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While insects use all five senses to gather information, the most common and advantageous is the sense of smell. Many insects have a very highly developed sense of smell, especially those insects that fly at night and those that must locate mates and/or food sources from long distances. For example, the male silk moth can locate a female silk moth from a distance of almost 3 miles (4.5 kilometers) using its large feather-shaped antennae (figure 1). Insects have evolved very intricate antennae, which serve to focus and amplify the detection of chemical odors (Vogt and Riddiford 1981).

Olfactory communication, or communication that relates to the sense of smell, is advantageous for insects in several ways: it allows them to communicate over long distances, the signal lasts longer than visual signals and auditory signals (signals that can be heard), and the communication is not dependent on daylight.

The chemical signals that insects use to communicate are called semiochemicals. Semiochemicals are classified into different categories depending on the sender of the signal, the receiver of the signal, and the beneficiary of the signal:

- **Pheromones** are semiochemicals produced by one insect to communicate with another insect of the same species (known as *intraspécific signaling*). Pheromones are typically used for mate finding, trail marking, aggregation, kin recognition, and alarming. A well-known example of pheromones is the trail-marking pheromone used by ant colonies to lead ants from the nest to a source of food and back to the nest. Additionally, many insect sex pheromones have been identified and developed into commercially available products designed to lure or bait insects.

- **Allelochemicals** are semiochemicals that are produced by an individual of one species to communicate with or signal to an individual of a different species (known as *interspécific signaling*). There are three types of allelochemicals, categorized by the

**FIGURE 1.** Feathered antennae of an adult silk moth.
beneficiary of the signal, although it is possible for one signal to fit into more than one category.

- **Allomones** benefit the sender of the message. An example of an allomone is the irritating spray produced by blister beetles when they are disturbed. The spray warns predators to keep their distance, thus protecting the insect.

- **Kairomones** benefit the receiver of the message. Kairomones typically are linked to feeding: the food source (either a plant or another insect) releases a smell that attracts the herbivore/predator to the food source. Common examples of kairomones are chemicals produced by plants, which attract herbaceous insects. For instance, the Colorado potato beetle senses chemical signals from potato plants, which inform the beetle that the plant is a desirable food and egg-laying site.

- **Synomones** benefit both the sender and receiver of the message. Examples of synomones include volatiles produced by flowers. The volatiles attract insects that gather nectar and pollen from the plant for food, and as the insects do so, they pollinate the flower.

Many plant–insect interactions are dependent on semiochemical signaling between the insect and host plant. Insect semiochemical communication can be taken advantage of to manage insect pests. Several methods that include the use of synthetic semiochemicals are a valuable part of an integrated pest management (IPM) program. Applications of these products include monitoring for pests, mass trapping, attract and kill, mating disruption, antifeedants and repellents, and push–pull strategies. Using semiochemicals for pest management is a very targeted approach as they can provide selective control of a single insect pest species. Some of the strategies using semiochemicals, such as mating disruption, are approved for organic production.

Since the identification of the first insect pheromone in 1959, scientists have isolated and identified the specific pheromone composition of many insects (Witzgall et al. 2010). Insect pheromones that have been identified can then be mass produced and loaded into a dispenser or lure; many pheromones are now available commercially. The lures can be placed inside some sort of trap, such as a sticky card or one-way funnel leading into a container. The majority of pheromones that have been identified come from moths, though there are many pheromones that have been identified from other insect orders, including flies and beetles.

The type of pheromone used for monitoring moths is typically a sex pheromone. Female moths produce these compounds to call males, which follow the scent to the female. When using a sex pheromone in a lure, only males will be caught in the trap because only males naturally respond to the female pheromone. An example of a sex pheromone used in pest management is the sex pheromone of codling moth, a common pest of apple. The codling moth pheromone has been identified and developed into a commercially available product as both a population-monitoring tool and for mating disruption in orchards.

Aggregation pheromones are more commonly used in lures for beetle species because beetles often do not rely so heavily on sex pheromones to find mates. For example, the Japanese beetle produces an aggregation pheromone that adults use to meet at feeding sites (figure 2). Even after a specific pheromone has been identified, there are other factors that may impact the effectiveness of applications of these pheromones. Experiments must be conducted to develop and evaluate the specific pheromone composition needed, as well as the release rate, delivery method, trap type, and trap placement that will be effective for specific applications (Witzgall et al. 2010).

**FIGURE 2.** Japanese beetle aggregation.
Monitoring pest populations

Pheromone trapping for monitoring purposes is a key component of integrated pest management for several reasons: insect populations can be detected at the onset of infestations when populations are still quite small, the time of peak adult activity can be identified, and pest populations can be estimated. This information allows for informed decision making. Additionally, many predictive degree day models that track insect development throughout the summer using outside temperatures are based on when the first insect of the target species is caught in a pheromone trap. It is estimated that each year at least 20 million lures containing insect pheromones are produced for either monitoring or mass trapping, covering over 24 million acres (Witzgall et al. 2010). Many insect pest species are detected and monitored with pheromone traps. The codling moth is one common example, but many other species, such as Indian meal moth, grape berry moth, and gypsy moth are also monitored in the same way (figures 3 and 4). Pheromones are also used to monitor for certain structural and stored product insect pests. Feeding attractants are another type of semiochemical used for pest detection and monitoring. For example, apple maggot adults are frequently monitored using a red sticky sphere (mimicking an apple) baited with a fruit odor attractant lure (see figures 5 and 6).

FIGURE 3. A sticky diamond trap with a lure containing an insect sex pheromone used for monitoring. This particular trap is staked in a cranberry marsh and contains a lure to attract male sparganothis fruitworm moths and monitor their activity to determine when and if it is necessary to apply an insecticide.

FIGURE 4. Codling moth adults caught inside a pheromone trap.

FIGURE 5. Red sticky sphere used for monitoring apple maggot adults (attractant bait not shown).

FIGURE 6. Apple maggot adult.
Mass trapping

Mass trapping was the first attempt made at controlling insect pest populations using semiochemicals (El-Sayed et al. 2006). The concept of mass trapping is similar to using pheromones as monitoring tools, but the goal is to attract as many insects of the target species into the trap as possible to reduce or eradicate the number in the field. Depending on the targeted insect species, difficulties with this method can arise since sex pheromones, which are often used in pheromone lures, often do not attract females. In this situation, because it is nearly impossible to trap absolutely every male, and males of many insect species will mate with multiple females, there will continue to be offspring and the population may be maintained at unacceptably high levels. Therefore, the use of sex pheromones has limited use for mass trapping. There has been some success with aggregation pheromones, especially those from various beetle pests, since in those situations both males and females are attracted to the trap. In addition to pheromones, food and food volatiles for the target species have also been used in lures to draw the target insects into traps. However, it is important to determine whether other non-target insects will also be attracted to the food before it is used as a lure for mass trapping.

Overall, there have been mixed results with the use of mass trapping as an insect management tool. Extensive studies evaluating the potential for mass trapping have been performed targeting the gypsy moth, a few species of boll weevils, pink bollworm, palm weevils, a few species of fruit flies, and bark beetles (El-Sayed et al. 2006). It appears that certain characteristics of the targeted insect species and the landscape are necessary for a higher level of potential control. First, if the insect species has only one generation per year and has a low mating frequency, there are fewer insects that need to be caught per season and the population is less likely to exponentially increase throughout the season. Also, the baseline population needs to be low for a successful mass trapping program. Isolated pockets of pests, pests that feed on only one host plant, and pests with limited mobility are also favorable candidates for mass trapping. These characteristics limit the number of insects that migrate into the area, and a single crop can be targeted rather than trying to catch insects that could be located throughout the entire landscape (El-Sayed et al. 2006). Trap design is also critical because the trap must successfully capture attracted individuals and be able to hold large numbers of insects without becoming saturated. Despite the mixed results, there is potential for mass trapping to be a useful method of pest control using semiochemical attractants in certain situations.

Attract and kill

Attract and kill is a method that uses a combination of either pheromones or kairomones as attractants along with insecticides to control insect pest populations. In this method, the semiochemical is mixed with or set amongst a toxic substance whereby when the insect is lured in, it will encounter the insecticide and die. The insect isn’t necessarily captured inside a trap; rather, it needs to come in physical contact with the semiochemical/insecticide mixture. This mixture could be located on a post or structure in the field, attached to the bark or branch of a tree, or coated over an appealing egg-laying site. Insect pathogens can also be used instead of insecticides, a method known as “attract and infect,” although this is less common.

The mechanisms and limitations of attract and kill are very similar to those of mass trapping, but with the added complexity of using an effective insecticide in the mixture. Most studies have found that in order for attract and kill to be a successful form of pest management, the pest population needs to be low and in an isolated area to limit insect immigration. The number of lures, distribution of lures, volume of pheromone being released, and the duration that the pheromone is released are also critical to the success of the program (El-Sayed et al. 2009). Because target insects must physically come into contact with the dispenser in order to be killed by the insecticide, the pheromone attractant must be more attractive than that of the naturally occurring source, especially when sex pheromones are being used. Also, if the pheromone density is too high, it will lead to disruption rather than attraction (see the following section on mating disruption), so the insect will not come in contact with the insecticide, leading to a failure of control. Due to these constraints, there have been mixed results with the use of attract and kill. The use with the most potential is to eradicate invasive species, since new invasive species are typically low in number and are in isolated areas. However, many invasive species are first found in urban areas, and including insecticides in the mixture can lead to a negative public perception, further limiting the use of this method (El-Sayed et al. 2009). Recently, there has been an increase in research on the use of attract and kill as an IPM tool with increasing promise for important economical pests such as codling moth and spotted wing drosophila.
“Attract and infect,” an interesting application of attract and kill, uses pheromone attractants to lure insects to inoculate them with a communicable fatal disease or parasite. The insects are then allowed to leave and infect other members of their species. Studies have evaluated an attractant/fungus trap for Japanese beetles with encouraging results (Klein and Lacey 1999).

**Mating disruption**

Mating disruption is a method of pest control that relies on pheromones (most commonly a sex pheromone) applied across a large area (figure 7). The goal of mating disruption is to decrease the probability of successful mate finding, thus reducing the number of offspring in the subsequent generation. Mating disruption is most efficient in areas of relatively low pest density, since in high pest density areas there is a greater probability that males and females will find each other by chance or by using visual cues. Often this limitation is addressed by using a preliminary insecticide spray to reduce the pest population before mating disruption is employed. Mating disruption is also most effective when applied over very large areas or isolated populations. Therefore, mating disruption is usually not practical for small-scale agriculture (less than ten acres) or for a backyard gardener.

A key consideration for successful mating disruption is the proper means of dispensing the pheromone. Different pheromone dispensers have been developed for different species so that they release the appropriate amount of pheromone for a certain length of time (i.e., the pheromone must be present for the full duration of time when the adult insects may be mating). Also, since pheromones are airborne signals, the dispenser must be placed in an area of the field where the pheromone will not rapidly blow off the field. Lures are commonly placed inside tree canopies where the insects mate or above crops where the insects fly when searching for a mate. Different types of pheromone dispensers can be used, such as rubber tubing, plastic wafers, hollow fibers, puffers, wax matrices, or sprays (figure 8).

**FIGURE 7.** A male moth normally finds a female moth by following the female’s pheromone trail (top). Two possible mechanisms of mating disruption (lower) include the male following a false trail (long dashed line) and the male being overwhelmed by the volume of pheromone so that he is unable to respond to any of the pheromone signals (short dashed line).
Often the pheromone used for mating disruption isn’t the complete insect pheromone but rather just a few of the major components. Therefore, the true female pheromone may be more attractive than the synthetic pheromone, but as long as the synthetic version is attractive enough, mating disruption can work. However, as with the mass trapping and attract and kill methods, particular characteristics of the target insect population and environment will have an impact when determining whether mating disruption will be a viable pest management strategy for a particular pest in a given location.

There have been many success stories using mating disruption, and it is a staple in many pest management programs in conventional as well as organic production systems. For example, mating disruption is a major component of the federal “Slow the Spread” program focused on reducing the rate of the invasive gypsy moth’s spread across the country. Mating disruption is also commonly used to control codling moth, a major insect pest of tree fruit.

**Antifeedants and repellents**

Antifeedants and repellents are naturally occurring or synthetic compounds used with the goal of preventing an insect from coming in contact with, landing on, or feeding on a particular surface, be it a plant or human/animal skin. They can act locally, as with a topical lotion or surface spray, or on a large scale, preventing an insect from entering an entire area or crop planting. Overall, there has been limited success with antifeedants used in large-scale agricultural settings (Isman 2006). Neem oil is one product that has been used as an antifeedant, but the majority of the benefit of the oil may be linked more closely to its insecticidal properties than to merely changing the insect’s behavior. The limited use of antifeedants in agriculture can be attributed to the challenge that substances used as antifeedants often have a wide range of efficacy even amongst closely related insect species. Also, compounds that may deter one pest from feeding can sometimes attract or increase the feeding of other pest species (Isman 2006). The length of time that the products are effective is often quite short due to rain, UV instability, and feeding by other insects or organisms. This short duration also limits the usefulness of potential products in an agricultural setting.

Antifeedants and repellents have been more successful for protection against insects that feed on humans and other mammals, most notably mosquitoes. The most effective and widely-used product that has been developed is DEET (N,N-diethyl-m-toluamide). DEET provides a high level of protection and good persistence. Other chemicals are not as effective as DEET, but some alternatives have demonstrated potential. Examples include the oil of citronella to repel mosquitoes in outdoor areas and a chemical extracted from citrus peels (d-limonene) to repel fleas and ticks on pets. Other plant essential oils are being examined for control of termites, cockroaches, flies, and other agricultural pest insects, and for managing mites in honeybee hives.
Push–pull system

The push–pull system was developed for smallholder farms in Africa as a method of pest control when insecticides were not available. This system uses both naturally occurring plant repellents (“push”) and attractants (“pull”) to move insect pests away from the desired crop. Under natural conditions, plants are constantly releasing volatiles that insects are sensing. These scents signal to an insect what is a good food plant or egg-laying site, as well as what is a plant to be avoided.

For the push–pull system to be a viable pest management program, there needs to be a plant or chemical lure that attracts the insect pest more than the crop, and another plant or chemical lure that repels the insect. The repellent plant or lure is placed within the desired crop, and the attractant plant or lure is placed outside of the desired crop. In this way, the insect senses the signals of the repellent plant or lure and stays away from them. But if only repellent plants or chemical lures are present, the insects will move onto the desired crop. Therefore, the more attractive crop or chemical lure is placed outside the crop, which draws the insects out of the desired crop. The insects are pushed out of the desired crop and then pulled into the non-target plants or traps.

The main success with this system has been protecting maize from stem-boring insects in sub-Saharan Africa. In the laboratory, semiochemicals that were repellant and attractant to the stemborers were identified. Native plants in the area were then screened to determine which ones produced those semiochemicals and were also available and economically viable to grow. A couple of legumes in the genus *Desmodium* and a grass species, molasses grass (*Melinis minutiflora*), were identified to be especially repellant to the stemborers, and Napier grass (*Pennisetum purpureum*) was selected as an attractant. Other plants were also studied to determine which ones were more drought tolerant so that this system could be used in drier areas or others that had beneficial properties like weed suppression. Currently, the push–pull system is being used by about 125,000 smallholder farmers in eastern Africa and has shown to be very successful at increasing maize yields with minimal inputs (Kahn et al. 2016).

Insect communication using smell is a critical factor in an insect’s ability to find mates, locate food, and avoid predators. When controlling an insect pest, these modes of communication can be manipulated in order to change the insect’s behavior. Synthetic versions of attractive scent molecules used by insects can be used in management strategies for pest monitoring, mass trapping, attract and kill, and mating disruption. Unappealing or repulsing scents (natural or synthetic) can be used as antifeedants and repellents or for crop protection using a push–pull strategy. Knowledge of these methods combined with the specific pest’s biology, can form a significant component of an effective integrated pest management program.

References


