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Semiochemicals of *Rhagoletis* fruit flies: Potential for integrated pest management

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ABSTRACT

Worldwide economic losses associated with *Rhagoletis* fruit flies (Diptera: Tephritidae) require an effective means of control. Most conventional insecticides used to control fruit flies have been banned, and fruit producers are seeking new economical fruit fly control options. Bait stations can be a suitable alternative, provided they are affordable, effective and pest-specific. Semiochemicals are important for fruit flies to locate their host fruit and to reproduce. They could therefore be good candidates to improve existing bait stations. In this literature review, we summarize the available data on *Rhagoletis* semiochemicals, including (1) the kairomones involved in fruit location, (2) mating and sex pheromones and (3) oviposition and host marking pheromones. We present the latest data on the chemical composition of these semiochemicals, as well as some field applications that have been successful at *Rhagoletis* fly control. Based on the available data on the semiochemicals of Rhagoletis species and other Tephritid flies, we believe that the association of an efficient food attractant with early applications of host marking pheromones could reduce the risk of oviposition that usually occurs rapidly after emergence. Also, traps baited with sex pheromones and/or fruit-associated kairomones could attract and kill emerging individuals. However, analytical work has still to be conducted, as most Rhagoletis semiochemicals have yet to be identified.

1. Introduction

Fruit flies of the genus *Rhagoletis* Loew (Diptera: Tephritidae) are major insect pests, responsible for significant economic damage in orchards worldwide. Their larvae develop inside the fruit, causing the fruit to fall or rendering it unfit for sale and/or consumption (Bateman, 1972). About one hundred species of *Rhagoletis* have been identified worldwide, with only some of them being considered important pests of agricultural production, including the apple maggot *Rhagoletis pomonella* Walsh, the blueberry maggot *Rhagoletis mendax* Curran, the cherry fruit flies *Rhagoletis cingulata* Loew, *Rhagoletis cerasi* L., *Rhagoletis indifferens* Curran, and *Rhagoletis fausta* Osten Sacken, and the walnut husk fly *Rhagoletis completa* Cresson (Daniel and Grunder, 2012; Yee et al., 2014a). Most *Rhagoletis* are specific to a plant species, with their respective life cycle adapted to their host plant phenology (Bateman, 1972), making it important to carry out specific research on each plant–insect association (Bush, 1966; Foote, 1981).

The current method for controlling *Rhagoletis* populations in conventional orchards is the application of insecticides, but alternatives have been sought to reduce the risk of developing resistance and reduce harm to the environment and human health. Fruit fly pheromones are indeed efficient at monitoring and mass trapping when they are added to pre-existing systems such as food attractant, as shown for *Ceratitis capitata* Wiedemann, *Bactrocera cucurbitae* Coquillett, *Bactrocera dorsalis* Hendel and *Bactrocera oleae* Gmelin (Bueno and Jones, 2002; Shelly et al., 2012). Because of their importance in mating and host finding behaviour, *Rhagoletis* semiochemicals have been identified and characterized, with the intention of including them in effective integrated pest management (IPM) programs. Although the number of published reports dealing with *Rhagoletis* semiochemicals has recently increased, efficient semiochemical-based control strategies are scarce. The chemical complexity of the semiochemical blends and their associated behaviour make their integration into IPM strategies difficult. The different compounds can act synergistically or antagonistically (Quilici et al., 2014) thereby substantial work in the

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laboratory is needed to apprehend all the factors that may influence the efficacy of semiochemicals in an IPM program. In this review, we list the main semiochemicals that have been identified in *Rhagoletis* species that are involved in host location, mating or host marking, and we summarize field trials with semiochemicals in control programs against *Rhagoletis*.

2. *Rhagoletis* semiochemicals and applications

Semiochemicals are organic molecules involved in the chemical interaction between two or more organisms. Allelochemicals are semiochemicals acting between individuals from different species, whereas pheromones are semiochemicals that act within a species. Three main groups of semiochemicals have been identified in *Rhagoletis* flies: (1) allelochemicals released by the host fruit that guide the flies towards oviposition site (kairomones), (2) sex pheromones and (3) host-marking pheromones (Table 1). We present the three groups of semiochemicals separately below.

2.1. Kairomones involved in fruit location

Rhagoletis have a simple life cycle because most species have a single host fruit species and are univoltine. Depending on the species, their emergence occurs between the late spring and late summer to coincide with the fructification period of the host, as observed in the European cherry fruit fly, *R. cerasi* (Boller and Bush, 1974). Two hours after emergence, adult flies start feeding on nectar, plant exudates, aphid honeydew and bird droppings rather than on the larval host fruit (Boller and Prokopy, 1976; Boyce, 1934; Prokopy et al., 1993). Feeding is a preliminary step towards reproduction, as proteins and amino nitrogen are needed for the development of the gonads (Allwood, 1996). This particular aspect of their life history has been exploited in that a wide variety of lures releasing ammonia (which is associated with protein decomposition) is used as a food attractant and is particularly effective for newly emerged fruit flies, which search for food to reach sexual maturation (Liburd, 2004). It is, however, less effective against mature individuals, which are more sensitive to volatile organic compounds (VOC) released by their host fruit. Ammonia bait trap is currently used for monitoring fruit fly populations, which can help to define the right timing for insecticide applications Ammonium better attracts females than males, as the former need to maturate their eggs before oviposition (Yee and Landolt, 2004). Ammonium acetate and also ammonium carbonate can be included in bait traps; the latter were shown to catch more *R. pomonella* than traps baited with lures containing fruit blends (Yee et al., 2014b). However, the ammonia releasing device is non-specific, and many non-target insects from other orders and both genders are also attracted and captured.

Host fruit VOCs are of importance, as they guide adults in their search for oviposition sites. Prokopy et al. (1973) first demonstrated the attraction of *Rhagoletis* to the VOCs emitted by their host fruits, using *R. pomonella* as an example. In 1982, Fein et al. (1982) identified seven organic compounds responsible for *R. pomonella* attraction to apples, *Malus domestica* Borkh. The chemicals identified after volatile collection performed on two apple varieties (Red Delicious and Red Astrachan) included hexyl acetate, (E)-2-hexen-1-yl acetate, butyl 2 methylbutanoate, propyl hexanoate, hexyl propanoate, butyl propanoate and hexyl butanoate. While none of the above-mentioned VOCs separately elicit significant olfactory responses from fly antennae, strong electrical depolarization was observed after exposure of the antenna to a synthetic blend comprising the seven chemicals (Fein et al., 1982). The synthetic blend was also attractive to sexually mature *R. pomonella* in laboratory bioassays. Since then, blends of attractive host fruit VOCs have been improved and complemented with additional behaviourally active chemical constituents, and preliminary experiments were performed in the field with success (Zhang et al., 1999). Fruit flies are supposed to acquire the ability to recognize their host VOC as larvae; *R. pomonella* flies originating from hawthorn (Crataegus spp) preferentially orient themselves towards a blend of volatiles collected from the hawthorn fruit over a blend collected from domestic apples (Nojima et al. 2003). After Solid-Phase Micro-Extraction (SPME) collection and bioassays conducted on different kairomonal blends, these authors identified a four-component mixture (made of 3-methylbutan-1-ol, 4,8-dimethyl-1,3(E),7-nonatriene, butyl hexanoate, and dihydro-β-ionone) that mediates the strong attraction of *R. pomonella* in a flight tunnel.

2.2. Mating and sex pheromones

After reaching sexual maturity, females begin to search for a male partner. The latter usually waits for a female on a fruit that he defends against competitors (Papaj, 1994). In *Rhagoletis* species, males often produce a sex pheromone to attract the mature female to the selected fruit (Katsoyannos, 1982). The existence of a sex pheromone was first suggested in two species, *R. pomonella* and *R. cerasi* (Prokopy, 1975; Katsoyannos, 1976). After mating, females become insensitive to the male sex pheromone for a few days, while the male continues to release sex pheromone, unaffected by his mating history (Katsoyannos, 1982). In *R. cerasi*, two different types of precopulatory behaviour are governed by chemical stimuli (Raptopoulos et al., 1995): males first produce a complex blend of volatile compounds that attracts females, while a second blend of fatty acids shows arresting properties. The exact composition of the attractive blend of male-produced volatile molecules has not been established but has been proposed to be a complex blend of chemicals (Raptopoulos et al., 1995). The sex pheromone

Table 1
Semiochemicals from Rhagoletis fruit flies.

Type of semiochemical	Rhagoletis species	Chemical identification	References
Fruit kairomone	*R. pomonella*	Apple Varieties: Red Delicious and Red Astrachan, Hexyl acetate, E−2-hexen-1-yl acetate, butyl 2 methylbutanoate, Propyl hexanoate, Hexyl propanoate, Butyl hexanoate, Hexyl butanoate	Fein et al., 1982
		Apple Varieties: Empire, Crispin, Cortland, Macintosh and Red Delicious, Butyl butanoate, Propyl hexanoate, Butyl hexanoate, Hexyl butanoate, Pentyl hexanoate	Zhang et al., 1999
		Dogwood *Cornus florida*, Ethyl acetate, 3-methylbutan-1-ol, Isoamyl acetate, Dimethyl trisulfide, 1-octen-3-ol, β-caryophyllene	Nojima et al., 2003
Sex pheromone	*R. cerasi*	Major compounds of male sex pheromone: 2-Ethoxy-2-methylbutane, 2-Pentanone, 4-Methyl-3-penten-2-one, 3-Hexen-2-one, 2-Hexanone, 2-Hexanol, 3-Heptanone, 3-Heptanol, Tetrahydro-5,6-dimethyl-2H-pyran-2-one, 2-Ethylhexanol, Limonene, β-Phellandrene, Nonanal, Decanal, Methyl heptanoate, Geranyl acetate	Raptopoulos et al., 1995
Host marking pheromone	*R. cerasi*	N[15(β-glucopyranosyl) oxy-8- hydroxypalmitol]-taurine	Hurter et al., 1987

composition is supposed to vary amongst *Rhagoletis* species, as sex pheromone constituents are usually synthesized from precursors taken from the host fruit (Landolt and Phillips, 1997), which differ among *Rhagoletis* species. Among the volatile chemicals identified in the headspace of *R. cerasi*, some have already been reported in other Tephritidae sex pheromones, such as geranyl acetate and (E,E)-α-farnesene, which have been reported as being constituents of the *C. capitata* sex pheromone (Heath et al., 1991). Unfortunately, no additional analytical characterization has been conducted to elucidate the chemical mechanisms involved in the sexual behaviour of *Rhagoletis* fruit flies despite their potential in pest management (Benelli et al., 2014; El-Sayed, 2014).

Consequently, no study documents the exploitation of *Rhagoletis* sex pheromones for monitoring or trapping (Tan et al., 2014). Yet, their specificity and biological activity at low doses are two major advantages that should favour their inclusion in IPM programs. Moreover, sex pheromones are usually non-toxic for animals (Howse et al., 1998). The use of sex pheromones in IPM still remains a challenge, as a pheromone blend can show very positive results in the laboratory but have no relevant activity under natural conditions under which insects are subjected to a very large number of different semiochemicals. Realizing a semiochemical blend capable of being stronger than natural emissions is an important challenge (Smart et al., 2014). Moreover, the bait station should release a consistent amount of attractant on a regular basis for a long time to avoid having to recharge the traps (IAEA, 2009). Because visual stimuli are supposed to be involved in *Rhagoletis* fruit selection, bait stations should have the shape and colour of the fruit being protected. Finally, the overall cost of the method should be minimized, as applied to all four constituents of the bait station: the trap, the insecticide, the attractant (including the semiochemical blend) and the attractant's diffusion matrix (Köppler et al., 2008; Daniel and Grunder, 2012; Bhagat et al., 2013; Piñero et al., 2014; Navarro-Llopis and Vacas, 2014).

2.3. Oviposition and host-marking pheromones

Following oviposition on a fruit, females produce and deposit on the fruit surface a second important group of *Rhagoletis* pheromones called host-marking pheromones (HMP) (Cirio, 1972; Prokopy, 1972). The main function of the HMP is to inform conspecific females that the marked fruit has already been infested and contains eggs. To reduce competition and therefore increase the chances of offspring survival, a second female perceiving the signal will likely look for an uninfested fruit to oviposit (Prokopy, 1972).

After mating, the females are able to fertilize between 300 and 400 eggs, which represents many infested fruits, as most *Rhagoletis* usually lay one egg per fruit (Bush, 1966; Boller and Prokopy, 1976). However, more eggs can be deposited on larger fruits (Prokopy and Webster, 1978). *R. completa* often lay over 15 eggs per sting, and many larvae can grow in a single walnut. *R. cerasi* deposits 3 to 5 eggs per cherry, but only a single egg usually reaches the pupal stage. After oviposition, females place their ovipositor on the fruit surface to release the HMP. Females are able to evaluate the fruit size and adjust the amount of HMP accordingly (Averill and Prokopy, 1987a). The fruit area being marked following a single oviposition is thought to be related to the amount of food required by one larva to grow to maturity (Averill and Prokopy, 1988). Oviposition-deterring pheromones also inform males of the presence of a mature female. The perceiving males reduce their mobility, thereby improving the probability of mating (Prokopy and Bush, 1972).

Fifteen years after the original suggestion of the existence of an HMP in a *Rhagoletis* species (Cirio, 1972; Prokopy, 1972), Hurter et al. (1987) isolated, in the faeces of *R. cerasi*, a single compound named N[15(β-glucopyranosyl)oxy-8-hydroxypalmitoyl]-taurine. This chemical possesses two chiral centres (on carbon 8 and carbon 15), making it possible to exist as four different stereoisomers (Hurter et al., 1987). Thus far, the stereometry of the *R. cerasi* HMP has not been elucidated.

Many field applications have been conducted using the HMP from *R. cerasi*. The first experiment started in 1975 using marking pheromones directly collected in the laboratory (Katsoyannos and Boller, 1976) without the chemical identification of the extract. The results were promising, with a fruit infestation reduction of 77% reached despite heavy rainfall that can shorten the lifetime of the HMP due to its high solubility (Averill and Prokopy, 1987b). Efforts have therefore been made to develop a formulation that allows the protection and continuous dispersal of the product over a period of time corresponding to the entire oviposition period. Two applications of the *R. cerasi* HMP on entire cherry trees (*Prunus avium* L.) in Swiss experimental fields allowed a 90% reduction in infested fruits (Katsoyannos and Boller, 1980). Taken independently, the four HMP stereoisomers do not have the same properties; isomers 8R−15S and 8S−15R showed the most effective results on *R. cerasi* in the field experiments. Aluja and Boller (1992a) then tested the efficacy of this synthetic *R. cerasi* HMP (a racemic mixture of the most effective stereoisomers, 8R−15S & 8S−15R) by applying it on cherry tree canopies and observed a significant reduction in fruit infestation (Aluja and Boller, 1992a). However, one of the major problems of using HMP in IPM is the risk of flies' acclimatization. Bioassays have shown that females exposed for prolonged periods to HMP were able to ignore it and oviposit on marked fruits (Aluja and Boller, 1992b). A rational use of HMP is therefore needed, and HMP should be associated with additional means of control in a long-term strategy. In this context, Aluja and Boller (1992b) proposed coupling the application of HMP on some trees in an orchard with colour traps placed on others.

In 1978, the kairomonal character of HMP was demonstrated for an egg parasitoid, *Opius lectus* Gahan (Hymnoptera: Braconidae) (Prokopy and Webster, 1978). In laboratory bioassays, the HMP promoted *O. lectus* retention on a fruit and elicited antennal tapping and oviposition probes. Because the HMP indicates the presence of eggs or first instars, it was not surprising to observe no attraction in *Opius. alloeus*, a parasitoid of late-instar larvae of *R. pomonella,* which are rather sensitive to chemical odours associated with the degradation of fruit by larval feeding behaviour (Vet and Dicke, 1992).

The HMP of *Rhagoletis* natural enemies could also be used in a similar way to protect the fruits; *Diachasma alloeum* (Muesebeck) (Hymenoptera: Braconidae) is a parasitic wasp attacking larval *R. mendax* which also deposits a HMP, signalling to conspecifics of a wasp-occupied host (Stelinski et al., 2009). The HMP is recognized by *R. mendax*, and female flies reject wasp-marked fruit for oviposition. The combination of mass trapping, HMP and natural enemies could lead to an effective multifaceted natural control program (Cook et al., 2007).

3. Conclusions: potential of semiochemicals in IPM programs

Because most conventional insecticides used to control fruit flies have been banned, fruit producers seek more economical and practical fruit fly control options. Bait stations, acting according to the "lure and kill" strategy, can be one of the most suitable alternatives, provided that they are affordable, effective and pest-specific. A wide variety of baits have been developed and tested. Affordable "attract and kill" strategies have been effective at controlling *R. pomonella* (Bostanian, 2001), but the lack of specificity of food attractants (e.g., butyl hexanoate) is still problematic. This is why a thorough study of semiochemicals is essential, as they could improve the efficiency and specificity of existing trapping methods. There are many examples of efficient attractants and killing compounds that target insect pests, so developing semiochemical-baited stations against fruit flies seems to be a feasible task.

Rhagoletis semiochemicals are still largely understudied with respect to the economic impact of individual species. The efficiency of the use of sex pheromones for detection/monitoring or for mating disruption/mass trapping has already been convincingly demonstrated, such as for olive fly *B. oleae* (Haniotakis et al., 1991). There is no reason not to reach similar conclusions for a *Rhagoletis* species, as sex pheromones have been suggested to play a role in the attraction of partners.

Based on what is presented above, the introduction of semiochemical-based products as control methods in IPM packages is likely feasible. Ammonium carbonate bait traps could allow an earlier detection of initial emergences in an orchard. Following the first detections, early applications of the active molecules of the host marking pheromone (along with host marking pheromones from parasitoids, if any), could reduce the risk of oviposition, that usually occurs rapidly after emergence. Finally, traps, baited with sex pheromones and fruit-associated kairomones and placed within the orchard, could attract and kill emerging individuals. The identification and formulation of *Rhagoletis* sex pheromones and fruit kairomones is therefore an important initial step to achieving more environmentally friendly agricultural methods.

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