

Effect of Plant Chemicals on the Behavior of the Mediterranean Fruit Fly

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INTRODUCTION

Throughout their lives insect herbivores are trapped between natural enemies and a deep sea of foliage or fruits of variable nutritional value (Lawton and McNeill, 1979). To navigate their way through this environment insects have developed complicated physiological and behavioral mechanisms that suit the needs of their chronological age and physiological requirements. These mechanisms drive decision making in insects and are aimed at maximizing fitness. Insect plant interactions have been studied extensively trying to give answers to both proximate and ultimate questions. Processing of visual, chemical and mechanosensory environmental information guide insects to locate host plants, and then feed and oviposit, through a series of steps that are neatly described by Schoonhoven et al. (2005). Besides host finding, feeding and oviposition, plant chemicals may also influence developmental rates and the progress of maturation (both leading to reproductive success) since they define the nutritional value of the consumed host. Also, in several insect species volatiles influence mating behavior. In some cases sexual signaling

and pheromone emission begin in the presence of plant volatiles, while in other cases plant compounds are used as pheromone precursors and thus become involved as behaviour modifying chemicals indirectly. There are several studies dealing with the host finding behavior of tephritids (true flies, Diptera: Tephritidae), and the influence of plant compounds on their reproductive success. Among the most studied species is the Mediterranean fruit fly (medfy) *Ceratitidis capitata* (Wiedemann), one of the most notorious pests of fruit trees. There are several studies on flies of the genus *Rhagoletis*, *Bactrocera* and *Anastrepha* (see Robinson and Hooper, 1989, and references therein) as well. Tephritids use both visual and chemical signals to locate and access habitat, adult food, oviposition sites and mating resources. Plant chemical cues play a crucial role in mediating host finding and oviposition (Fletcher and Prokopy, 1991). Soon after attaining adulthood both males and females need to locate food rich in proteins and carbohydrates. The availability, quality and quantity of adult food has significant effect on the ovarian maturation and egg development (Carey et al., 1998; Carey et al., 2002) but also on the reproductive success of males (Blay and Yuval, 1997; Field and Yuval, 1999; Kaspi et al., 2000; Papadopoulos et al., 1998; Shelly et al., 2002a; Yu-

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val et al., 2002). Therefore, both sexes share the same nutritional interests and may use similar cues to locate habitats bearing high quality food. Sources of food can be located on host plants in the form of fruit juice, and other plant exudates, but also on other niches such as bird droppings. Nevertheless, the interests of the two sexes might diverge later in their lives. After attaining maturity and becoming mated, females search for suitable oviposition sites, while sexually mature males search for receptive females. At this point in their lives males and females employ different cues to maximize fitness. This results in temporal differences in the spatial distribution of the two sexes (Papadopoulos et al., 2003). As insects age, their response to cues may shift, but this requires further study.

This paper reviews current information on the relation between plant chemicals and the Mediterranean fruit fly. It addresses the influence of age and adult physiology on the response of medflies to plant chemicals and the effect of plant chemicals on medfly behavior during host finding, mating and oviposition. It also addresses the issue of how plant chemicals may influence the dispersion patterns and spatial distribution of the fly.

ADULT AGE AND PHYSIOLOGY

The response to plant cues may vary with the physiological condition and age of individual insects. Aging may bring about physiological changes or result in senescent sensory systems and reduced responsiveness to specific stimuli. Major physiological alterations take place during reproductive maturation and mating. An example of this would be olfactory mediated behaviors of female *C. capitata* after they have mated. Virgin females choose the odor of male pheromone over the odor of host fruits; however, after mating they switch

preference and select the odor emanating from host fruits (Jang, 1995). Male accessory gland fluids contain compounds responsible for the noted change of behavior. Virgin females injected with male accessory gland fluids switched odor preference likewise to mated ones.

Host plant stimuli may substantially influence the physiology of medflies. In other fruit flies the physical properties of artificial oviposition devices influence ovarian maturation and egg development (Lachmann and Papaj, 2001). The presence of chemical and visual properties of olive fruits affect egg maturity and oviposition in the olive fruit fly *Bactrocera oleae* (Rossi) (Girolami et al., 1982). Females reabsorb eggs when no such stimuli are available, and they resume egg maturation when fruits reappear. In fruit flies of the genus *Anastrepha* host odor and male pheromone have a significant effect on ovarian development (Aluja et al., 2001). The effect of chemical properties of the host plants, and especially that of fruits, on the ovarian dynamics of female medflies is not yet well studied. Preliminary laboratory observations indicate a neutral influence of citrus odors on ovarian maturation in medflies (Ioannou, 2005).

The effect of aging on the response to plant chemicals remains largely unknown. Differences in response to synthetic attractants of medfly adults of four different age classes have been discovered. In a field cage study male and female medflies older than 30 days exhibited reduced responsiveness to the synthetic compounds of ammonium acetate and trimethylamine (BioLure, Oregon) compared to younger flies (N. Koulooussis, N. Papadopoulos and B. Katsoyannos unpublished). Whether old age attenuates response to natural plant chemicals similarly with younger flies remains to be investigated. Studies addressing the behavioral adjustments of the older individuals may shed important light on the role of older in-

dividuals in nature and provide basic information on aging dynamics of fruit flies and other animals.

HOST FINDING

Visual and chemical stimuli emitted from host plants direct fruit flies to host trees (Katsoyannos, 1989a; Katsoyannos, 1989b). Adult medflies respond to plant derived olfactory cues and use them to orient towards host trees. The distance over which visual or plant odor stimuli are first detected and elicit a response remains largely unknown (Prokopy and Roitberg, 1989). The only documented case of attraction were females of *Rhagoletis pomonella* that have been shown to respond to fruit odor emitted from a distance of approximately 20 m (Fletcher and Prokopy, 1991). Upon landing on a host tree, the shape, size, and color of the fruits and other visual properties attract female medflies to fruits suitable for oviposition. Fruit density may also play a role. Physical properties of the fruit surface, gustatory and/or short range olfactory stimuli influence decision to accept or reject the specific fruit. The insect will oviposit or depart respectively.

OVIPOSITION

Mature mated medfly females search for ripening or ripe fruits for oviposition. Upon landing on a fruit that is suitable for oviposition, a gravid female engages in a series of steps that define preoviposition behavior (Levinson et al., 2003). This behavior involves examination of the fruit with her proboscis, tarsi, and probably olfactory sensilla. This process is performed to assess suitability and the possible presence of host marking pheromone deposited by other females. She then locates a suitable spot to oviposit, preferably a depressed or injured site on the

fruit surface. After finding a suitable location the female uses her ovipositor to lay a group of eggs in a perforated cavity.

As suggested by Levinson et al. (2003) medfly oviposition is favored by high fruit humidity and appropriate tactile and optical stimuli, while the odor of fruits plays a secondary role. Though odors from small amounts of orange peel oil did not affect oviposition, higher doses of orange oil had deterrent effects. Electrophysiological studies showed that olfactory sensilla on medfly antennae are sensitive to orange oils (Hernandez et al., 1996). Under natural conditions this sensitivity may manifest itself as avoidance by females to lay eggs on fruits loaded with citrus peel oils. High doses of citrus oils have toxic allelopathic effects on immature medflies. Therefore, females might use the odor from citrus peel as a signal to avoid oviposition where offspring survival may be low. However, essential oils are not the only odors emitted from mature fruits and it seems that other chemicals encourage oviposition. Guava juice has been used as oviposition stimulant and preferential oviposition on ripe coffee berries has been reported (McInnis, 1989; Vargas et al., 1995). Jang et al. (1994) reported intensive egg-laying in hollow plastic spheres perforated with holes emanating odor from host fruits.

The extent fruit odors influence the oviposition behavior of medflies became clearer from studies utilizing citrus odors. Peel and pulp odors differ substantially in many fruits, even though some of the compounds that constitute them are the same. In citrus fruits, essential oils account for the peel odor, whereas the odor of the pulp comes from other compounds. In a field cage study, female medflies did not respond to the odor of orange peel oil, but responded to the odor of juice from the pulp; males responded to both orange oil and to pulp odors (Katsoyannos et al., 1997). Both sexes search for food, so pulp chemicals may direct them to feeding sites.

However, gravid females might also use pulp odor to locate oviposition sites. It is well documented that females exploit natural or artificial peel-penetrating fruit wounds to lay their eggs (Papaj et al., 1989). Therefore, females may be able to discriminate between odors from the peel and odors from the pulp and use them appropriately to maximize fitness. High concentrations of citrus oils might indicate an oviposition site with deleterious properties that would result in reduced hatchability of eggs, enhanced mortality of early instar larvae, or suppression of larval growth (Katsoyannos et al., 1997). Conversely, juice volatiles might indicate a highly suitable oviposition site that would enhance egg hatch and larval performance. Other workers have reported juice odors to either increase medfly oviposition (Jang and Light, 1996; McInnis, 1989) or to be neutral (Stark et al., 1991). Recent laboratory studies that addressed this phenomenon showed that females ovipositing in response to citrus juices are induced to start reproduction at a younger age, remain oviposition-active for a longer proportion of their lives, and lay more eggs than females ovipositing in response to water (Ioannou, 2005; N. Kouloussis, B. Katsoyannos, N. Papadopoulos, unpublished data).

Another group of compounds that affects oviposition of medfly females and other tephritids is referred to as "green leaf volatiles" (Jang and Light, 1996). This group comprises six-carbon aliphatic aldehydes and alcohols and forms the main odor emitted from green leaves and unripe fruits. Green leaf volatiles repel medflies from landing on objects emanating this odor and also deter oviposition. Green leaf volatiles provide a cue of poor larval food and may assist females in making wiser choices of oviposition sites, thus contributing to increased offspring survival. Other volatiles that deter gravid females from oviposition are emitted from fermenting fruits (Jang and Light, 1996).

SEXUAL BEHAVIOR

Medfly males form loose aggregations termed leks, usually on host plant leaves, performing sexual signaling by emitting a sexual pheromone and defending territories (Prokopy and Hendrichs, 1979; Yuval and Hendrichs, 2000). Receptive females visit leks and choose mates following a process that is not well understood. Males are likely evaluated and selected as mates on the basis of their physical characteristics and their courtship performance. Overall male mating success relies on the ability to establish or join leks, perform sexual signaling, convince courtship, and finally mate and transfer sperm.

Males of *C. capitata* and other Tephritidae display a strong attraction for certain plant-derived substances, such as the essential oils contained in the peel of citrus fruits and the root of ginger, as well as for certain laboratory synthesized chemicals, such as trimedlure. A well studied plant substance is α -copaene, a sesquiterpene hydrocarbon that is found in a wide range of medfly hosts and in the above mentioned oils (Nishida et al., 2000). Males are attracted to α -copaene from a long distance and select treated over untreated leaves. It has been suggested that α -copaene triggers lek establishment by functioning as an aggregating stimulus for males (Nishida et al., 2000). In the same study Nishida et al. showed a short range attraction of female medflies to α -copaene sources and reported "abnormal" female behaviors. In a field cage study, males, not female medflies, were attracted to the odor of essential oils emanating from peel wounds on oranges (Katsoyannos et al., 1997). Shelly and Villalobos (2004) reported tight aggregations of males on the trunk and branches of specific guava trees where natural α -copaene occurred. Males in both studies appeared to feed on the odor source on orange peel wounds or on the bark of guava (Katsoyannos et al., 1997; Shelly and Villalobos, 2004).

Convincing explanations for this affinity between *C. capitata* males and certain host-derived substances has only recently been provided. Over the past few years a wealth of information have been gathered on the effect of orange peel oil and ginger root oil on *C. capitata* males. Exposure to these oils confers to males a significant mating advantage over non exposed males (Papadopoulos et al., 2006; Papadopoulos et al., 2001; Shelly, 2001; Shelly and McInnis, 2001; Shelly and Kennelly, 2004). Exposure of males to natural sources of α -copaene or/and other compounds, emitted by wounded oranges or guava bark, increase mating competitiveness as well. The behavioral and physiological mechanisms underlying these phenomena have not been fully elucidated. Both orange oil and ginger root oil increase male sexual signaling (Papadopoulos et al., 2006; Shelly, 2001), and high signalers mate at higher rates (Shelly, 2000). Part of the explanation may, therefore, rely on the elevated signaling activity of exposed males. Nevertheless, the above two oils might also function in other ways. In wind tunnel experiments females tended to become arrested more on objects emitting pheromone from males previously exposed to orange oil than to objects emitting pheromone from non exposed males. However, in the same experimental set up the pheromone emitted from males exposed to ginger root oil did not have such an effect (Papadopoulos et al., 2006). Female arrestment might provide males exposed to orange oil with extra courting time and increase their mating probabilities, whereas ginger root oil might act differently. Video recording of pre-copulation behavior of males exposed to ginger root oil showed that females accept more readily males exposed to ginger root oil over unexposed males (Briceno et al., 2005). These males may be successful in mating because they display one or more courtship elements in a distinctive form or rate and/

or because they emit distinctive close-range olfactory cues (Papadopoulos et al., 2006).

The physiological mechanisms underlying the function of the above two plant chemicals have only recently been studied. It has been hypothesized that (a) males ingest the responsible chemicals to use them in pheromone biosynthesis, thereby producing pheromone of higher quality; (b) males perceive volatile chemicals olfactorily from some distance and this triggers production of pheromone of higher quality; (c) volatiles from the above two compounds aromatize males by interacting with cuticular odor, thus rendering these males more attractive to females. However, topical application of orange or ginger root oil on the wings of males had a negligible effect on their mating performance (Papadopoulos et al., 2006).

SPATIAL DISTRIBUTION

The ecological factors selecting for particular spatial patterns rest on the spatiotemporal pattern in the distribution of food resources, climate and probably other critical parameters (Koenig, 1999). Plant sources and plant chemicals are distributed in patches, and there is also a temporal availability of the respective chemicals. As we discussed above, plant chemicals affect host finding, oviposition, habitat selection and mating behavior of medflies which might affect their temporal and spatial distribution. Therefore, adult medflies in specific times of the season will be distributed in patches as a result of their response to above plant compounds (Nestel et al., 2004; Papadopoulos et al., 2003). Spatial distribution might differ between the two sexes because of the different ecological and behavioral needs. In a recent field study that examined the temporal and spatial distribution of medflies in a mixed deciduous fruit orchard in northern Greece (Papadopoulos et al., 2003), it was found that females exhibit ag-

Summary diagram

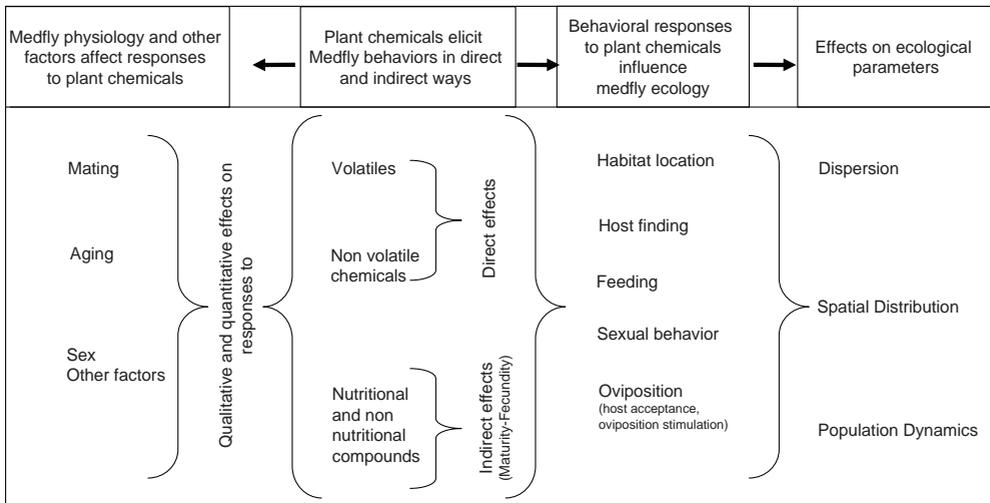


Fig. 1. Summary diagram of the complex interactions of plant chemicals with medfly behaviors including those factors affecting the response of medfly to plant chemicals and the ecological consequences of these responses.

gregated distributions that are tightly related to host fruit availability and maturity, and that low populations tend to be more clustered than high populations. Males exhibit aggregated distributions that are not closely related to host fruit maturity and availability, and are different from those of females in specific times of the season. A dramatic increase of the population size, and exhaustion of fruit resources at the end of fruiting season, results in random distribution indicating a dispersion drive. The spatio-temporal dispersion pattern of the medfly populations in an orchard is a dynamic process that might also reflect the individual fly foraging behavior. Essential resources for adults constitute adult food, mating sites, mating partners, oviposition sites, and refugia (Prokopy et al., 1994). Differences between the two sexes reflect the differential use and need for resources. On the other hand, male spatial distribution might be affected by the patchy availability of plant chemicals, which may vary between and within plant species and male distribu-

tion may affect female distribution via attraction to male sex pheromone. Therefore, plant chemicals might directly affect male spacing and indirectly female spatial distribution (Shelly and Villalobos, 2004). Figure 1 summarizes the complex interactions of plant chemicals with medfly behaviors and the resulting ecological consequences.

PRACTICAL IMPLICATIONS AND CONCLUSIONS

The successful application of the Sterile Insect Technique (SIT) for the control of the Mediterranean fruit fly and other fruit flies hinges on the quality of the released males that has to be comparable with that of wild males. Sterile males should exhibit a battery of qualities such as adequate mobility and survival, ability for habitat orientation, mating compatibility with wild females, and a capacity to compete successfully with wild males (Katsoyannos et al., 1999a). The im-

portance of specific host trees for the sexual behavior of medflies has been documented. In field studies, most of the leks were established on fruiting *Citrus* trees and most matings were observed in the foliage of these trees (Hendrichs et al., 1991; Prokopy and Hendrichs, 1979). Therefore, to be competitive sterilized released males need to be responsive to plant odors that would drive them to specific trees to ensure mating success and survival. Host location and response to plant chemicals should be included to the routine quality control tests for mass-reared sterilized males. In field cage tests conducted in a green house mass-reared males of the genetic sexing strain Vienna-42 performed sexual signaling and mating on *Citrus* trees and not on other plants (Katsoyannos et al., 1999a). Also, in field cage tests conducted in a citrus orchard sterile males of the same strain responded similarly to wild males to odor emanating from several citrus fruits that were wounded on the peel. The above findings showed that mass-reared males that had been held in the laboratory for more than 150 generations and had undergone artificial selection, still maintained a clear preference for citrus foliage and volatiles.

Host fruit chemicals reduce preoviposition period and increase oviposition rates (Ioannou 2005). Wild flies accept artificial oviposition devices easier when host fruit chemicals are present to stimulate oviposition. Therefore fruit chemicals could be used to (a) increase production in laboratory rearing of medflies, (b) increase production in mass rearing facilities, and most importantly, (c) avoid bottleneck effects during new introductions of wild strains to laboratory conditions.

Host fruit chemicals could be also used to assess the fertility of wild females in Sterile Insect Release Programs (Katsoyannos et al., 1999b; McInnis, 1989). So far this has been done with indirect labor intensive methods, such as with sampling of wild hosts and examining them for medfly eggs. An alternative

method relies on collecting wild females from the field using female specific traps, keeping them individually, and having them lay eggs in artificial oviposition devices (Katsoyannos et al., 1999b). The use of host juice or other host fruit chemicals that stimulate oviposition promotes quick adaptation to artificial oviposition devices and could save time and labor while providing important data for the fertility of the captured females that is directly related to the success of a SIT Program.

The mating-enhancing properties of orange peel oil and ginger root oil (Papadopoulos et al., 2006; Papadopoulos et al., 2001; Shelly, 2001; Shelly and Kennelly, 2004) could be put into use to increase mating success of the sterilized flies in Sterile Insect Release Programs. The exposure of sterile males to ginger root oil has been implemented recently with success. Sterilized, mass reared males were exposed to ginger oil and acquired a mating advantage over wild non exposed males (Shelly and McInnis, 2001; Shelly et al., 2004; Shelly et al., 2002b; Shelly et al., 2003). Exposure to ginger root oil not only increases the efficacy of the SIT programs but may also result in substantial decrease of the cost of these programs. Exposure to ginger root oil increases mating competitiveness; therefore, lower numbers of males need to be released to achieve the same result (Barry et al., 2003). Here we attempted to present a review of the recent advances on the influence of plant chemicals on the behavior of the Mediterranean fruit fly and to highlight the practical implications of the acquired knowledge. Before concluding we should point out that despite the progress made in understanding the complex interactions between plants and the Mediterranean fruit fly behavior, there are still plenty of challenging questions to answer. For example it would be very interesting to chemically identify the exact compounds responsible for attracting medflies or eliciting various responses. Such chemicals could be used to develop more powerful at-

tractants for monitoring and managing the medfly, as has been attempted for the control of the apple maggot fly using fruit blends and other attractants (Prokopy et al., 2001; Reynolds et al., 1998; Rull and Prokopy, 2001). Basic research aimed at investigating the evolutionary mechanisms and the response of medflies to chemicals should also be conducted (Papadopoulos et al., 2006). It would also be challenging to know the function of these compounds within the plants producing them. Alpha copaene, for example, might serve a defensive role against plant herbivores by attracting predators (Shelly and Vilalobos, 2004), but this has not been proven. Plant compounds that are ingested by tephritids of the genus *Bactrocera* increase male mating success but also confer to these species partial defense against herbivores (Tan and Nishida, 1998). They also attract pollinators to plants serving as synomones that directly benefit both the plant and the fruit fly (Tan and Nishida, 2000). The investigation of other roles that plant compounds involved with the behavior of the medfly might play is definitely a worthy subject.

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