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The Host Marking Pheromone Application on the Management of Fruit Flies - A Review

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ABSTRACT

The aim of this work was to review the role of the host marking pheromone (HMP) and its application in integrated management programs for the fruit flies. Initially the oviposition behavior of tephritids has been analyzed with emphasis on Ceratitis capitata. *The deposition of HMP, which consists in the last stage of the oviposition behavior has been characterized and discussed about evolutive aspects and the biological meaning of the tephritidae communication through the HMP. Finally, the perspectives on the use of HMP in the integrated management of fruit flies have been discussed.*

Key words: Oviposition behavior, host marking pheromone, oviposition deterring pheromone, IPM, fruit flies

INTRODUCTION

The fruit flies (FF) belong to the Diptera order (which has later wings transformed in halteres), Brachycera suborder (with short antenna, usually with three segments), Schizophora series (with ptilinal fissure), Acalyptratae section (without calyptras) and Tephritidae family (with subcostal nervure turned in angle) (Zucchi 2000). In Tephritidae family, 4,448 species and subspecies are known and organized in 484 genera (Norrbom 2008). The genera represented by the species of economic importance are classified in the subfamily Trypetinae, Toxotrypanini tribe (*Anastrepha* and *Toxotrypana*) and Carpomyinae tribe (*Rhagoletis*) in Dacinae subfamily, Ceratitidini tribe (*Ceratitis*) and Dacini tribe (*Bactrocera* and *Dacus*) (Norrbom 2008). After mating on the host plant, fruit flies females show a sequence of behaviors that are interpreted in terms of "decisions", which are taken as they cumulate information about the potential host (Prokopy and Roitberg 1989; Fletcher and Prokopy 1991; Díaz-Fleischer et al. 2000; Sugayama and Malavasi, 2000). The oviposition behavior has been studied in several fruit flies species and for the *Ceratitis capitata* (Wied.), medfly, it happens in four steps: arriving the fruit, searching, puncture and drawing (Prokopy and Roitberg 1989; Fletcher and Prokopy 1991). When the female arrives on the fruit, she uses, at short distance, visual stimuli and appraises the fruit about its size, color and shape (Prokopy and Roitberg 1984). The female surveys all the surface of the fruit during the searching, touching it with the anterior part of the head, the labelo and the 7th sintergosternito (ovipositor). In that step, she analyses the physical (size and shape) and chemical properties of the fruit (Prokopy and Roitberg 1989; Fletcher and Prokopy 1991; Yuval and Hendrichs 2000; Díaz-

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Fleischer et al. 2000). The female inserts its aculeus in the fruit pulp, keeping her ovipositor in a perpendicular position to the surface (Yuval and Hendrichs 2000; Díaz-Fleischer et al. 2000). The female does not lay eggs obligatory but, in some cases, she removes the aculeus making only the puncture (Barros 1986). At last, in the drawing step, the female surveys again the fruit surface, but with the aculeus protract. At this point, she lays a pheromone, the host marking pheromone (HMP) (Prokopy et al. 1978). The behavior of marking the host is an evident and well-studied aspect of the oviposition behavior of many tephritids, especially in the species that attack the fruits. In this review, the host marking pheromone of fruit flies is discussed and some perspectives of its use in integrated management of fruit flies are suggested.

HOST MARKING BEHAVIOR

Finding a host that is nutritionally suitable and without the presence of competitor organisms requires a sophisticated mechanism of detection of the environmental signals, such as visual, soundly, tactile and smelly signals (Chapmann 1998; Dicke 2000). The oviposition behavior of herbivorous insects is often modified by the presence of conspecifics (eggs and or larvae). Typically, females avoid laying eggs in the resources already explored (Nufio and Papaj 2001). The variation in the compounds released by the plant related to the damage provoked by the oviposition or by the tissues destroyed by the immature or adults represent important tools for the intraspecific and interspecific recognition (Dicke 2000; Nufio and Papaj 2001). However, the fruit flies lay their eggs inside the plant structures, provoking a small visible damage. No evidences of variability in the emission of volatiles when the plant is infested only with the fly eggs are known. In this case, during the embryonic stage of the plague, additional evidences of conspecific presence are necessary to the exploitation of a particular resource, what suggests the host marking as such evidence. Competition for tephritids is the key ecological factor for the evolution of the host marking pheromone (Díaz-Fleischer et al. 2000). Porter (1928) was the first scientist to describe precisely this behavior, observing *Rhagoletis pomonella* (Walsh). Later, Wiesmann (1937) reported a similar behavior for *Rhagoletis cerasi* (Linnaeus), suggesting a host marking before the oviposition. For that species, however, it was proved that the marking occurred after oviposition (Katsoyannos 1975). A decade later, Hafliger (1953) was the first to speculate the biological meaning of the drawing of the ovipositor. He got impressed by the fact that rarely more than one egg of *R. cerasi* per fruit was found. The author speculated that the uniformity on the eggs dispersion of *R. cerasi* used to occur due to a fruit marking procedure when the female drew the ovipositor on the surface of the host. Bush (1966) reported that when *Rhagoletis* species infested small fruits, more than one larva per fruit was rarely found. This author agreed with Hafliger and suggested that multiple ovipositions were inhibited by the deposition of the pheromone after oviposition. Experimentally, Prokopy (1972) was the first to demonstrate that fruit flies let a host marking pheromone during the draw of the ovipositor just after the oviposition.

The action of marking the oviposition site has been reported for 23 frugivorous species of the genus *Anastrepha*, *Ceratitis* and *Rhagoletis* (Table 1). On the other hand, the non-host marking has been reported in *Toxotrypana curvicaudata* Gerstaecker, which is reported to be a species close to *Anastrepha*. Considering now the *Bactrocera* genus, the drawing of the aculeus without deposition of HMP has been reported in *Bactrocera cucurbitae* (Coquillett) (Prokopy and Koyama 1982), *Bactrocera dorsalis* (Hendel) (Prokopy et al. 1989) and *Bactrocera tryoni* (Froggatt) and *Bactrocera jarvisi* (Tryon) (Fitt 1984).

Individuals of the *Rhagoletis* genus that belongs to a group of species that became specialists in small hosts (e.g., groups of *alternata*, *indifferens* and *pomonella*) tend to pledge the host marking behavior (Prokopy and Papaj 2000). By contrast, flies of the *suavis* group were observed marking occasionally (Círio 1972; Papaj 1994). Not surprisely, members of the *suavis* group often lay eggs on already infested fruits (Lalonde and Mangel 1994; Papaj 1993; 1994). There are two possible explanations for the inconsistence on host marking in the group of *suavis* species. The first is related to the host, all the members of the *suavis* group infest the nuts (*Juglans* spp.), a host not used by other flies of that genus in the North America (Prokopy and Papaj 2000). The nuts are large, allowing abundant food for the larvae and reducing larval competition (Prokopy and Papaj 2000) and the concern to the success of the

offspring. The second explanation is about the occurrence of host marking behavior by the male. Papaj et al. (1996) found that the males of *Rhagoletis boycei* Cresson usually touched the host fruit, leaving on it a viscous substance and the females preferred to oviposite in the fruits without this mark. It is possible that the host marking by the males replaces the mark of the own females, leading to a loss or reduction in female marks. Male marks have been reported for two members of the *suavis* group, *R. boycei* and *Rhagoletis suavis* (Loew) (Díaz-Fleischer et al. 2000).

Table 1 – Records for frugivorous species (Diptera: Tephritidae) showing the host marking behavior.

Tribe	Genus	Species	Reference
Toxotrypanini	*Anastrepha*	*A. suspensa*	Prokopy et al. 1977
		A. sororcula	Simões et al. 1978
		A. fraterculus	Prokopy et al. 1982
		A. pseudoparallela	Poloni and Silva 1986
		A. bistrigata	Selivon 1991
		A. grandis	Silva 1991
		A. ludens	Papaj and Aluja 1993
		A. striata	Aluja et al. 1993
		A. obliqua	Aluja and Díaz-Fleischer 2006
		A. serpentina	
Carpomyinae	*Rhagoletis*	*R. completa*	Círio 1972
		R. pomonnela	Prokopy 1972
		R. cerasi	Katsoyannos 1975
		R. fausta	Prokopy 1975
		R. cingulata	Prokopy et al. 1976
		R. cornivora	
		R. indifferens	
		R. mendax	
		R. tabellaria	
		R. basiola	Averill and Prokopy 1981
		R. zephyria	Averill and Prokopy 1982
		R. alternata	Bauer 1986
Ceratitidini	*Ceratitis*	*C. capitata*	Prokopy et al. 1978

There are no records of males marking in any other member of the genus, including the species that have been characterized regarding the use of HMP (Prokopy and Papaj 2000). In non-frugivorous tephritid, there are few records of the behavior of drawing the aculeus with simultaneous deposition of HMP. Among the few known cases of host marking behavior are *Tephritis bardanae* (Schrank) (Straw 1989), *Chaetorellia australis* Hering (Pitarra and Katsoyannos 1990), *Terellia ruficauda* (Fabricius) (Lalonde and Roitberg, 1992) and *Rhagoletis alternata* Fall (Bauer 1986). Non- frugivorous tephritid have been less studied in comparison to the frugivorous species.

BIOLOGICAL MEANING OF HOST MARKING

The main goal of the communication through the host marking pheromone is the reduction of competition among the offspring. The fruit or the part of the plant used by the tephritid represents limited resources. Reducing the larvae loss of energy in already infested fruits, the females

possibly increase the chances of success of their offspring.

The theoretical model of the evolution of host marking remarks that the marking behavior may involve the ability of the females in avoiding a second oviposition in the hosts previously used by other females (Roitberg and Mangel 1988). The host marking even on a secondary level may avoid the oviposition on the same fruit by the same female, but this is unlikely. Even in such case, the host marking reward is the reduction of larval competition.

In principle, the use of HMP might be related to host characteristics that tend to increase the competition level (Prokopy 1981; Fitt 1984; Roitberg and Prokopy 1987; Averill and Prokopy, 1989a), such as (1) small size of the fruit; (2) the provisory status of the larval diet (fruit); (3) limited feed resources and/or shelter places in the host plant; (4) size of the host plant; (5) host plant of high longevity (such that insect communities develop several generations at one single plant); and (6) random distribution of hosts in time and space. The use of HMPs might also be related to life-time characteristics of the own insects, e.g., limited mobility of the parents or offspring and potential larval cannibalism (Roitberg and Prokopy 1987; Díaz-Fleischer et al. 2000).

For the species that attack large fruits, such as the medfly, Papaj et al. (1992) and Papaj (1993) proposed that HMP should act as an indicator of the level of larval competition. The accumulation of high levels of HMP could finally prevent the females of laying more eggs. A dosage pattern in response to HMP could be considered a mechanism through which the females could respond to an increasing level of competition in large fruits. The females adjust the use of an infested fruit in response to the host size, and the probability of re-infestation of large fruits is higher than in small fruits (Papaj and Messing 1996).

The HMPs induce numerous and complex effects on the males and females of fruit flies. In general, the HMP causes suppression of the oviposition activity, disruption of oviposition, stimulates the migration from high infested areas and reduction of the number of eggs per oviposition (see Table 2).

Table 2 – Effects of host marking pheromones (HMP) in tephritids.

HMP effect	Reference
Suppression of the oviposition tentative	Averill and Prokopy 1989b; Papaj et al. 1992
Disruption of oviposition	Papaj et al. 1989
	Papaj et al. 1989
Stimuli for emigration from high infested areas	Roitberg et al. 1982; Roitberg et al. 1984
Reduction of the number of eggs laid	Papaj et al. 1989; 1990

HMP APPLICATION ON THE INTEGRATED MANAGEMENT

On the 1970's, Katsoyannos (1975) demonstrated that *R. cerasi* marked its hosts with a substance, the host marking pheromone. Later, it was demonstrated that the application of HMP in cherry orchards reduced the *R. cerasi* infestation up to 90% (Katsoyannos and Boller 1976; 1980). On the 1980's, research efforts were made for the complete purification, chemical characterization and synthesis of the *R. cerasi* HMP, now also called of oviposition deterring pheromone (ODP) (Hurter et al. 1976; Boller and Hurter 1985; Hurter et al. 1987; Boller et al. 1987; Ernst and Wagner 1989). The HMP of *R. cerasi* is a complex molecule {*N*[15(*β*-glucopyranosyl) oxy-8-hydroxypalmitol]-taurine} showing four stereoisomers (Hurter et al. 1987).

Subsequently, Boller and Aluja (1992) verified under laboratory conditions that the synthetic pheromone, isomer A (8R-15R) and the racemic mixture of the isomers A (8R-15R) + B (8S-15R) = 8RS-15R showed oviposition deterrence similar or higher than to the natural HMP. In the field, the racemic mixture of the isomers (A + B = 8RS-15R) provoked a reduction of the infestation about 90% (Aluja and Boller 1992b). Another study developed by Aluja and Boller (1992a) aimed to evaluate the behavioral response of *R. cerasi* to the isomer A (8R-15R) and the racemic mixture of the isomers (A + B = 8RS-15R) in field cage tests.

The objective of these authors was to establish what control mechanisms were involved (see Table 2). First, the authors registered that the behavioral response of the females to the isomer and the raceme mixture were similar to the results of other studies using natural HMPs. That the isomer and the racemic mixture induced either a reduction in infestation as a migration of the pest to other host trees. Third, it was shown that the continuous exposure to the synthetic HMP increased the possibility of the pest laying eggs in the treated fruits, probably due to the habituation or sensorial adaptation (Aluja and Boller 1992a). The efficacy of the synthetic HMP was later confirmed by Boller and Hurter (1998) in different regions of Switzerland, where reductions in the infestation of *R. cerasi* up to 100% were reached in cherry fields. Motivated by the results obtained with *R. cerasi*, the team of Martin Aluja initiated a long project aiming the synthesis of HMP analogs for the flies of the genus *Anastrepha*, especially for *Anastrepha ludens* (Loew). Initially, the temporal dynamic of the drawing of the ovipositor was studied and the host marking by *A. ludens* (Papaj and Aluja 1993). From 1993 to 1995, the host marking behavior in *Anastrepha obliqua* (Macquart) and *Anastrepha serpentina* (Wiedemann) were demonstrated, as the interspecific recognition of the HMP among the three species, *A. ludens*, *A. obliqua* and *A. serpentina* (the HMP of one species provoked oviposition deterrence besides other behavioral effects over the three species) (Aluja and Díaz-Fleischer 2006). Using an electrophysiological bioassay, Aluja et al. (2000) demonstrated that the Mexican fruit fly, *A. ludens*, recognized the compounds present in its own feces and from *A. obliqua*, *A. serpentina*, *Anastrepha suspensa* (Loew) and *Toxotrypana curvicaudata* Gerstacker. In laboratory bioassays, Aluja et al. (2000) observed that the feces extracts of *A. obliqua*, *A. ludens*, *A. serpentina*, *Anastrepha striata* Schiner, *Anastrepha leptozona* Hendel, Anastrepha bezzii Lima and *T. curvicaudata* provoked oviposition deterrence over *A. ludens*. For *A. obliqua*, oviposition deterrence was noticed when using *Anastrepha* feces (*obliqua*, *ludens*, *serpentina*, *striata* and *bezii*) and *T. curvicaudata*. The oviposition deterrence for *A. serpentina* was also reported for some *Anastrepha* feces (*obliqua*, *ludens* and *serpentina*). In 1994, field application of *A. ludens* feces extract with HMP over *Spondias purpurea* L. fruits reduced an *A. obliqua* infestation (Aluja et al. 2009). After isolation and structural determination, the synthetic HMP was evaluated according to its biological activity, first by electrophysiological bioassay and then in behavioral assays under the laboratory conditions (Aluja et al. 2000; Edmunds et al. 2010). Two synthetic molecules were selected for the field evaluation in 1997 (Aluja et al. 2009). The results demonstrated a reduction of infestation of *S. purpurea* by 64 and 77% using the molecules (R)-L-(22) and ((R/S)-L-(22)), and the later was named Anastrephamide (Aluja et al. 2000; Aluja et al. 2009; Edmunds et al. 2010).

FINAL THOUGHTS

So far, there has been three successful cases of HMP application in the field, achieving significant reductions in the pest incidence: for *R. cerasi* (Katsoyannos and Boller 1976; 1980; Aluja and Boller 1992b; Boller and Hurter 1998), *C. capitata* (Arredondo and Díaz-Fleischer 2006), and *A. obliqua* (Aluja et al. 2009). The use of HMP in the management of fruit flies was proposed initially as a *push-pull* strategy (Prokopy 1972; 1981; Boller 1981; Aluja et al. 2009; Edmunds et al. 2010). The *push-pull* system, however, is not indicated for the species with high population growth rates; another drawback is the risk of insect learning (Cook et al. 2007). Currently, there are evidences that the flies can lay eggs in the fruits treated with HMP, especially under continuous exposure to the pheromone (Aluja and Boller 1992a; Papaj and Aluja 1993). Such behavior is probably due to the habituation or sensorial adaptation by the insect (Aluja and Boller 1992a; Papaj and Aluja 1993). A feasible alternative for the use of the HMP would be the application in commercial orchards in which the tephritid populations are not resident, what implies in low populations to be suppressed and also in less risk for the occurrence of learning process.

Another strategy would be the release of parasitoids with the previous knowledge of the odors emitted by the HMPs would probably reduce the loss of the parasitoids in searching for the hosts and could increase the efficiency of the strategy. Some parasitoid species [e.g., *Diachasmimorpha longicaudata* (Ashmead)], originally recovered from the tephritid that do not leave HMPs, such as *Bactrocera* spp., may have their performance improved when released in regions where the local

fruit flies show that behavior (see Table 1). The parasitoids of fruit flies are able to localize the host through the marking pheromone left by the female. According to Prokopy and Webster (1978), host marking pheromone of *R. pomonella* stimulates the oviposition of the parasitoid *Opius lectus* Gahan (Hymnoptera: Braconidae). In the studies performed with *Halticoptera rosae* Burks (Hymenoptera: Pteromalidae), a parasitoid wasp of *R. basiola*, the parasitoid increased the chances in finding the host, and therefore, its efficiency in the presence of the host marking pheromone (Roitberg and Lalonde 1991). Actually, *H. rosae* can even host marking pheromone trail to find the oviposition site of the fly (Hoffmeister et al. 2000). These results indicated that these two parasitoids had the ability to distinguish the odors (i.e., the HMPs) among the volatiles emitted by the plants, which suggested the occurrence of an associated learning process. The HMP could easily be incorporated to the mass rearing process of the parasitoid, once spraying the HMP over the parasitism units could result in associated learning. This could induce a behavioral change in the parasitoid, but investigations are still required in order to maximize the parasitism efficiency.

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