses, such that plant volatiles may lead to increases in virus transmission (Kennedy et al., 1959).

Taking into consideration all the signals used by insects in host location and mate finding, and the potential synergistic interactions between them, studying the behavioral response of insect pests to host-plant volatiles can become a challenging task. Here we provide a sequence of steps for conducting such studies. The first step when considering the use of host-plant volatiles for IPM is to understand the behavior of the insect. This is the most critical, and possibly most time consuming, of all steps. The initial questions to answer are: Is the insect attracted to intact host plants? Is the insect attracted to host plants that are damaged by conspecifics or other herbivores? And, what specific part of the plant is attractive? To answer these questions researchers will require the use of behavioral arenas such as wind tunnels or Y-tube olfactometers.

Management of an insect pest using plant volatiles to manipulate host-finding behavior will also require knowledge of the insect's life history. For instance, results from studies on host finding behavior most likely will differ when comparing insect herbivores adapted to a crop versus non-adapted herbivores. On one hand a plant volatile can be attractive to an adapted herbivore, while it might be repellent to a non-adapted herbivore (i.e., non-host volatiles). The results may also differ when studying adapted herbivores that differ in their degree of specialization (Bernays and Chapman, 1994). For example, different responses to plant volatiles might be expected when comparing a specialist herbivore that feeds on one or few plant species to a generalist herbivore that feeds on a wide range of plant species in different families. This degree of specialization should be considered when developing behavioral-based strategies using host-plant volatiles for pest management. In fact, specialists might use specific signals from their host-plant while generalists might use more generalized plant signals. This specialization may be due to a greater degree of sensitivity to host-plant volatiles mediated by more sophisticated detection mechanisms (but see Bruce et al., 2005). On the other hand, specialists may use more complex signals than generalists by obtaining more information from blends of host-plant volatiles in specific ratios. Even within a species there can be differences between sympatric or allopatric populations. One of the most well-known studies of host race formation on alternative hosts is that of the apple maggot fly, *R. pomonella* (Linn et al., 2003). In this species there are differences among populations in preference for different host plants, such that flies of apple origin chose apples significantly more often than flies of hawthorn origin and vice-versa.

It is also important to consider the insect's physiological state and gender differences in their response to host-plant volatiles. The integration of external stimuli and internal physiological state will determine the threshold and ultimate outcome of the response of insects to plant volatiles (Miller and Strickler, 1984). For example, males and virgin females are often less responsive than gravid females to host-plant volatiles (e.g. Hern and Dorn, 1999; Yan et al., 1999; Mechaber et al., 2002; Masante-Roca et al., 2007). However, altering the internal state of an insect is often not feasible and therefore most efforts to manipulate insect behavior focus on altering the insect's response to an external stimulus. In addition, plant phenology often has an effect on volatile emissions. Different plant parts may emit distinct volatile blends (e.g. Bengtsson et al., 2001; Vallat and Dorn, 2005). Volatile emission can also vary among cultivars (Loughrin et al., 1996b). All of these factors add to the complexity of studying insect behavioral response to plant volatiles.

Once researchers have an understanding of the behavioral responses of the target pest to its host plant and have identified the source of attractive volatile emissions from plants, the next step is similar to the identification of insect pheromones. It involves the detection and analysis of behaviorally-active compound(s) through the use of EAG, gas chromatography (GC), and coupled GC-EAD. The identified compounds can then be tested individually or as a blend(s) in the laboratory to determine if they act as attractants or repellents. The third step is to test the active compound(s) under field conditions. Most of the research on the effects of host-plant volatiles has been limited to the first two steps, i.e., to controlled laboratory conditions. Only few studies have been able to make the transition from the laboratory to the field successfully and they are discussed below. The final step is to incorporate the active volatile blend into an IPM-based program and achieve adoption.

11.3.1 Manipulation of Host Finding

According to their effects on insect behavior, plant volatiles can be classified as attractants or repellents (Dethier et al., 1960; Bernays and Chapman, 1994). This classification is not always clear because a plant volatile can act as an attractant or a repellent depending on its concentration. For instance, many attractants will repel herbivores at high concentration (e.g. Finch, 1978; Hern and Dorn, 1999; Mewis et al., 2002). In addition, host-plant volatiles are often induced by different environmental factors (Karban and Baldwin, 1997). For example, herbivore feeding increases emission of volatiles in plants; these volatiles are referred to as herbivore-induced plant volatiles (HIPVs; e.g. Arimura et al., 2005) (Fig. 11.4). Examples of host-plant attractants and repellents and of the effects of HIPVs on insect behavior are presented below.

11.3.1.1 Attractants

Plant attractants are those volatiles that cause an insect to orient its movement towards the emitting source (Dethier et al., 1960; Bernays and Chapman, 1994). Most research on host-plant volatile effects on herbivore behavior has focused on the

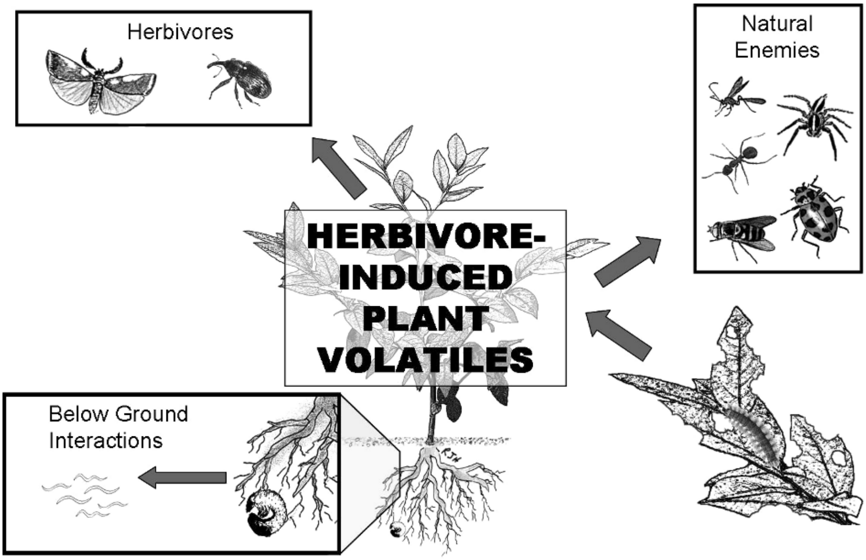


Fig. 11.4 Herbivore-induced plant volatiles (HIPVs) effects on herbivores and their natural enemies. Herbivory often induces a volatile response in plants than can attract or repel herbivores. HIPVs also can serve as long-distance cues for natural enemies during host/prey searching. These effects are not only found aboveground, but also belowground. Herbivore feeding on roots releases HIPVs that attract entomopathogenic nematodes. Graphic designed by Robert Holdcraft

discovery of new insect attractants. Here we discuss four general examples where an individual chemical or blend of host-plant volatiles has been isolated, identified, and shown to attract agricultural pests. We include examples of attractants derived exclusively from plant odors. These examples are summarized in Table 11.3. We do

Table 11.3 Examples of insect attractants derived from host plant volatiles

Insect pest	Host	Plant volatiles	References
Coding Moth (*Cydia pomonella*)	Apple	Butyl hexanoate *E,E*-α-farnesene	Hern and Dorn (2004) Hern and Dorn (1999)
	Pear	Ethyl(*E,Z*)-2,4 decadienoate (pear aster)	Light et al. (2001)
Grapevine Moth (*Lobesia botrana*)	Grape	(*E*)-β-caryophyllene (*E*)-β-farnesene (*E*)-4,8-dimethyl-1,3,7-nonatriene	Tasin et al. (2006)
Colorado Potato Beetle (*Leptinotarsa decemlineata*)	Potato	(*Z*)-3-hexenyl acetate Linalool Methyl salicylate	Martel et al. (2005)
Plum curcuiio (*Conotrachelus nenuphar*)	Plum Apple	Benzaldehyde	Piñero and Prokopy (2003)

not include examples of volatiles from other food sources such as protein baits (e.g. NuLure or Mazoferm), that attract and stimulate feeding in fruit flies and are widely used in IPM programs worldwide (e.g. McQuate and Peck, 2001).

Codling Moth

As indicated previously, sex pheromones have been used for monitoring and in various formulations to disrupt mating. The codling moth, *C. pomonella*, is a major pest in pome fruits and walnuts. The sex pheromone, however, only attracts males; finding a plant volatile that is attractive to both sexes and especially to females is an important research goal. Wearing et al., (1973) and Yan et al., (1999) found that females are attracted to the odor of apples. Sutherland (1972) and Hern and Dorn (1999) found that larvae and adults of codling moth, respectively, respond to the plant volatile *E*,*E*-α-farnesene. This terpene attracted female codling moth at low doses and repelled them at high doses (Hern and Dorn, 1999). Because of its low environmental stability, *E*,*E*-α-farnesene has limited value in the field. A recent breakthrough in the development of an effective kairomonal lure was the identification of the pear ester, ethyl (*E*,*Z*)-2,4-decadienoate, a volatile present in the odor of ripe Bartlett pears (Light et al., 2001). Field tests showed that pear ester lure-baited traps capture more codling moths than pheromone baited traps in orchards treated with mating disruption. This kairomone attracts both males and females. The pear ester also attracted codling moth neonates in laboratory studies (Knight and Light, 2001). This chemical is stable, inexpensive to synthesize, and readily released from dispensers such as rubber septa. The use of kairomone-baited traps for codling moth has recently been developed to establish accurate action thresholds (Knight and Light, 2005a), and for monitoring females (Knight and Light, 2005b). However, the pear ester is found only from the odor of ripe pears but not in other host plants of the codling moth. Therefore, it is likely that codling moth females use other volatiles from non-pear hosts to recognize suitable oviposition sites (Witzgall et al., 2005). An apple-derived ester, butyl hexanoate, attracts mated codling moth females in laboratory studies (Hern and Dorn, 2004); however, it has not been proven to attract adults in the field.

Grapevine Moth

The European grapevine moth, *L. botrana* (Lepidoptera: Tortricidae), is a polyphagous insect and one of the most serious pests of vineyards. Females oviposit on flower buds, green berries, and mature grapevine berries. Adults are attracted to odors from grapevine berries (Tasin et al., 2005). Headspace volatile collections from green berries elicited antennal responses of mated *L. botrana* females. Masante-Roca et al. (2005) showed that plant volatiles are processed in the moth's antennal lobe. In wind tunnel assays, females responded to volatiles from grapevine branches and green berries (Tasin et al., 2005). Masante-Roca et al. (2007) also showed attraction to flower buds and ripe berries (both infested and uninfested with the pathogenic fungus *Botrytis cinerea*) but not to flowers. A recent breakthrough was the development of a complex attractive kairomonal lure for the grapevine moth (Tasin et al., 2006). They identified a blend of volatiles that attracts mated females consisting of (*E*)-β-caryophyllene, (*E*)-β-farnesene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene. Attraction to the blend in the wind tunnel was achieved only when the individual compounds were mixed at a 100:78:9 ratio.

Colorado Potato Beetle

McIndoo (1926) first determined the attraction of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), an important pest of solanaceous crops, to potato foliage in the laboratory. Recently, Dickens (1999) identified a synthetic blend of volatiles released by potatoes that attract Colorado potato beetle. Using GC-EAD analyses, nine volatiles contained in the potato blend elicited an antennal response in adult Colorado potato beetle (Dickens, 1999). Seven of these nine compounds were also detected by antennal receptors of two of its predators, the generalist *Podisus maculiventris* (Say) and the specialist *Perillus bioculatus* (F) (Dickens, 1999). Behavioral studies showed that adult Colorado potato beetles and the generalist predator are attracted to a blend of five compounds: (*E*)-2-hexenol, (*Z*)-3-hexenol, nonanal, linalool, and methyl salicylate. Further studies showed that Colorado potato beetle adults and larvae were attracted to blends comprised of (*Z*)-3-hexenyl acetate, linalool, and methyl salicylate (Dickens, 2000; Dickens, 2002). Recent field experiments by Martel et al. (2005) showed that pitfall traps baited with this blend captured more Colorado potato beetle adults than unbaited pitfall traps.

Plum Curculio

The plum curculio, *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae), is a serious pest of stone and pone fruit in eastern North America. Behavioral studies showed that adult plum curculio use olfactory cues to locate its host fruit trees (Butkewich and Prokopy, 1993; Leskey and Prokopy, 2001). Further studies revealed that apple and plum odors released during bloom and 2 weeks after bloom attract adults (Leskey and Prokopy, 2000). Adults were attracted to fruit volatiles, particularly (*E*)-2-hexenal, hexyl acetate, ethyl isovalerate, limonene, benzaldehyde, benzyl alcohol, decanal, and geranyl propionate (Leskey et al., 2001; Prokopy et al., 2001). In field experiments, only benzaldehyde synergized the response of plum curculio to its aggregation pheromone grandisoic acid (GA) (Piñero and Prokopy, 2003). Although the combination of benzaldehyde and GA has yielded higher adult trap captures in baited traps than in non-baited traps, baited traps have failed to reliably monitor plum curculio activity in apple and peach orchards because captures decline rapidly after fruit set suggesting that traps were out-competed by fruit volatiles (Prokopy et al., 2003; Leskey and Wright, 2004).

11.3.1.2 Repellents

Plant repellents are volatiles that cause an insect to orient their movement away from the emitting source (Dethier et al., 1960; Bernays and Chapman, 1994). Compared to attractants, fewer plant-derived insect repellents have been studied, and as a result the use of repellents for exogenous applications to prevent pest infestations in agriculture has not been widely practiced. The role of non-host volatiles as repellents has been tested mainly in forest systems (e.g. Byers et al., 2004). Among agricultural pests, host-plant repellents have been mostly studied in aphids. (*E*)-(β)-Farnesene, a common sesquiterpene host-plant volatile and the major component of the alarm pheromone of several aphid species, repels some aphid species (Pickett et al., 1992; Bernasconi et al., 1998). Methyl salicylate and (-)-(1*R*,5*S*)-myrtenal were repellent to the black bean aphid, *Aphis fabae* Scop, and inhibited attraction to its host, the broad bean (Hardie et al., 1994). *A. fabae* and *Brevicoryne brassicae* (L.) were repelled by volatiles from tansy and summer savory (Nottingham et al., 1991). The authors found that *A. fabae* was repelled by 4-pentenyl isothiocyanate. Isothiocyanates are catabolites of glucosinolates and characteristic of the Brassicaceae, and most likely repellent to non-adapted insects. Limonene, a common monoterpene volatile from plants, has also been shown to repel some insects (e.g. Ibrahim et al., 2001). Other plant monoterpenes such as (*E*)-ocimene and sesquiterpenes such as (-)-germacrene D repel herbivores (Bruce et al., 2005).

11.3.1.3 Herbivore-Induced Plant Volatiles

Herbivory often increases volatile emissions from plants (Karban and Baldwin, 1997). Studies on the effects of HIPVs on insect behavior have been viewed mainly in a tritrophic context (Vet and Dicke, 1992). Natural enemies of herbivores may use volatiles from herbivore-damaged plants to locate their host or prey (see discussion below). Recently, however, HIPVs have been shown to also influence the behavior of phytophagous insects (Dicke and van Loon, 2000) (Fig. 11.4). For example, grape volatiles induced by insect feeding (conspecifics) attracted Japanese beetles in the field (Loughrin et al., 1996a). Similarly, Colorado potato beetles are attracted to potato plants damaged by conspecific larvae (Schutz et al., 1997; Landolt et al., 1999). HIPVs can also repel insect herbivores. For example, undamaged wheat seedlings arrested, and damaged wheat seedlings repelled, the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Quiroz et al., 1997). Four compounds, 6-methyl-5-hepten-2-one, (–)- and (+)-6-methyl-5-hepten-2-ol, and 2-tridecanone, were present in volatile blends from aphid-infested but not from un-infested wheat seedlings. De Moraes et al. (2001) showed that caterpillars induce volatiles at night from tobacco plants that are repellent to female *Heliothis virescens* (Fabricius) moths.

HIPVs can also affect the behavioral response of immature insects towards plants. For example, neonate larvae of the codling moth are attracted to larval-infested apple fruit (Landolt et al., 2000). (*E*,*E*)-α-Farnesene was emitted in greater amounts from infested compared to un-infested apples. Previous studies had shown that neonate codling moth is attracted to α-farnesene, as previously discussed. Similarly, *Spodoptera frugiperda* (J.E. Smith) larvae were attracted to volatiles from herbivore-damaged maize seedlings (Carroll et al., 2006).

11.3.2 Applications

To a large extent, plant volatiles can be used in a similar manner to sex pheromones. Plant volatiles can be used to bait traps for monitoring, or in pest control strategies such as in mass trapping and attract-and-kill approaches, or to disrupt host-finding behavior.

Figure 11.1 provides a comparison of different attributes of insect sex pheromones and host-plant volatiles. The development of plant-based kairomones in IPM offers several advantages over sex pheromones, which typically attract only one sex or only males in the majority of cases. This is important because most efforts in pest management are directed towards attraction and control of females. For example, monitoring for the presence of females, which mate and lay eggs offers a distinct advantage in terms of predicting crop damage. Plant volatiles are also advantageous because they may attract both immature and adult stages. A third advantage of plant volatiles over pheromones is that they are often simple, commercially available, and cheap chemicals. Plant-based kairomones can serve as an alternative to sex pheromones when the pheromone is absent or produced at amounts undetectable by GC, has low volatility, or is difficult and/or expensive to synthesize.

A major disadvantage of host-plant volatiles is their limited specificity, or lack thereof, compared to sex pheromones. Plant volatiles are ubiquitous and plant species often share similar biosynthetic pathways in volatile production; the most prominent being the lipoxygenase, leading to the production of green leaf volatiles, and the isoprenoid pathways, leading to the production of terpenes (Paré and Tumlinson, 1999). Thus, plant-derived attractants will often attract several species of non-target insects. This might be problematic if the blend attracts beneficial insects, such as bees and predators; thus potentially disrupting pollination or biological control. Also, host-plant volatiles may be less effective than sex pheromones because they have to compete with abundant surrounding odor sources for attraction. This might be more problematic in agriculture than in forest systems because most crops are grown as monocultures. Under these crop conditions, a good understanding of the pest's behavior will be important when testing plant-based kairomones in the field. For example, if the pest migrates from the forest into the crop, attractants could be placed near the forest edge to avoid competition with the host plant.

11.3.2.1 Monitoring

Host-plant volatiles can be deployed in the same manner as described for sex pheromones, and may provide a natural source for the development of attractants for monitoring insect pests that are safe to the environment. Attraction to kairomone-baited traps by insect pests will require the detection of a specific blend of host-plant volatiles or specific ratios of these volatiles. However, finding the right combination of plant volatiles at the correct ratio is often a challenging task. As indicated previously, attractants from plant volatiles are currently under development for various species of moths and beetles (Table 11.3). Yet, the best-known success case is the use of food-derived attractant traps to monitor and control fruit flies (e.g., Morton and Bateman, 1981; Prokopy et al., 1992; Prutuele et al., 1993; Cornelius et al., 1999). The use of kairomone-based lures for pest monitoring may feature more prominently in future pest management as our understanding of plant-based attractants for both generalist and specialist herbivores increases. Currently, the number of potent pheromone-based insect attractants vastly outnumbers the number of effective known kairomones.

11.3.2.2 Mass Trapping

The host-plant volatiles used for monitoring insect pests can be used in a mass trapping approach. Only few studies have investigated this approach to protect plants in an agricultural system. For example, Ruther and Mayer (2005) tested synthetic plant volatiles in a mass trapping experiment to control the garden chafer, *Phyllopertha horticola* L., in an apple orchard. They found that orchards treated with attractant traps had about 7% less disfigured fruit by adult feeding compared to control orchards.

11.3.2.3 Attract-and-Kill

Although attract-and-kill strategies have mainly used sex pheromones and food lures (see Section 11.2.1.3), host-plant volatile attractants can also be employed with an insecticide to increase its efficacy in crop protection. An attract-and-kill tactic that uses a kairomone-based attractant to target females would have a much greater effect on pest population growth compared with those that target males only. Some important chemicals, including methyl eugenol, 1-(p-acetoxyphenyl)-butan-3-one (cue-lure), and t-butyl 4 (or 5)-chloro-2-methyl-cyclohexanoate (trimedlure), have been used as attractants for fruit flies. For example, methyl eugenol was used in the eradication program for the oriental fruit fly, *Dacus dorsalis* (Hendel), on the island of Rota in the Marianas (Steiner et al., 1965). Other volatiles used for monitoring fruit flies are derived from food sources (food baits), such as from the protein hydrolysates of corn, soybeans, or yeast. Fermentation of these baits results in volatile emissions attractive to fruit flies. Several attractants (baits) for fruit flies are commercially available (e.g., Nu Lure, GF-120, Naturalure).

The attract-and-kill concept has also been tested in trap crops, where more attractive plants are used to lure insects away from the economic crop, and then reduce the pest populations by either killing the insects in the trap crop with an insecticide or destroying the trap crop (Hokkanen, 1991). The attractiveness of trap crops to insect pests can be enhanced by the use of host-plant volatiles. This approach has been called "semiochemically assisted trap cropping" (Shelton and Badenes-Perez, 2006). For example, Martel et al. (2005) evaluated the potential of a synthetic host-plant attractant blend for the Colorado potato beetle to enhance efficacy of trap cropping. More colonizing adults, eggs, and larvae were found in attractant-treated trap crops than in untreated trap crops. This resulted in reduced amounts of insecticides applied to plots bordering the attractant-treated trap crops.

11.3.2.4 Push-Pull Strategy

Push-pull (Pyke et al., 1987), or stimulo-deterrent diversion (Miller and Cowles, 1990), is a strategy where a host-plant attractant(s) and a repellent(s) are used in combination. This concept has been tested using a repellent intercrop and an attractant "trap" plant. Here insects are repelled by volatiles emitted from the intercrop (push) and simultaneously attracted by volatiles from the trap plant (pull). The most successful work on push-pull to date has been conducted in Africa to control stem borers in maize and sorghum (Cook et al., 2007). This work has lead to the adoption of push-pull strategies among thousands of small and medium scale farmers in eastern Africa (Khan and Pickett, 2004). The strategy works not only by decreasing stem borer damage to maize, but also by enhancing the efficacy of natural enemies (Khan et al., 1997a,b). Here, the two most successful trap crops are Napier and Sudan grasses; they receive greater stem borer oviposition than maize. Six volatiles found in Napier grass attractive to female stem borers are octanal, nonanal, naphthalene, 4-allylanisole, eugenol, and linalool (Khan et al., 2000). Napier grass also produces larger amounts of green leaf volatiles hexanal, (*E*)-2-hexenal, (*Z*)-3-hexenol, and (*Z*)-3-hexenyl acetate than maize and sorghum (Chamberlain et al., 2006). These green leaf volatiles might be responsible for female stem borer attraction to trap plants because they are emitted at the beginning of the scotophase, when females seek plants for oviposition (Khan et al., 2008). The intercrops with greatest repellent effects are molasses grass and two legumes: siverleaf and greenleaf desmodium. Six volatiles are emitted from molasses grass but not in the trap plants; these are (*E*)-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, β-caryophyllene, humulene, and α-terpinolene (Khan et al., 2000; Pickett et al., 2006). The ocimene and nonatriene were found repellent to stem borer (Khan et al., 1997a). These compounds were also found in the desmodium intercrops (Khan et al., 2000). Volatile chemicals from molasses grass that repelled female stem borers attracted females of its parasitoid *Cotesia sesamiae* (Cameron) (Khan et al., 1997a).

11.3.2.5 Disruption of Host Finding

Host-plant volatiles can be sprayed on a crop to disrupt the pest's host finding behavior. For example, an attractant crude oil was used to disrupt the host-finding behavior of the navel orangeworm, *Amyelois transitella* (Walker), a pest of almonds in California (Van Steenwyk and Barnett, 1987). Spraying a formulation of 5% crude almond oil on trees suppressed egg deposition in egg traps and reduced the infestation of nuts. An approach recently employed is to apply an elicitor of plant defenses that can activate the production of volatiles in plants. For example, Thaler (2001) showed that application of jasmonic acid (JA), a hormone known to induce plant resistance and HIPVs, reduces the number of caterpillars, aphids, flea beetles, and thrips on tomato plants. Whether the negative effects of JA treatment on herbivores were due to an increase in HIPVs was not investigated. Disruption of host finding by spraying a synthetic volatile attractant or repellent has rarely been tested to control an agricultural pest, possibly because it might unintentionally attract other pests into the crop.

11.3.3 Synergism with Other Stimuli and Control Strategies

11.3.3.1 Visual Cues

As indicated above, host-plant selection by insects usually requires visual (color, shape, or size) and chemical (pheromones or host-plant volatiles) signals. Therefore, combinations of these signals might work better in attracting insects than a single stimulus. Several examples exist where visual stimuli enhance insect responses to host-plant volatiles (Prokopy, 1986; Blackmer and Cañas, 2005; Kendrick and Raffa, 2006). Colored traps have historically been used to monitor insect pests. Yellow sticky traps have been used to monitor whiteflies (e.g. Gillespie and Quiring, 1987), plant bugs (e.g. Prokopy et al., 1979), and leafhoppers (e.g. Meyerdirk and Oldfield, 1985). Red spheres attract female apple maggots, *R. pomonella*, by mimicking ripe fruit (Prokopy, 1968). Sticky red spheres have been used to protect apples against this fruit fly species (Prokopy, 1975); however, a combination of visual and chemical cues proved to be more attractive (Prokopy et al., 1990; Aluja and Prokopy, 1993). Prokopy et al. (1990) found that sticky spheres baited with butyl hexanoate placed in the perimeter of orchards provide protection similar to unbaited spheres on every tree. Adding an insecticide and/or a food stimulant can further enhance the efficacy of sphere traps (see Sections 11.2.1.3 and 11.3.2.3).

11.3.3.2 Pheromones

Probably the most effective method for using host-plant volatiles is in combination with insect pheromones. Host-plant volatiles, particularly green leaf volatiles, can enhance the insect's response to their sex pheromone. For example, male corn earworm, *Helicoverpa zea* (Boddie) response to the sex pheromone is enhanced when combined with (Z)-3-hexenyl acetate (Light et al., 1993). Males were not attracted to this green leaf volatile when presented alone, indicating that it acted synergistically with the sex pheromone. (Z)-3-hexenyl acetate also acts synergistically with the sex pheromones of the codling moth, *C. pomonella*, the diamondback moth, *Plutella xylostella* (L.), and the tobacco budworm, *H. virescens* (Reddy and Guerrero, 2004).

Host-plant volatiles can also enhance the insects' response to their aggregation pheromone. Reddy and Guerrero (2004) provide a list of examples where synergistic effects of plant volatiles and aggregation pheromones have been reported. For example, the response of the boll weevil, *Anthonomus grandis* Boh., to their aggregation pheromone (grandlure) is enhanced when combined with the green leaf volatiles (*E*)-2-hexenol, (*Z*)-3-hexenol, or 1-hexanol (Dickens, 1989).

Host-plant volatiles can also inhibit the insect's response to their pheromone. This concept has been investigated for forest pests but not for agricultural pests. Non-host, green leaf volatiles have been shown to inhibit the response of several species of bark beetles to their pheromone (e.g. Dickens, 1992; De Groot and MacDonald, 1999; Poland and Haack, 2000). Whether non-host volatiles can be used to protect plants in agricultural systems requires further investigation.

11.3.3.3 Biological Control

Plant volatiles are critical in host finding not only for insect pests but also for their natural enemies, i.e., insect predators and parasitoids (Price et al., 1980) (Fig.11.4). Natural enemies may use plant volatiles to find a habitat where their host or prey can be found. However, more reliable cues for natural enemies are herbivore-induced plant volatiles (HIPVs). The role of HIPVs on natural enemy host finding behavior has been studied extensively in the past few decades and several reviews have been written on the subject (e.g. Dicke et al., 1990; Lewis and Martin, 1990; Vet and Dicke, 1992; Tumlinson et al., 1993). Here we will only discuss examples where synthetic HIPVs have been used to manipulate natural enemy behavior. These chemicals may increase biological control success in agriculture by "enhancing the searching efficacy of natural enemies, bringing the natural enemies into a searching mode, and making novel or artificial host-prey species acceptable in a mass rearing program" (Khan et al., 2008). In contrast, when applied to agricultural crops, HIPVs may reduce searching efficacy of natural enemies by attracting them to areas where the prey or host are absent. Thus, it might be important to consider the abundance and distribution of the pest when using HIPVs to enhance biological control.

To date, field demonstrations on the use of HIPVs to manipulate the behavior of the natural enemies of herbivores remain limited. James (2003a) was the first to demonstrate attraction of predators to synthetic HIPVs in an agricultural system. In hop, sticky traps baited with synthetic methyl salicylate (MeSA) caught greater numbers of lacewings than unbaited traps (James, 2003a). In another study, traps baited with (*Z*)-3-hexenyl acetate caught more predatory mirids, *Deraocoris brevis* (Uhler), and anthocorids, *Orius tristicolor* (White), than unbaited traps; whereas traps baited with MeSA attracted more geocorids, *Geocoris pallens* Stal., and hover flies (James, 2003b). Subsequently, James and Price (2004) showed similar results in juice grape vineyards, with sticky traps in MeSA-baited blocks attracting greater numbers of predatory insects than traps in unbaited blocks. Significantly greater numbers of the parasitoid *Anagrus* spp. were also found in MeSA-baited blocks

(James and Grasswitz, 2005). (*Z*)-Jasmone is another HIPV that attracts natural enemies of aphids (Powell and Pickett, 2003; Pickett et al., 2006). Another approach is to spray specific plant hormones, such as JA, to induced HIPV emissions and orient predators and parasitoids to plants (e.g. Thaler, 1999).

The mode of action of HIPVs on natural enemies remains unknown. However, two mechanisms have been proposed; HIPVs may influence the natural enemies' behavior directly by attracting them and increasing their searching behavior, or indirectly by making plants more responsive to insect damage for increased volatile emissions (Khan et al., 2008). The later mode of action has been referred to as "priming" (Engelberth et al., 2004), and is expected to be less disruptive to biological control because plant volatile emissions are activated only when under attack by herbivores, thus increasing the detectability of volatiles to natural enemies. Predalure (AgBio Inc.) is a commercially available lure to attract multiple species of insect predators.

HIPVs are not only important in attracting natural enemies aboveground but also belowground (Fig. 11.4). Recently, Rasmann et al. (2005) reported the first identification of an insect-induced belowground plant signal. (*E*)-β-caryophyllene was released from maize roots in response to feeding by the beetle *Diabrotica virgifera virgifera* LeConte, and shown to strongly attract an entomopathogenic nematode.

Biological control agents can enhance the efficacy of strategies for the manipulation of pest behavior, such as in trap crops and push-pull approaches. For instance, trap plants often serve as reservoirs for beneficial insects (van Emden and Dabrowski, 1994). Molasses plants, when intercropped with maize, increased parasitoids and predators of stem borers (Khan et al., 1997a, 1997b, 2008). Furthermore, the use of insect pheromones with host-plant volatiles can reduce pest populations by increasing natural enemy populations, a research area that needs further investigation. On the other hand, some approaches may reduce the abundance of beneficial arthropods such as the use of attract-and-kill strategies that attract natural enemies.

11.4 Farmer Education and Adoption

A list of technical, socio-economic, and policy-related constraints for the development and adoption of behavior-modifying strategies is provided in Table 11.4. For many growers, farming is a family affair, with the older generation teaching the younger about the practice. Educating farmers on a new strategy for pest management, such as manipulation of a pest's behavior, can be challenging because it requires changes in the farmers' current management practices. Here communication between researchers and farmers is key and can be achieved through an extensive education/demonstration program showing the benefits of new strategies. These educational programs should focus on subjects that provide farmers with a better understanding on general aspects of the pest, such as pest identification, biology, and behaviors, as well as aspects on pest-monitoring such as trap efficacy,

Table 11.4 Constraints hindering development and adoption of behavior-modifying strategies in IPM

Technical	• Specificity. Sex pheromones are highly specific, and thus their use in strategies such as mating disruption might be limited when there is need to control several pests. • Complete control is rarely achieved. This is most critical when controlling a pest with "O" or very low tolerance. • For some pest species, these strategies are not sufficient for control as a stand alone treatment. • Often low efficacy under high pest pressure. • Need for large-scale (area-wide) implementation (i.e., for mating disruption programs).
Socio-economic	• High input costs. • High competition with pesticides. Pesticides are often cheaper and have broader spectrum activity. • Need for multi-grower implementation. • Require intense education and on-farm demonstrations. Need for change in farmer perception of benefits compared to other strategies.
Policy related	• Regulatory: certain chemicals of natural origin may not have tolerance exemptions. • Registration: market volume will dictate the interest from industry to pursue registration. In most cases, interest will be biased towards highly valuable, widely cultivated, and vastly consumed crops.

assemblage, timing, and position. Educational programs also need to focus on the type of field data to be recorded by farmers, which will provide information on the occurrence and possibly the distribution of pests depending on the number and location of traps within farms. Trap information can be combined with geographic information systems (GIS) for an area-wide approach to manage insect pests (e.g. Carrière et al., 2006). Geographical information can be used to target insecticide applications to specific areas of infestation, and thus may result in reduced pesticide use.

Ultimately, the adoption of semiochemicals for control of insect pests will depend on the farmers' perception of these strategies, i.e., costs, compared to their current practices. Current pest management is dominated by the use of broad-spectrum insecticides. However, due to increased restrictions on the use of broad-spectrum insecticides in agricultural crops worldwide (e.g. Matteson, 1995), there is a growing demand for the study of alternative pest management methods. These new regulatory measures will likely increase adoption of new technologies including the use of semiochemical-based strategies for monitoring and management of insect pests. Manipulation of insect behavior through the use of semiochemicals may provide farmers with a highly specific, minimally or non-toxic, and environmentally friendly alternative to insecticides. Although semiochemicals are expected to be less toxic than broad-spectrum insecticides, their toxicity has not always been thoroughly tested.

The trend towards restricting the use of broad-spectrum insecticides in the 1990s was one of the motivating factors that led to the large-scale adoption of mating disruption in regions such as the U.S. Pacific Northwest (Brunner et al., 2002). Today, the majority of apple orchards in Washington State (USA) rely on mating disruption as part of an integrated strategy for managing pests such as codling moth. In this state, farmer adoption of mating disruption has been due to the concerted team effort between industry, academia, and U.S. government researchers, who worked together to demonstrate the effectiveness of the technology and spread awareness of its benefits. In addition to producing clean fruit, farmers have become keenly aware of the other benefits mating disruption provides, such as increased worker safety, greater positive impact of unaffected natural enemies, and reduced environmental pollution. However, large-scale adoption of mating disruption remains an economically-driven decision, and has been slower in tree fruit growing regions where a complex of multiple Lepidopteran pests affects production such as in Michigan (USA). One of the main impediments is that the most effective mating disruption technology available today still requires hand application. Cost of labor for such formulations remains an economic limitation even though these technologies are applied only once a year. The species specificity of pheromones as tools for monitoring pests is unfortunately one of their greatest drawbacks as tools for direct pest suppression or control. In regions where a complex of pests concurrently affects fruit production, use of species-specific control technologies is an economic burden that many growers cannot afford. Fortunately, multi-species formulations of pheromones have been developed, which simultaneously disrupt the communication of several moth species (e.g., Stelinski et al., 2007c). Such formulations may feature prominently in farmer management programs in tree fruit areas affected by multiple pests. The codling moth is a potent example of the broad-scale adoption of mating disruption with over 160,000 ha of pome fruit treated with pheromone for control of this pest annually (Witzgall et al., 2008). The development of effective new generation insecticides for use in tree fruit such as neonicotinoid insecticides and spinosad (Thompson et al., 2000; Tomizawa and Casida, 2003) may slow the adoption of mating disruption, as broad-spectrum insecticides are phased out, because these new generation pesticides are often less expensive than pheromone active ingredients and often target multiple pests simultaneously. However, as the deployment of mating disruption technology is further mechanized and as more effective technologies are developed based on knowledge of the actual mating disruption mechanisms, adoption of this biorational management tactic will likely increase. Pheromone or kairomone-based monitoring of Lepidopteran and Dipteran pests to determine action thresholds has become a commonplace component of many tree fruit management programs throughout the world and will likely only increase as the available number of effective semiochemicals continues to increase.

Furthermore, adoption of semiochemical-based strategies is most likely when farmers have limited alternative options for controlling a pest. For example, in highbush blueberries in New Jersey (USA) the only control for oriental beetle is soil treatment with the neonicotinoid insecticide imidacloprid. However, several blueberry farmers refuse to use this insecticide because of unsupported beliefs that imidacloprid applications reduce blueberry yield through decreased pollination. Several other growers have used imidacloprid for many years without any reductions in pollination or yield. Under this condition, the use of an alternative strategy, such as mating disruption, is likely to be adopted, not only by those farmers who do not want to use imidacloprid, but also by organic farmers. Making the cost of mating disruption more comparable to imidacloprid will also help increase its adoption among farmers. Adoption of mating disruption will reduce the use of imidacloprid, and in turn reduce the amount of pesticide in the environment and serve as a good practice for managing resistance.

Another limitation is the difficulty in obtaining registration for certain semiochemicals, such as the pheromone of the oriental beetle, which can cause delays in the commercial application of a product for several years. The oriental beetle pheromone is a ketone and this chemistry does not have a tolerance exemption for fruit crops. This has delayed the registration of the pheromone for mating disruption. In addition, the cost of registration of semiochemicals can be high, and thus interest from companies to register a product will depend on the size of the market. In fact, there is low interest from companies to register a product that is species-specific and that controls a regional pest. This is the case for oriental beetle mating disruption because blueberries are a minor crop and oriental beetle is a pest only in the Northeast USA. Oriental beetle is also a pest in ornamentals, turf, and cranberries, and mating disruption has been effective in controlling this pest in these crops (Polavarapu et al., 2002; Koppenhöfer et al., 2005; Wenninger and Averill, 2006). However, several other Scarab pests also attack them, making it unlikely that mating disruption for oriental beetle will replace the use of insecticides, which target all soil species in these systems.

A few other concerns that farmers have expressed in relation to using attractants for insect control are that deploying sex pheromones for mating disruption may inadvertently attract more pests into treated fields, thus potentially increasing the pest population, and that natural enemies attracted to the crop can unintentionally end up in the harvested fruit, especially during machine harvest, and thus be a source of contamination. These are examples where farmer education on the mechanism of these technologies is most crucial. Therefore, successful communication between industry, academia, extension personnel, members of the agri-business, and farmers is imperative when developing technologies to manipulate insect behavior.

11.5 Future Directions

Sex pheromones will likely continue to be an integral part of IPM programs in agriculture, particularly for monitoring insect pest populations. Research on mating disruption will continue to focus on understanding underlying mechanisms and developing more effective and economical release technologies. Fundamental research directions should include testing the recently formulated predictions of Miller et al. (2006a) by developing moth catch versus dispenser density profiles for various pest species. These analyses, combined with direct observations of insect behavior in the field, will determine the possible mechanism(s) of disruption. Generating such data will allow development of optimal formulations as well as facilitate determining optimal dispenser density for maximum efficacy against a particular pest. Practical research should focus on development of multi-species formulations that can be applied mechanically to large areas. Finally, although mating disruption exploits insect behaviors that are under intense selection pressure to maintain species isolation, development of resistance following prolonged use remains a possibility (Mochizuki, 2002; Roelofs et al., 2002), and should not be ignored.

More research is needed to better understand insect behaviors towards host-plant volatiles. Comparative studies should be conducted to determine the role of plant volatiles in host finding by insects with different life histories, i.e., specialists versus generalists. Although some plant-based attractants have proven successful in IPM, the use of plant repellents to control insect pests has yet to be exploited in agriculture. The best chance for implementing host-plant volatiles in IPM programs is in combination with other strategies. For instance, host-plant volatiles may enhance the efficacy of sex pheromones and biological control. Given that plant volatiles often synergize the insect's response to pheromones, the efficacy of mating disruption formulations that co-release pheromones and key behaviorally active plant volatiles requires prompt investigation. Whether a combination of host-plant volatiles and sex pheromones increases attraction of natural enemies also requires evaluation. Advances in molecular technology will lead to new ways of exploiting host-plant volatiles in IPM. Plants could be genetically-engineered to be more or less attractive to herbivores, or to be more attractive to natural enemies.

To increase farmer adoption, future research should focus on making these strategies more effective and less costly.

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