Population Dynamics of Moths Under Mating Disruption

VINCENT P. JONES
Assistant Entomologist
Tree Fruit Research and Extension Center
Washington State University
1100 N. Western Ave.
Wenatchee, WA 98801
vpjones@wsu.edu

The Food Quality Protection Act (FQPA) is eliminating or restricting the use of many organophosphate (OP) pesticides commonly used for control of codling moth (CM) and leafrollers (LR) in apple and pear. Although several "softer" alternatives pesticides are available, for control of CM mating disruption (MD) is clearly the best alternative in most situations. Currently, MD is used in Washington for CM control on nearly 93,000 acres of apple and pear (Brunner et al. 2001). In organic orchards in particular, MD is the best method of managing CM.

While MD appears to be the likely future for pest management programs in Washington apples, the implementation of MD is not without problems. First, it does not cause mortality of the pest, and using it in the same fashion as a pesticide will result in poor or inconsistent control. Secondly, understanding control failures and how to prevent them requires a knowledge of not only the pest, its behavior, and population dynamics, but also an understanding of the mechanisms by which mating disruption may act. The purpose of this paper is to clarify some of the mechanisms by which MD acts, and some broad guidelines for its use.

How moths find females in the absence of MD
The pheromone communication system of moths has developed so that males can find females over a relatively large area, even when the population density of the females is quite low. Pheromones are typically composed of 2-5 components that occur in relatively constant ratios. If the pheromone blend is altered, inactivity or a reduced response may occur.

Virgin females typically release pheromone, a behavior referred to as "calling", beginning at dusk and continuing for several hours a night. Calling normally occurs when the wind speed is quite low, so that a recognizable pheromone "plume" can be generated. Males normally move upwind and when they encounter a plume composed of the correct pheromone, they begin a searching behavior. This behavior is flight at an angle to directly upwind – they are searching for the edges of the plume, and when they fly out of the plume, they turn abruptly back into the plume. This results in them being able to narrow the location of the female down with each pass through the plume, until they finally land on the same leaf and begin courtship behavior. Once mated, females generally no longer call or produce pheromone.

How mating disruption acts in theory

A number of mechanisms have been proposed to explain why MD works in theory. The number of mechanisms varies by author, but five mechanisms can be used to broadly cover the likely ones (Bartell 1982, Brunner 1991). First, the pheromone blanket in the orchard may cause sensory habituation so that the male antennae don't respond to the pheromone correctly. Secondly, the males may not find the females because they spend so much time following the false trails of the dispensers that they rarely find a female. The greater the number of point sources of pheromone (i.e. dispensers) compared to the number of females, the more important this mechanism may be. Thirdly, the blanket of pheromone may simply mask any of the pheromone plumes put out by females. Fourth, by putting out a large concentration of one of the pheromone components, the blend perceived by the male moth may not match the ratio to which it normally responds. Finally, certain materials may act as anti-pheromones in that they bind to the receptors and prevent the pheromone from being detected.

The result of the five methods mentioned above is that they prevent the males from finding the females. With moths in particular, unmated females produce only sterile eggs. Thus, population growth declines at a rate directly proportional to the percentage of the population that is unmated. For example, if 80% of the female moths in a mating disruption area are unmated (i.e. 20% are mated) and all the females in a nearby area are mated, then the growth rate in the mating disruption area is only 20% of the control area. Factors such as movement of mated females into the area are of concern because MD does not affect them in any way.

How mating disruption works in practice

While the mechanisms mentioned above are important to understand, the key question is whether they are the only mechanisms that could help MD work in practice. If they are the only mechanisms that reduce population growth under MD, then a simple test to determine the effectiveness of MD is to determine the differences in the percentage of females that are mated in MD treated areas and control areas. For oriental fruit moth in California, there did appear to be significant differences in mating success under mating disruption, suggesting for this insect that prevention of mating may be important (Rice and Kirsch 1990). For codling moth and leafrollers, the results have been that there is little to no differences in the percentage of mating between control and treated areas (Agnello et al. 1996, Knight 1996) suggesting that mating prevention is not likely a key mechanism. While movement of mated females could be important in these situations, it is minimized in large plots, suggesting that other mechanisms might be behind the success of MD for CM.

Population biology gives some important clues as to why MD works for CM. Studies of population growth clearly show that the time of first mating is the most important factor governing the growth rate of a population. In reviewing the literature, I found 13 studies that examined the effect of delayed mating in moths. Four effects were noted in these studies: As the delay in mating increases, (1) the longevity of the females increases, (2) eggs produced per female decreases, (3) gross percentage fertility of eggs laid decreases, and (4) the period after mating but before egg deposition (pre-oviposition period) increases. However, these effects were not constant for a particular duration of delay between the different species examined nor did all species exhibit all four effects. Codling moth was one of the pests studied, and two of the studies suggest that it is sensitive to delays in mating. For example, Knight (1996) states that a 2 day delay in mating caused a 40% reduction in egg production, and (Vickers 1997)) showed a 8% reduction in egg production if mating is delayed 2 days and 30% reduction if delayed 4 days.

To determine which effects apply to any particular pest, laboratory studies must be performed to determine the overall sensitivity of the pest to delays and that data must be combined with simulation studies to determine the effect on the pest population growth rate. Unfortunately, these studies are not simple to perform, and virtually all the studies we surveyed gave only broad generalities and were based on small sample sizes which makes the data useless for population models necessary to test the importance of delayed mating in field situations.

An example from afar

When in Hawaii, I worked with koa seedworm, which is a tortricid pest of macadamia nuts and performed the experiments required to determine how important delayed mating is with that particular moth (Jones and Aihara-Sasaki 2001). We reared moths in culture and collected pupae before they emerged. Female moths were paired with males either 1-day after emerging (normal time) or males were withheld for 4 or 6 days. We then followed the daily mortality, egg production and hatch rate for the entire female life span. We found that there was no difference in mortality rate between moths mated at the different times, but there was a major difference in the production of daughters. Females experiencing no delay in mating produced an average of 68 daughters while females experiencing a 4-day delay produced 57 daughters (a 17% reduction) and females experiencing a 6-day delay produced only 35 daughters (a 49% reduction). The large drop between the females exposed to the 4 and 6-day mating delay suggests that there is a threshold that must be surpassed for MD to be effective. Thus, if a MD technology (dispensers, puffers, sprayable formulations) cannot delay mating so that this threshold is surpassed, MD by itself would not be expected to suppress population levels of the pest.

The Hawaii study also allowed us to examine the effect of adding small amounts of mortality during the first week of a female's life span to simulate an effect of natural enemies on population growth when mating was delayed 4 or 6 days longer than normal. We found that natural enemies acted synergistically with mating delay to decrease population growth rate. For example, if 10% mortality was added to females experiencing a 6-day delay in mating, the percentage decrease in growth rate was higher than for the females experiencing a 4-day delay. Females experiencing a 4-day delay also had a greater percentage decrease in growth rate than the females where mating was not delayed. These data suggest that if our MD technology can delay mating only 4-days, and if an additional 28% natural enemy mortality can occur during the first week of a female's life, that MD may work as if the full 6-day delay in mating is occurring.

Mating Disruption + Biological Control

The Hawaii study showed that BC can have a major positive impact on a MD program. The relatively low rates of natural mortality required to stabilize a marginal MD program should cause entomologists to reconsider the importance of many of our natural enemies that previously had been considered to be of minor importance. Unfortunately, the marginal systems augmented by natural enemies will probably be less stable than systems where the MD technology can delay mating beyond the threshold because pesticide sprays for secondary pests may disrupt the natural enemies. These types of systems will probably also show variability in efficacy of the MD program that is related to different natural enemy complexes found in the different areas.

The data also suggest that the reason that rates of MD dispensers can be reduced over time may be caused by increasing biological control related to decreased pesticide applications. However, as mentioned above, the decreased rate of dispensers comes at the cost of decreased stability of the MD program.

Considerations in use of mating disruption

MD requires a different way of looking at pest suppression than that used in evaluating or using insecticides. First, the pheromone MD programs cause no direct mortality to the moths or larvae. This, coupled with the fact that CM (and other moths) can often mate on the day of emergence, means that MD dispensers must be in place before the first moths are caught in pheromone traps. I suggest putting the CM dispensers out during the pre-pink or at least by the pink stage of apple bud development – this is before any codling moth should be caught anywhere in Washington. The longevity of the dispensers should not be a concern because early in the season the release rates of the dispensers are so low. Secondly, when placing the dispensers, make sure they are in the upper third of the canopy – mating occurs primarily in this region and if dispensers are placed too low, will not interfere as effectively with the mating process. Third, if MD is working, a normal pheromone trap will not catch any moths. For codling moth, a 10x pheromone lure will enhance some of the efficacy of traps, but they will still be less effective than a normal 1x pheromone lure in a non-MD orchard. Food-based lures are being developed for both CM and LR and should be on the market in the next year (CM) or two (LR). However, these new food lures will require careful calibration so that growers and consultants will be able to understand what the catches mean compared to catches in pheromone traps. Fourth, pheromone concentrations will be the lowest at the upwind side of the orchard, or on highest sites within the orchard. These areas should be supplemented with extra dispensers or pesticide sprays (borders) to prevent damage or mating from occurring there. Finally, while MD is a great control tactic in many ways, it should not be used if CM pressure is excessive. In these circumstances, suppress CM populations to as low a level as possible and then try MD. Most growers are still applying a single cover spray for CM, even though using a full rate of MD.

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