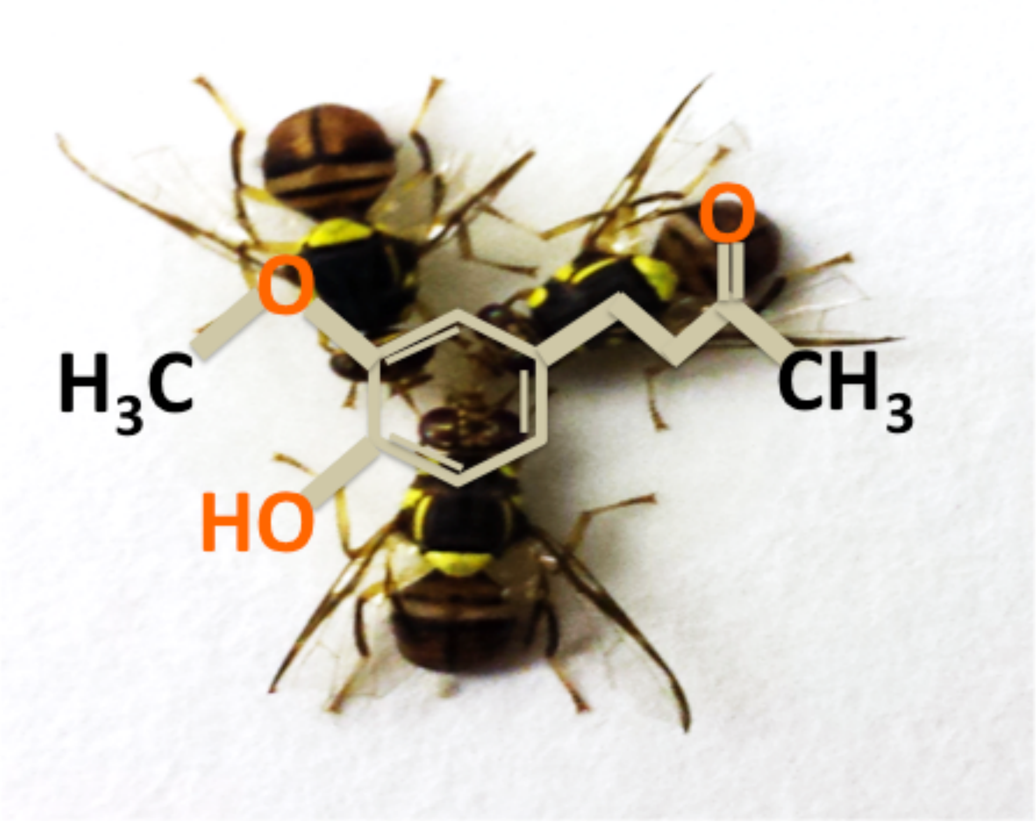
Chemical Communication In Economically Important Fruit Flies (Diptera: Tephritidae)

Tibebe Dejene

Introductory Paper at the Faculty of Landscape Architecture,
Horticulture and Crop Production Science 2015: 4
Swedish University of Agricultural Sciences
Alnarp, October 2015



Summary

Fruit fly is a common name given for two distantly related families: Tephritidae and Drosophilidae. Flies in the family Tephritidae, unlike most of Drosophilidae are referred to as true fruit flies, as they damage fruits before they are overripe or rotten. There are about 500 genera in this family, of which several are serious pests of commercially grown fruits and vegetables. Flies in the subfamily Dacinae are of considerable agricultural concern in the tropics and sub-tropics causing direct damage through infestation and indirect damages via quarantine restrictions. Control strategies include trapping with protein baits and male annihilation, both of which are based on olfactory behaviour of the flies. Protein baits and host volatiles attract both sexes, but are less effective compared to parapheromones that attract only males of Dacinae. Parapheromones not only attract, but also strongly induce phagostimulation. Males that fed on parapheromone appear to gain selective advantage. Alternatively, but not mutually exclusive, parapheromones may act as rendezvous site marking. Apart from its function, the mechanism by which males recognize parapheromone is not understood. In order to clarify this, it is crucial to look further into the peripheral olfactory system and find the sensory neurons that are responsible for detecting parapheromones. Structure-activity studies and comparative studies on homologous sensory circuits in females and in closely and distantly related species of tephritid flies might elucidate the evolutionary origin of parapheromones and identify new avenues for use in the control of these global pests.

Table of Contents

1. Background

The family Tephritidae comprises more than 5000 species worldwide, of which around 1400 species develop in fleshy fruits (Norrbom et al. 1999). Nearly 250 of these species are regarded as pests of vegetables and fruits (White and Elson-Harris 1992) and they are globally distributed (Christenson and Foote 1960). Most are phytophagous, with larvae developing in the seed-bearing organs of plants (Han and McPheron 1997). Flies in the subfamily Dacinae such as *Ceratitis capitata* (the mediterranean fruit fly), *Bactrocea cucurbitae* (the melon fly), *Bactrocera dorsalis / Bactrocera invadens* (the oriental fruit fly / the African invader fly), *Bactrocera zonata* (peach fruit fly) and *Bactrocera olea* (olive fruit fly) are of considerable agricultural concern in the tropics and sub-tropics. Despite the effort to combat these pests, they are still causing excessive damage in horticulture produce almost everywhere in the world.

The damage caused by fruit flies could be direct due to infestation or indirect due to loss of export market through quarantine restrictions and transmission of phytopathogenic microbes (Ordax et al. 2015). Direct damage starts when female flies pierce the skin of the fruit to deposit eggs. The eggs then hatch to larvae that feed actively on the fleshy part of the fruit. While inside the fruit the larvae moults twice and the last instar makes an exit hole to exit the fruit to the ground. The larvae then bury themselves in the soil where pupation occurs. Once emerged, adults crawl up the soil surface and start searching for food. Carbohydrates, protein in the form of free amino acids, minerals, B-complex vitamins and water are essential for survival but also for the sexual maturation of fruit flies (Hagen 1953).

Although adults of both sexes are attracted to protein and ammonium derived food lures and fermentation products, males are also attracted to pheromones and parapheromones (Tan et al. 2014). Parapheromones are compounds usually derived from plants that attract sexually mature males and hence they are termed male lures (Sivinski and Calkins 1986, Renou and Guerrero 2000). The most common parapheromones in tephritidae are trimedlure (TML), methyl eugenol (ME) and Cuelure (CUE). The former attracts males of the genus *Ceratitis* while the latter two attracts males of the genus *Bactrocera*. Spiroketal and Pyrazine are the only known pheromones that attract males of the olive fruit fly (*B. olea*) and the papaya fruit fly (*Toxotrypana curvicauda*) respectively (Tan et al. 2014).

Fruit fly attractants (both fermentation products and parapheromones) combined with toxicants have been utilised in fruit fly management since long ago. Adults are attracted towards fermentation products for the sake of energy and sexual maturation, however, it is not clear for why males are attracted to these plant derived chemicals, though it is believed that feeding on it boosts their sexual competitiveness (Tan et al. 2014). Regardless of their function, these attractants are used in management techniques such as protein bait sprays and male annihilation techniques (MAT).

MAT is a control strategy that involves parapheromones combined with insecticide to attract and kill male fruit flies. Protein bait sprays are also control strategies, but mainly target female fruit flies.

Protein-based substances and fermentation products are used to attract fruit flies to toxic bait. However, this technique is not species specific, hence, non-target species could also be attracted and killed (Uchida et al. 2006, Leblanc et al. 2010).

.

In addition to protein-based attractants (hydrolysates and ammonium salts) females may also be proportionally more attracted to leaves and fruits of host plants compared to males. Female lures when compared to male lures are less effective in attracting tephritid fruit flies (Ekesi and Billah 2007). Female specific or at least female biased attractants are crucial for effective interference of fruit flies. Female lures constitute an important complement to parapheromones when for instance assessing the efficacy of fruit fly management. In addition, their use may also directly reduce damage (Siderhurst and Jang 2006).

1.1. Economically important fruit flies

The most economically important agricultural pests belong mainly to the genera *Anastrepha*, *Bactrocera, Ceratitis, Dacus* and *Rhagoletis* (Fletcher 1989, Thompson 1998). *Anastrepha* and *Rhagoletis* are fruit flies of the new world whereas the genera *Bactrocera, Ceratitis* and *Dacus* are fruit flies of the afro-tropical region. *Bactrocera and Ceratitis* are documented as the worst of all fruit fly pests and are the focus of this introductory paper. These pests devastate fruit production and put serious constraints on domestic and international trade of horticultural products. In the afro-tropical region, where environments are favourable, these pests are among the main causes of poor production and trade of horticultural products and hence are a main cause of poverty and malnutrition.

1.1.1 The Genus Bactrocera

Bactrocera, previously known as *Dacus* (Drew 1989), is a tephritid fruit fly genus in the subfamily Dacinae with more than 500 described species subdivided into 28 subgenera (Drew and Hancock 2000, Drew 2004). A number of species in this genus are of major economic importance since they pose a substantial threat in the production of fruit crops and vegetables throughout the world, causing both direct (fruit damage or drop) and indirect (export shut down) losses (Clarke et al. 2005, Clarke et al. 2011). Most of these pest species such as *B. zonata*, *B. tryoni, B. cucurbitae* and *B. dorsalis / invadens* are polyphagous utilizing a variety of fruit species in numerous plant families, whereas a few, such as *B. olea* and *B. cacuminata* have monophagous larvae utilizing closely related host species (Drew 2004).

The taxonomy of members of this group, particularly of those in the *B. dorsalis* complex, is unsettled and constantly reassigned with the addition_/_omission of new siblings or species. For instance, the African invader fruit fly *B. invadens* was described as a new species a decade ago (Lux et al. 2003, Drew et al. 2005). However, recent literatures are showing that it is the same species as the oriental fruit fly *B. dorsalis* (Bo et al. 2014, Schutze et al. 2014). Advanced technologies such as DNA sequencing are being used to resolve the complexity of the identification process (Van Houdt et al.

2010, Asokan et al. 2011, Boykin et al. 2014). The potential of phenylpropanoid metabolites from the rectal gland of male flies, for usage of chemo-identification is also acknowledged (Tan et al. 2011).

Some species in the genus, particularly those that are polyphagous, are r-strategist; hence they are well known for their high reproductive rate and dispersive abilities (Fletcher 1987). These traits, supported with the globally increasing fruit trade, human movement, global warming and poor quarantine infrastructure, have enabled *Bactrocera* flies to be successfully invading new areas (Duyck et al. 2004, Malacrida et al. 2007). It is documented that some of the species such as *B. invadens / dorsalis*, *B. zonata* and *B. cucurbitae* have recently invaded Africa (Duyck et al. 2006, De Meyer et al. 2010).

Another important behavioural characteristic of the genus *Bactrocera* is that, males of many species are highly attracted to either of the parapheromones: methyl-eugenol (ME) (4-allyl-1,2-dimethoxybenzene) or cue-lure (CUE) [4-(p-ace- toxyphenyl)-2-butanone] (Drew and Hooper 1981) and structurally related compounds such as raspberry ketone and zingerone (Khoo and Tan 2000, Khoo and Tan 2005, Fay 2012). These are structurally related organic compounds produced from carbohydrates by the shikimate or shikimic acid pathway and they are collectively known as phenylpropanoids (Raghu 2004). It has been shown that both CUE and ME responding flies are attracted to Zingerone (Tan and Nishida 2007). The chemical structures of these lures are displayed in Fig 1.

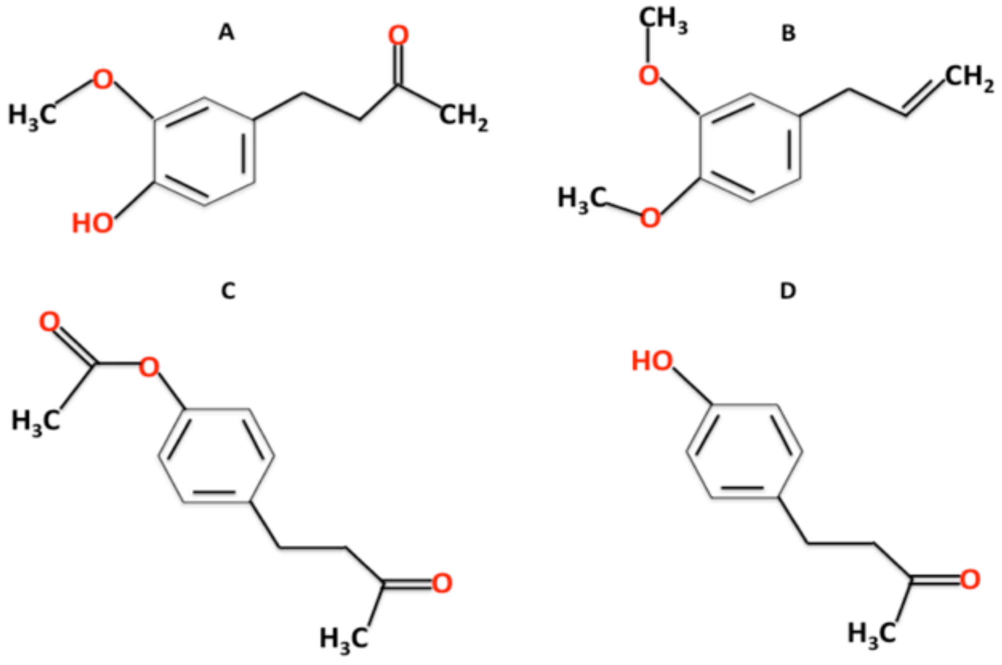


Figure 1. Chemical structures of Zingerone, Methyl eugenol, Cuelure, and Raspberry Ketone; signified by letters A, B, C, and D respectively.

1.1.2 The Genus Ceratitis

Ceratitis is a tephritidae fruit fly genus in the family Dacinae that encompasses 89 recognized species subdivided in to six subgenera (De Meyer 2000). Except for *Ceratitis capitata,* which is virtually worldwide, almost all species in the genera are biogeographically restricted to the Afro-tropical region (De Meyer et al. 2008). The major economically important pests in these genera are the Mediterranean fruit fly *C. capitata*, the Natal fruit fly *C. rosa,* C. *fasciventris* and the mango fruit fly *C. cosyra*. They are highly polyphagous and attack a wide variety of plants. Although, most *Ceratitis* pests are biogeographically restricted to the Afro-tropical region, they are major quarantine pests almost everywhere in the world.

Ceratitis capitata is the most studied of all fruit pests in the genus and it is known to have a broad host range utilizing more than 300 fruits and vegetables (Copeland et al. 2002, De Meyer et al. 2002, Malacrida et al. 2007). Its origin has been traced back to Sub-Saharan Africa (Silva et al. 2003), *C. capitata* has spread to all countries neighbouring the Mediterranean Sea, hence the name Mediterranean (Med) fruit fly. Its life strategy (r-selected), polyphagous nature and wind assisted flight capacity (Thomas et al. 2001, Thomas et al. 2010) are amongst the success for its worldwide distribution and invasion.

Mating in this species is initiated by aggregation of males displaying visual, chemical (sex pheromone / parapheromone) and acoustic communication (buzzing sound due to wing fanning to disseminate the pheromone (Landolt et al. 1992, Briceño et al. 2007). The pheromone, which is released by male rectal gland, appears to be a blend of various compounds (Gonçalves et al. 2006, Alfaro et al. 2010). However, the composition seems to differ between studies and populations of origin (Baker et al. 1985, Gonçalves et al. 2006, Alfaro et al. 2010). The parapheromones in *Ceratitis* are not species specific and they are synthetic compounds developed after tedious chemical analysis.

1.2. Reproductive Behaviour

Tephritidae fruit flies exhibit complex reproductive behavior, with the mating component not yet clarified. Males of most species aggregate / lek on specific plants around dusk or dawn and settle on the leaf under-surfaces (Burk 1984, Iwahashi and Majima 1986, Shelly and Kaneshiro 1991). Calling behavior ensues by bending the abdomen upward (Liimatainen et al. 1997), and in some species followed by releasing anal secretions, and wing fanning, the latter presumably to evaporate the exudate, which is believed to act as a sex pheromone attracting virgin females (Marchini et al. 2003).

Female flies prefer to visit groups of males rather than solitary males (Shelly 2001, Weldon 2007). The male activates wing fanning, which provides potential dispersion of the pheromone cues and an audible buzzing sound (Fletcher 1987). After detecting the appearance of the female, the male stops wing fanning and tries to mount the female (Shelly and Kaneshiro 1991). Female mate acceptance is typically preceded by a head-to-head display followed by copulation, whereas escape evidences rejection by the female.

Mated female fruit flies puncture the fruits with their ovipositor and oviposit their eggs in batches of 1 to 8 depending on the species, quality and density of the host (Aluja et al. 2001). Within 3 to 12 days, the eggs develop into larvae that feed on the fleshy part of the fruit. When fully grown, the maggots exit the fruit and bury themselves in the soil, where they pupate (Vargas et al. 1996). In a few species, pupation may occur inside the host. Approximately one week after emergence, flies become sexually mature and mating ensues. Depending on the climatic conditions and abundance of host fruits, fruit flies of the tropics may complete more than twelve generations in a year (Wih-Kwasi 2008).

2. Control strategies

Several techniques including male annihilation, sanitation, bait sprays and use of biological control agents have been used to supress or eradicate fruit fly population from an infested area (Vargas et al. 2010). There are also numerous preventive and post harvest methods that include bagging or wrapping, early harvesting and post-harvest cold and heat treatments (Ekesi and Billah 2007). Some management techniques adopt the concept of chemical ecology by combining semiochemicals (male and female attractants) with killing agents in traps (Cunningham and Steiner 1972, Sivinski and Calkins 1986).

2.1. Male Annihilation Technique (MAT)

MAT is a control strategy that involves the deployment of traps consisting of male specific lures (parapheromones) combined with a killing agent. Suppression or eradication of fruit fly without the involvement of MAT has been impossible (Cunningham 1989). The traditional killing agents in MAT are generally organophosphorus compounds, such as Naled, Malathion, and Dichlorvos (DDVP) (Vargas et al. 2003). However, in the light of the ban on systemic and broad spectrum insecticides such as organophosphates, recent studies are focusing on developing environmentally friendly bio-insecticides such as spinosad (Vargas et al. 2014).

MAT could also be applied as spot treatments by using many types of dispensers as carriers of the lure and the toxicant (Vargas et al. 2012). The use of lure-and kill stations (*i.e.* dispensers impregnated with the parapheromone-insecticide mixture) is often successful. Recently, a novel attract-kill formulation that contains male attractant and spinosad formulated into a specialized pheromone and lure application technology (SPLAT) has been shown to be promising for effective suppression of fruit flies without any adverse environmental impact (Vargas et al. 2009, Vargas et al. 2014).

The aim of MAT is to diminish the number of male fruit flies in a population to such low levels that mating and subsequent population build-up is reduced (suppression) or does not happen (eradication). Fiberboard blocks impregnated with methyl eugenol and various insecticides (e.g., Naled, Malathion and Fipronil) were used successfully to eradicate oriental fruit fly, *Bactrocera dorsalis* (Hendel) in Okinawa, Japan (Koyama et al. 1984, Koyama et al. 2004); Asian papaya fruit fly, *Bactrocera papayae* in Australia (Cantrell et al. 2002) and *Bactrocera* species in Nauru, South Africa (Allwood et al. 2002).

African Insect Science for Food and Health (icipe) and the International Institute of Tropical Agriculture (IITA) in Africa, are promoting the use of MAT as a component of the IPM strategy for *Bactrocera*, *Ceratitis* and *Dacus* fruit fly pests (Ekesi and Billah 2007). However, for effective fruit fly management, it is important to target females as well, removing female fruit flies has additional advantage of reducing oviposition-induced damage and removing the potential for offspring (Jang and Light 1996).

2.2. Protein bait techniques

Traps baited with proteins have been used historically to detect, monitor and suppress fruit flies from a given area (Dowell and Penrose 1995, Vargas et al. 2002). The proteins in these baits often provide nutrients essential for development and sexual maturity of flies (Perez-Staples et al. 2007). Bait sprays and bait stations are fruit fly suppression techniques that combine food-based attractants with insecticide to target mainly female adult flies. Protein hydrolysates and their ammonium mimics combined with a killing agent are used to attract flies and kill them before they lay eggs on the fruit. An advantage of these techniques is the bait has a potential to attract both male and female fruit flies. In addition, it reduces the proportion or land area covered with conventional pesticide sprays (Prokopy et al. 1992). However, a number of non-target flies could also be attracted and killed (Uchida et al. 2006, Leblanc et al. 2010).

2.3. Integrated pest management (IPM)

As often a complex of fruit fly species infest fruit and vegetable production systems, no single management or control technique would be sufficient. In fact single techniques seldom result in sustainable and effective suppression of pests. As a result, the approach being promoted in today's agricultural practise is a combination of control methods, Integrated Pest Management (IPM). The use of single suppression techniques to reduce fruit flies from an area where they are well established has proven insufficient in many cases, and consequently, most successful programs have resorted to the use of integrated suppression techniques. For instance, a nation-wide program was initiated to eradicate *Bactrocera dorsalis* from Taiwan in 1994. By the year 2002, a large amount of methyl eugenol (40 metric tone) was used to supress 75% of the population, but further reductions with male annihilation alone was impossible. They subsequently incorporated bait sprays, sanitation, and fruit bagging and accomplished further suppression of *B. dorsalis* population (Vargas et al. 2010).

On Hawaii, a combination of six different management techniques suppressed *Ceratitis capitata* and *Bactrocera dorsalis* to a significant level (90.7% and 60.7% respectively) in a 40-km^2 area during a six-year period (Vargas et al. 2010). A successful eradication of another pest *Bactrocera cucurbitae* was made possible by combining sterile insect technique (SIT) with other techniques that include mass trapping and bait sprays (Koyama et al. 2004). In South Africa, male annihilation combined with orchard sanitation and protein bait sprays with malathion eradicated *Bactrocera dorsalis / invadens* from the northern most part of the Limpopo province (Manrakhan et al. 2011).

For successful result, IPM system should also consider coexisting species of flies in the area of management. Because, a suppression of a major fruit fly pest to a significant level may through competitive exclusion cause other fruit fly species in the area to become pests.

3. Lures

Lures are excellent tools for fruit fly pest management. Lures of fruit flies are either male specific or female biased (Tan et al. 2014) that is there is no female specific attractant for tephritid flies. Citronella oil was the first male specific attractant found attracting *B. zonata* males, later its main ingredient methyl eugenol was obtained. Similarly, Kerosene was found to attractant males of *C. capitata*, and further analysis revealed, trimedlure (TML). Female biased attractants are mainly derived from food and host odours.

3.1. Bactrocera male lures

Fruit flies in the *Bactrocera dorsalis* complex are classified into three different groups, ME responders, CUE responders and non-responders, based on the response to CUE and ME lures (Drew and Hooper 1981, Tan and Nishida 2012). Nearly 200 species of *Bactrocera* are CUE responders and 81 are ME responders, but most of these are not economically important (IAEA 2003) (Table 1).

While ME is widely distributed in nature and occurs in over 200 plant species representing 80 families (Tan and Nishida 1996a, Tan and Nishida 2012). CUE on the other hand has not been isolated directly as a natural product, although it is rapidly hydrolysed to form a naturally occurring compound raspberry ketone (RK) (Metcalf 1990, Metcalf and Metcalf 1992). Raspberry ketone is the main attractive component of CUE (Metcalf and Metcalf 1992). Although, RK is more attractive than CUE (Jang et al. 2007), it is less stable in the field. Nevertheless, the primary role of these lures in the fly ecology is still under investigation (Shelly and Villalobos 1995, Shelly 2010).

There are two hypotheses speculating about the main role of these plant-derived substances in *Bactrocera* males; in both cases, the role is ecological rather than nutritional. The first hypothesis suggested by (Metcalf 1979) is that, these lures serve as rendezvous stimuli used by males to locate mates or to bring the sexes together in proximity to a suitable host. This hypothesis is further supported by the incident that the day to day activities of adult fruit flies is partitioned spatially depending on their physiological status (Raghu and Clarke 2003). The partition is that, immature and unmated adults spend most of their time searching for protein and sugar, while mature male flies and unmated mature females search for sugars during the day and respond to lures at dusk (Raghu et al. 2002), mating often follows the later. In contrast, mature and mated females search for suitable hosts for egg laying and do not respond to the parapheromones. This finding, where immature males are not as responsive as mature males during the day and, mature unmated females respond during dusk, suggests that the lures serve as a meeting site (Raghu and Clarke 2003).

Table 1. Species of the *B. dorsalis* complex with types of lures and economic importance (Modified from Clarke et al 2005)

B. abdolonginqua	🟪	⬜	*B. laticosta*	🟩	⬜
B. aemula	🟩	⬜	*B. latilineola*	🟪	⬜
B. affinidorsalis	🟩	⬜	*B. lombokensis*	🟩	⬜
B. amarambalensis	🟪	⬜	*B. makilingensis*	🟩	⬜
B. arecae	🟦	⬜	*B. malaysiensis*	🟩	⬜
B. atrifemur	🟪	⬜	*B. melastomatos*	🟩	⬜
B. bimaculata	🟩	⬜	*B. merapiensis*	🟩	⬜
B. cacuminata	🟪	⬜	*B. mimulus*	🟪	⬜
B. carambolae	🟪	🟨	*B. minuscula*	🟪	⬜
B. caryeae	🟪	⬜	*B. muiri*	🟦	⬜
B. ceylanica	🟩	⬜	*B. neoarecae*	🟪	⬜
B. cibodasae	🟩	⬜	*B. neocognata*	🟩	⬜
B. cognata	🟦	⬜	*B. neopropinqua*	🟦	⬜
B. collita	🟪	⬜	*B. nigrescens*	🟪	⬜
B. consectorata	🟩	⬜	*B. occipitalis*	🟪	🟨
B. dapsiles	🟪	⬜	*B. opiliae*	🟪	⬜
B. diallagma	🟪	⬜	*B. osbeckiae*	🟦	⬜
B. dorsalis	🟪	🟨	*B. papayae*	🟪	🟨
B. dorsaloides	🟦	⬜	*B. paraverbascifoliae*	🟪	⬜
B. endiandrae	🟪	⬜	*B. pedestris*	🟩	⬜
B. fernandoi	🟩	⬜	*B. penecognata*	🟩	⬜
B. floresiae	🟪	⬜	*B. philippinensis*	🟪	🟨
B. fuliginus	🟩	⬜	*B. profunda*	🟩	⬜
B. fulvifemur	🟩	⬜	*B. propinqua*	🟩	⬜
B. fuscitibia	🟩	⬜	*B. pyrifoliae*	🟦	🟨
B. gombokensis	🟩	⬜	*B. quasipropinqua*	🟦	⬜
B. hantanae	🟩	⬜	*B. raiensis*	🟦	⬜
B. holtmanni	🟩	⬜	*B. selnophora*	🟩	⬜
B. inconstans	🟩	⬜	*B. sembaliensis*	🟩	⬜
B. indecora	🟩	⬜	*B. sulawesiae*	🟪	⬜
B. indonesiae	🟪	⬜	*B. sumbawaensis*	🟩	⬜
B. infulata	🟪	⬜	*B. syzygii*	🟦	⬜
B. involuta	🟦	⬜	*B. thailandica*	🟦	⬜
B. irvingiae	🟦	⬜	*B. trivialis*	🟩	🟨
B. kanchanaburi	🟦	⬜	*B. unimacula*	🟪	⬜
B. kandiensis	🟪	🟨	*B. usitata*	🟩	⬜
B. kinabalu	🟩	⬜	*B. verbascifoliae*	🟪	⬜
B. lateriaenia	🟩	⬜	*B. vishnu*	🟩	⬜

🟪 ME	🟩 CUE	🟦 No lure	🟨 Ec. imp	⬜ Not Ec. Imp.

The second hypothesis states that the lures are precursors of sex pheromones. Males of *Bactrocera* that feed on ME or CUE or plants containing ME or RK are known to store or sequester metabolites in their rectal gland, the site where they are converted into compounds that appear to increase competitiveness between males and increase mating success (Nishida et al. 1988, Shelly and Nishida 2004, Hee and Tan 2006). It is believed that, males ingest these plant substances for the purpose of having a better chance of being selected by the female (Shelly 2010). Even though the process is not clearly defined, females prefer males who fed on these substances.

When an insect actively searches for secondary plant metabolites and feed on it for a specific purpose other than metabolism, the insect is termed as pharmacophagous and the process is known as pharmacophagy (Boppré 1984). Pharmacophagy of ME in *Bactrocera* results in the emission of compounds such as 2-allyl-4,5-dimethoxyphenol (DMP), (E)-coniferyl alcohol (E-CF), (Z)-coniferyl alcohol, (Z)-3,4-dimethoxycinnamyl alcohol (Z-DMC), *N*-3-methylbutyl acetamate, spiroacetals, pyrazines, ethyl 4-hydroxybenzoate and propyl 4-hydroxybenzoate along with other endogenously produced compounds (Baker and Bacon 1985, Perkins et al. 1990, Tan and Nishida 1996a, Tan et al. 2011). These plant substances are converted in different combinations depending on the species. For example, after feeding on ME *B. dorsalis* males transform and accumulate the phenylpropanoids in the form of DMP and E-CF whereas *B. zonata* males convert and accumulate phenylpropanoids in the form of DMP and Z-CF and *B. correcta* males accumulate in the form of Z-DMC and Z-CF in their rectal sac (Tan et al. 2011).

The second hypothesis is further supported by a laboratory observation where male *Bactrocera* flies are attracted to the rectal gland secretions of other ME fed flies, feed on it and form leks (Wee and Tan 2007). Lekking is a communal competitive display by which males gather to compete for the visiting females (Fletcher 1987). Males calling in aggregation are more effective in attracting females than males calling singly (Shelly 2001, Weldon 2007). In the *Bactrocera dorsalis* complex lekking may also have a purpose of mating disruption by a male releasing the sex pheromone, which immediately acts as an aggregation pheromone to distract attracted males' from a potential female mate (Tan and Nishida 1996a).

Another, but not well developed hypothesis states that feeding on ME may provide a defensive role against vertebrate predation (Tan and Nishida 1996b). An Asian house lizard *Hemidactylus frenatus* has been observed to prefer feeding on ME deprived males than ME fed males and avoid feeding on ME fed males after its first day encounter (Tan and Nishida 1998).

3.2. Ceratitis male lures

The first known attractant for the Mediterranean fruit fly known was kerosene (Severin and Severin 1913). Later it was discovered that the kerosene attracted only males of *C. capitata*. Despite extensive trapping using kerosene, fruit orchards were highly infested and the use of kerosene was superseded. In 1956, the uses of angelica seed oil became popular in Florida for the same purpose of trapping

Mediterranean fruit flies (Steiner 1957). Further analysis and bioassay of this oil components resulted in the production of medlure. Subsequently, the chlorination of medlure, resulted in todays widely used and powerful male attractant tert-butyl 4 or 5 chloro-2-methylcyclohexane-1-carboxylate Trimedlure (TML) (Beroza et al. 1961). TML is a male specific lure that attracts *C. capitata* as well as another fruit fly native to Africa (*C. rosae*).

Commercial TML is a mixture of mainly four isomers designated as A, B1, B2 and C, in which the methyl group is trans to the ester group (McGovern et al. 1986) (Fig 2A). The C isomer in its trans configuration with an axial 4-chloro group is the most attractive to *C. capitata* (McGovern et al. 1987). In subsequent studies, substituting the chlorine with iodine resulted in ethyl ester of iodo-TML, which is found to be more attractive and long lasting than the chloro-TML. This product (the iodinated analogue of TML) was later named as Ceralure (CRL) (McGovern and Cunningham 1988) (Fig 2B). CRL (ethyl 4-(5) iodo-trans-2-methlcyclohexane-1-carboxylate) also have four major isomers designated in the same way as its analogue TML. Unlike TML, the B1 isomer in its trans configuration with an equatorial 5-iodo group is the most attractive to *C. capitata*. Not only CRL-B1 was superior to its isomers but also it was twice as attractive as TML-C (Warthen et al. 1994).

There is no evidence for the natural occurrence of TML (Drew 1987). However, it is more likely that there exist natural substances that are important for the synthesis of the male sex parapheromone. This speculation is further supported by the observation that some male *Ceratitis* flies forage and aggregate on particular plant species (McInnis and Warthen 1988). It is shown that, male flies exposed to volatile of the synthetic TML manifest an increased mating success. Similarly, males exposed to a naturally found sesquiterpene that is found in many essential oils (α copaene) and α copaene containing essential oils exhibited a significant mating advantage over unexposed control flies. Thus, α copaene is supposed to be the major compound, which facilitates aggregation of the male flies to the lek site (Nishida et al. 2000).

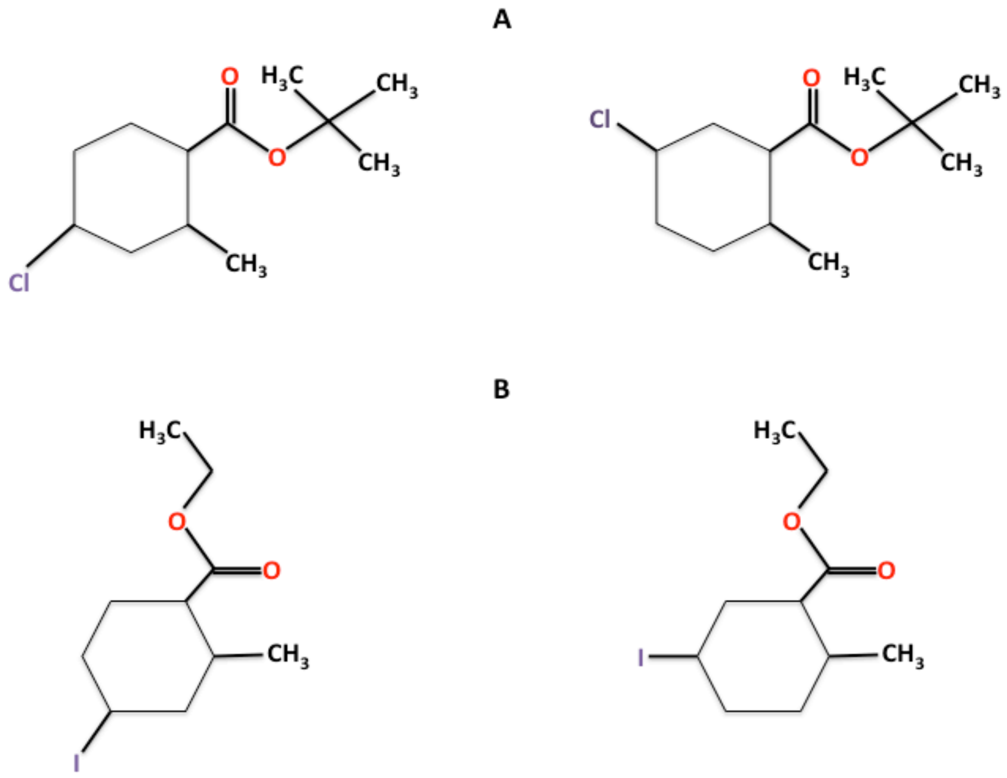


Figure 2. Structural isomers of *Ceratitis* male attractants, A = trimedlure (TML) and B = ceralure (CRL).

A field cage containing oranges wounded on the peels have been shown to attract only male *Ceratitis* flies and those attracted were feeding on the exudates of the wound (Katsoyannos et al. 1997). Similar feeding responses were observed when an essential oil of the citrus was smeared on a plastic sphere (Katsoyannos et al. 1997). In line with this, under laboratory condition, males observed to be highly attracted to wounded orange compared to woundless orange (Papadopoulos et al. 2001). Furthermore, males that openly contacted the wounded fruit and ingested the exudates manifested a better competitive advantage during courtship over unexposed males (Papadopoulos et al. 2001). Hence, it is more likely that the flies use this exudate in the synthesis of the pheromone.

Currently, enriched ginger root oil (EGO lure) has been proved to be as equally attractant as TML, and has the additional benefit of attracting *Ceratitis cosyra*, a species that is not attracted to TML (Mwatawala et al. 2013).

3.3 Female biased Lures

Food lures are less effective in attracting tephritid fruit flies compared to the number of males attracted to male lures (Ekesi and Billah 2007). Unlike the male lures, which are highly volatile and attract male flies from a long distance, food lures are less volatile and attract both sexes from short distances (McQuate and Follett 2006). Both sexes are attracted to food lure because; they require protein for development and enhancement of their reproductive success (Hagen and Finney 1950, Fabre et al.

2003). Males that feed on protein are more successful in gaining copulation than protein-deprived males and females that copulate with protein fed males are less likely to re-copulate than females copulated with protein-deprived males (Blay and Yuval 1997) this is because females mated with well-fed males store sperm in greater abundance (Taylor and Yuval 1999).

The attraction of fruit flies to protein sources has been harnessed in control measures. Although, not efficient as male lures (parapheromones), protein lures have been used as food baits for controlling fruit flies (Varikou et al. 2014). Based on volatiles emanating from food lures, various food-based synthetic attractants have been produced and commercialized and are available in both dry and liquid forms. Among these are Torula yeast, hydrolysate protein, Nulure, Biolure, GF 120 and Ammonium Bicarbonate (Ekesi and Billah 2007). Most of the research on food-based lures studies the efficacy and possibilities of improvement either through combining baits or using synthetics.

Torula Yeast is an autolysed yeast protein and is available commercially as dry pellets. Biolure is a commercially available dry attractant and it consists of three components: ammonium acetate, trimethylamine and putrescine (AA + TMA + PT). These components are available as membrane-based dispensers (Ekesi and Billah 2007). Biolure is a female biased attractant and it is highly effective in attracting females of *C. capitata*, *C. rosa* and *C. cosyra* (McQuate et al. 2005), and appears more attractive than commonly used protein baits such as Torula yeast and hydrolysate proteins (Sookar et al. 2006, Quilici et al. 2007). On the other hand, species that are more host-specific such as the guava fruit fly, *A. striata* and the olive fruit fly, *B. oleae* has poor response to the synthetic lures compared to the conventional protein baits (bicarbonate and spiroketal), Nulure in combination with borax is the best lure for these species (Sookar et al. 2006, Quilici et al. 2007).

.

Eliminating one constituent from Biolure minimizes the cost significantly. The response of some of the economically important *Anastrepha* species to a two-component synthetic food lure (AA + PT) is equal or better compared to torula yeast and Nulure in subtropical condition and dry season. Likewise, *Bactrocera* species responded better to different concentrations and combinations of the synthetic food lures than to the conventional protein baits (Sookar et al. 2006, Quilici et al. 2007).

Results appeared to differ between studies at different geographic localities. For example, on Reunion only a double dose of AA was better than the conventional bait to attract *B. zonata*, whereas on Mauritius TMA was required in addition to the double dose of AA. In Pakistan PT was added to TMA for the same purpose of trapping *B. zonata*. Similarly, in Reunion a half dose of AA was enough to attract *B. cucurbitae*, whereas a double dose was required in Mauritius (Sookar et al. 2006, Quilici et al. 2007).

Other examples of research with lure combinations showed that male *B. olea* are highly attracted towards hydrolysed protein and female flies are more attracted to torula yeast, but when these two lures are combined, fewer flies of both sexes were attracted (Varikou et al. 2014).

3.4. Host volatiles: potential female attractants

Polyphagy contributes to the biological success of tephritidae fruit flies. This success was made possible primarily due to morphological adaptation in the ovipositor and behavioural adaptations in oviposition preference of the female (Fletcher 1987). There usually exists a positive association between the choice of the ovipositing female and the performance of the larvae. The process of oviposition site choice thus requires a sophisticated behavioural mechanism which involve the integration of olfactory, gustatory and visual cues plus physical information such as colour, shape and texture of the fruit (Robacker 1992, Cardé and Willis 2008) and is probably regulated by short term memory (Prokopy et al. 1989, Liu et al. 2015).

Numerous studies have shown that fruit flies strongly rely on odorants in host searching behaviour (Siderhurst and Jang 2006, Jayanthi et al. 2012, Biasazin et al. 2014). Fruits and leaves of host plants are the most extensively assessed organs for fruit fly attracting volatiles. However, the search has been extended to include volatiles from non-host plants and animal wastes including human urine and bird faeces (Piñero et al. 2003, Robacker et al. 2009). Electrophysiological studies have shown that fruit flies are sensitive to organic compounds such as monoterpenes, sesquiterpenes, pyrazine, carboxylic acids, alcohols, aldehydes, ketones and esters, most of which are typical volatiles of ripening fruits (Gikonyo et al. 2005, Jayanthi et al. 2012, Biasazin et al. 2014).

4. Antennal Morphology and Types of Antennal Sensilla

The antenna is the most important olfactory organ of all insects. Different insect orders have different antennal forms, but share three basic segments: scape, pedicel and flagellum. The segments are covered with cuticular protrusions called sensilla, which harbour sensory neurons. The sensilla are of various forms, basiconic, clavate, coeloconic, trichoid, styloconic and chaetica that house chemoreceptor neurons, mechanoreceptor neurons, thermoreceptor neurons and hygroreceptor neurons, which are crucial for survival and reproduction.

4.1. Antennal Morphology of Tephritidae

In Tephritidae, the antennae are of arista type (Fig 3), and it is the primary channel in detecting odorants (Rice 1989, Keil 1999). On the dorso-proximal end of the flagellum arises a trichoid arista having two short basal segments and on the medial side of the flagellum is a single sensorial pit. However, (Hu et al. 2010) has recently reported the absence of a sensorial pit in six different species of *Bactrocera* flies.

In most of the economically important fruit flies studied so far, the antennal morphology is similar with regard to type and shape. Sexual dimorphism is reported with regard to difference in length of specific antennal segments, presence and absence of sensilla types in either of the segments and density of specific sensillum types (Arzuffi et al. 2008, Awad et al. 2014, Awad et al. 2015). Awad et al. 2015 have recently observed sexual dimorphism on the antennae of *B. zonata* depending on the host fruit they colonize (Fig 3). Some studies reported that males having longer antennal segments and females having more abundant sensilla in the funiculus. However, in some cases such differences in length of segments and density of sensilla are minor (Levinson et al. 1987, Mayo et al. 1987, Castrejón-Gómez and Rojas 2009) and some authors have reported the contraries (Dickens et al. 1988).

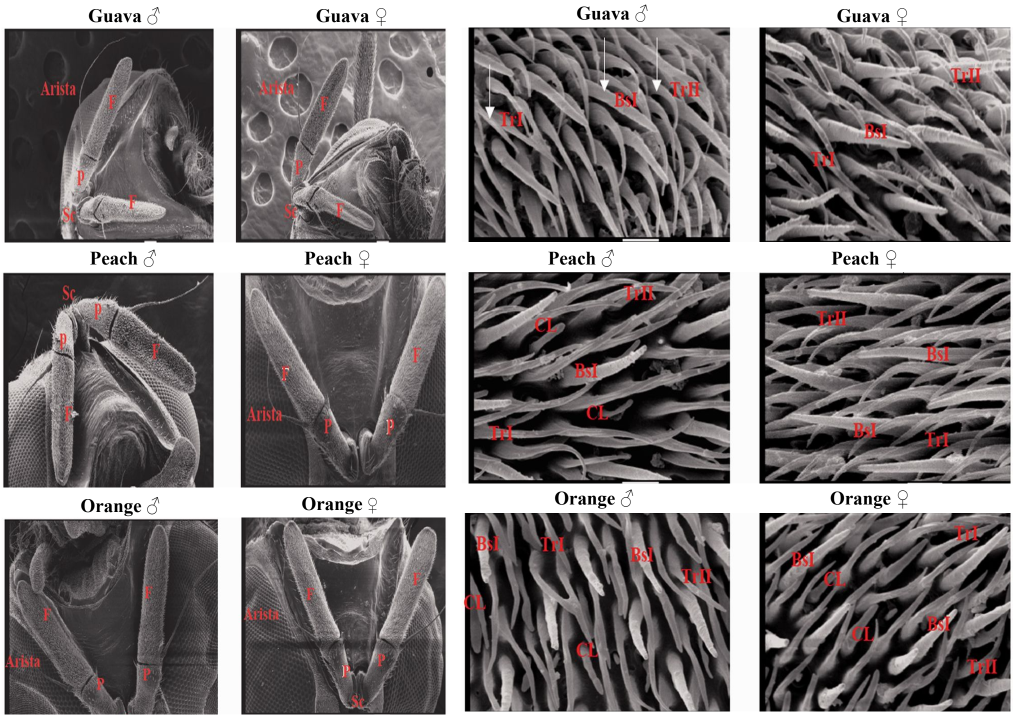


Figure 3. Antennal segments and funicular sensilla of male and female *Bactrocera zonata* on different host species (guava, peach and orange), showing trichoid type I, II (TrI, TrII), basiconic type I (BSI) and clavate (CL) sensilla (modified from Awad et al. 2015)

4.2. Types of Olfactory Sensilla

A thorough understanding of the morphology, function and distribution of tephritidae olfactory sensilla is a prerequisite for future electrophysiological and neuroethological studies of the insect sensory system involved in chemical communication. Integration of this knowledge with inputs from behavioural and molecular studies may lead to an effective practical use of pheromones, parapheromones and other semiochemicals in chemical ecology related pest management strategies (Keil 1999).

Different types of sensory structures cover the surface of all the three segments of the antennae and the sensorial pit (Sivinski and Calkins 1986, Mayo et al. 1987, Dickens et al. 1988). Morphologically a sensillum can be either single walled or double walled with numerous pores that allows the access of odour molecules into the lumen of the sensillum. Several authors have documented microtrichial, basiconic (types I and II), clavate, chaetica, coeloconica, trichoid (types I and II), campaniform, and styloconic sensilla on several species of tephritidae fruit flies (Sivinski and Calkins 1986, Levinson et al. 1987, Mayo et al. 1987, Dickens et al. 1988, Hu et al. 2010).

It should be noted that the same types of sensillum have been named differently in different fruit flies. For instance, non-porous sensilla (NPS) was used for sensilla chaetica, multiporous grooved sensilla (MPGS) for styloconic sensilla, and multiporous sensilla (MPS) for trichoid and basiconic sensilla (Bisotto-de-Oliveira et al. 2011). Short type of sensilla basiconica (SSB) was a name given to type II basiconica sensilla (Hu et al. 2010). Trichoid, basiconic and clavate sensilla are single walled with pores, whereas, styloconic is double walled with pores (Mayo et al. 1987).

4.3. Distribution and function of sensilla

Every type of sensillum has a particular abundance and distribution pattern along the antennae and fulfils presumably a distinct function (Hu et al. 2010). The distribution pattern and morph is more or less similar between sexes of same species, but might be different between different species of tephritidae flies. In *Anastrepha fraterculus*, sensilla chaetica are not detected on the flagellum (Bisotto-de-Oliveira et al. 2011). Most of the sensilla types on the scape and pedicel are non porous and believed to have a mechanoreceptor function related to movement of the antennae (Arzuffi et al. 2008).

Basiconic sensilla are characterized by swollen base and neck shaft; the two subtypes are similar in morphology, but different in size (Hu et al. 2010). Sensilla basiconica on the flagellum are with numerous pore and socketed base. Several authors have suggested the olfactory function of these types of sensilla (Mayo et al. 1987, Dickens et al. 1988, Arzuffi et al. 2008). In addition, (Hull and Cribb 2001) have reported its role as CO_2 receptor in *B. tryoni* and (Ross and Anderson 1991) have suggested its role in thermo reception.

Trichoid sensilla are the longest and most conspicuous sensillum types with slender and conical structure and smooth wall. There are two types of such sensilla, the first type is the most numerous type on the flagellum, whereas the second type, which is slightly more curved, is less numerous (Hu et al. 2010, Awad et al. 2014). They are regularly distributed over the flagellum and they are believed to function in chemoreception, olfaction and parapheromone reception (Dickens et al. 1988, Levinson et al. 1990). Type 1 trichoid sensilla are known to respond to a wide range of plant volatiles including aldehydes, esters and short chain alcohols and pheromones (Hull and Cribb 1997). Dickens et al 1988 reported responses from trichoid sensilla of *Ceratitis* males to the attractant trimedlure.

Styloconic sensilla are characterized by finger like processes with distinct longitudinal groves in their walls (Arzuffi et al. 2008). These types of sensilla are present on the whole surface of the funniculus, but are more abundant on the medial region (Hu et al. 2010). They have a dual function of chemoreception and thermo-reception (Hull and Cribb 1997).

In *C. capitata*, basiconic and grooved peg type sensilla are distributed all over the funiculus whereas sensilla chaetica are found only in the proximal region of the flagellum surface. Trichoid type sensilla are found all over the flagellum except for the proximal region where sensilla chaetica are present (Bigiani et al. 1989).

Clavate sensilla are very similar to basiconic types. The only difference is, these are shorter and club like (Mayo et al. 1987, Arzuffi et al. 2008). These types of sensilla are multi-porous (Liscia et al. 2013) and they are the least abundant (Bigiani et al. 1989). According to their distal diameter, these types were classified as types I and II, type I being larger (Bisotto-de-Oliveira et al. 2011).

Sensilla chaetica are one row of bristle-like structures with a stout and a very long shaft. These type of sensilla are nonporous and absent in the flagellum (Bisotto-de-Oliveira et al. 2011, Awad et al. 2014). They probably function as contact chemoreceptors.

Sensilla coeloconica are the shortest and least abundant sensillum types and irregularly distributed (Hu et al. 2010). They arise from a depression of the integument called sacculus. In *B. olea* these types of sensilla were reported as non-porous but other authors have described them as multi-porous (Mayo et al. 1987, Dickens et al. 1988). In *B. zonata* two types of sensilla coeloconica (types I and II) are reported. Sensillum coeloconica II was found only in male antennae of *B. zonata* whereas coeloconica (I) is found in female antennae (Awad et al. 2014).

5. The Olfactory Transduction Pathway

Tephritid flies detect parapheromone with high sensitivity (Wee et al. 2002) that may be comparable to pheromone detection in moths. Parapheromones are believed to be pheromone precursors and some such as methyl eugenol and raspberry ketone are found naturally from plant sources. In insects, pheromone perception is somehow different from general odour perception. Moth sex pheromones are detected in a ‘labelled line’ fashion. That is, each single component of the sex pheromone is individually detected by male specific pheromone olfactory receptor neurons (Pher-ORNs) that project to a specific enlarged sphere, the macroglomerular complex (MGC) in the antennal lobe (AL), and directly to the higher brain centre. So one could ask how are parapheromones detected? Do parapheromones have specific ORNs like moth sex pheromones? Or are they detected as a general (non-pheromonal) odorant? Do these OSNs project to an MGC in the brain, and do these send information to higher brain centers through another mode than ‘normal’ odors? Below a brief overview of what we know about the signalling cascade in other insect species.

Pher-ORNs in many insects are embedded within long trichoid sensilla. At the base of any sensillum are auxiliary cells that surround cell bodies of the ORNs. The auxiliary cells function in secreting both the aqueous lymph that fills the space within the cuticle and odorant binding proteins (OBPs) (Park et al. 2000, Shanbhag et al. 2000). ORNs extend their dendrite in to the sensillar lymph filed cavity and project their axons to glomeruli in the antennal lobe (AL). On the dendrites of each ORN one or rarely a few different olfactory receptor genes (ORs) are expressed

An odorant that enters through the porous cuticle of the sensillum is subjected to the aqueous sensillar lymph, and binds with odorant binding proteins (OBPs). Pheromone components have special type of odorant binding proteins named as pheromone binding proteins (PBPs). The OBPs capture the hydrophobic odorant and transport the molecule in a hydrophilic medium to the ORs. ORs are expressed along with a conserved odorant receptor co-receptor (Orco). This interaction forms a heterodimer, which has an inverted topology in the plasma membrane compared to other G protein coupled receptors. This heterodimer either function in ionotropic manner as a direct ligand gated ion channel (Sato et al 2008) or as a metabotropic cascade (Witcher et al 2008), but it could also function in a combination of both ionotropic and metabotropic manners (Wicher 2010). One OR can recognize multiple odorants, but one odorant can also be recognized by multiple ORs (Hallem and Carlsson 2006). Again, in tephritid flies we have almost no information on which OSN types respond to parapheromones, whether they are housed in tirchoid or other types of sensilla, or whether these are highly sensitive and specific compared to ordinary odors.

Similarly, we lack of information on signalling downstream from the antenna in tephritid fruit flies. Whereas it is established that ORNs that express the same OR coalesce into a single glomerulus in the AL, it is unknown if the glomeruli targeted by parapheromone-sensitive OSNs are sexually dimorphic (enlarged in males), such as is observed in male moths. Or whether these OSNs synapse with projection neurons (PNs) via a different tract and target specific areas in the higher brain regions mushroom body (MB) and lateral horn (LH) different from ordinary odors. Projection neurons (PNs) branch in a single glomerulus in the AL (uniglomerular) or branch in many glomeruli (multiglomerular) and send their axons to the calyx (Galizia and Lledo 2013). Unlike, the axons of PNs of non-pheromonal glomeruli that are widely distributed in the MB calyx, the axons of PNs that innervate MGC are relatively confined to a small area within the calyx (Namiki et al. 2013).

6. Research Gaps

The surface of the maxillary palps of tephritid fruit flies is also covered by sensory structures that probably have olfactory roles (Zhang et al. 2011). The morphology and distribution of sensilla both on the antenna and maxillary palps of most teprhitid fruit flies are more or less similar across different species (Arzuffi et al. 2008, Hu et al. 2010, Awad et al. 2014, Awad et al. 2015). But, the sensilla types that house ORNs responsible for detecting male lures have not been clearly identified. It is also unknown if ORNs housed in sensilla of maxillary palps are involved in parapheromone detection. Identifying and characterizing these sensilla types should be the first step for future neuroethological studies.

Males of most polyphagous fruit flies are attracted to parapheromones of different types, For example *B. dorsalis* and *B. zonata* are attracted to ME, *B. cucurbitae* is attracted to CUE and *C. capitata* is attracted to TML. On the other hand, *B. oleae*, which specialize on olive fruits, are dependent on pheromones for sexual communication between conspecifics. Both pheromones and parapheromones are directly or indirectly associated with reproductive success. Insects that depend on pheromone for sexual communication, such as moths and cockroaches manifest a sex specific enlargement of glomeruli in the AL referred to as macroglemerular complex (MGC). MGC could also be associated with plant odours (Dekker et al. 2006). It is also important to ask if ORNs that respond to parapheromones may coalesce into such an enlarged sphere in the AL. Or if *B. oleae* has such modulation in the AL in order to adapt to olive fruit specific volatiles.

Most tephritid fruit flies, even those that are polyphagous, have some sort of fruit preferences (Rwomushana et al. 2008). This preference is largely based on headspace volatiles of ripe fruits (Biasazin et al. 2014). Fruit flies in the genus *Bactrocera* have variety of fruit preferences ranging from being specialist to generalists. For instance, *B. dorsalis* prefers to oviposit on ripe mango and ripe guava than other fruit volatiles, *B. cucurbitae* has a special preference for cucurbitaceous plants and *B. oleae*, is monophagous on olive fruits. A small shift in fruit preference of *Rhagholetis palmonella* has lead to modification in the olfactory system and speciation (Linn et al. 2003). It would be important to see if this variation in *Bactrocera* fruit preference is correlated with change in the olfactory system of the flies. Maybe those with similar feeding types (generalists) have conserved ORN clusters and those that specialize on a single host, as observed in *Drosophila sechelia*, have lost some of the clusters (Dekker et al. 2006).

Peripheral sexual dimorphism with reference to presence and absence of sensilla types and density of specific sensilla types has been observed (Arzuffi et al. 2008, Awad et al. 2014, Awad et al. 2015). One could ask if these sensillum types in males are related to detection of parapheromone or other structurally related compounds. This could also be compared between closely and distantly related species of tephritidae fruit flies. The next question would be, what are the homologous sensilla types in females? What are they tuned to? It would also be important to investigate if these peripheral differences are correlated with the glomerular organization in the AL with regard to size, shape, number and position. This would be a very important step towards development of specific attractant for female flies of different species that would be as equally attractant as male lures. Otherwise it may explain why females are not attracted to male lures

References

Alfaro, C., S. Vacas, M. Zarzo, V. Navarro-Llopis, and J. Primo. 2010. Solid phase microextraction of volatile emissions of Ceratitis capitata (Wiedemann)(Diptera: Tephritidae): influence of fly sex, age, and mating status. Journal of agricultural and food chemistry 59: 298-306.

Allwood, A., E. Vueti, L. Leblanc, and R. Bull. 2002. Eradication of introduced Bactrocera species (Diptera: Tephritidae) in Nauru using male annihilation and protein bait application techniques, pp. 19-25, Turning the tide: the eradication of invasive species. . IUCN Species Specialist Group. IUCN,, Gland Switzerland and Cambridge, UK.

Aluja, M., F. Dıaz-Fleischer, D. R. Papaj, G. Lagunes, and J. Sivinski. 2001. Effects of age, diet, female density, and the host resource on egg load in Anastrepha ludens and Anastrepha obliqua (Diptera: Tephritidae). Journal of insect physiology 47: 975-988.

Arzuffi, R., N. Robledo, and J. Valdez. 2008. Antennal sensilla of Toxotrypana curvicauda (Diptera: Tephritidae). Florida Entomolgist 91: 669-673.

Asokan, R., K. Rebijith, S. K. Singh, A. Sidhu, S. Siddharthan, P. K. Karanth, R. Ellango, and V. Ramamurthy. 2011. Molecular identification and phylogeny of Bactrocera species (Diptera: Tephritidae). Florida Entomologist 94: 1026-1035.

Awad, A. A., N. A. Ali, and H. O. Mohamed. 2014. Ultrastructure of the antennal sensillae of male and female peach fruit fly, Bactrocera zonata. Journal of Insect Science 14: 45.

Awad, A. A., H. O. Mohamed, and N. A. Ali. 2015. Differences in Antennal Sensillae of Male and Female Peach Fruit Flies in Relation to Hosts. Journal of insect science 15: 8.

Baker, R., and A. Bacon. 1985. The identification of spiroacetals in the volatile secretions of two species of fruit fly (Dacus dorsalis, Dacus curcurbitae). Cellular and Molecular Life Science 41: 1484-1485.

Baker, R., R. H. Herbert, and G. G. Grant. 1985. Isolation and identification of the sex pheromone of the Mediterranean fruit fly, Ceratitis capitata (Wied). Journal of Chemical Society: 824-825.

Beroza, M., N. Green, S. Gertler, L. Steiner, and D. Miyashita. 1961. Insect Attractants, New Attractants for the Mediterranean Fruit Fly. Journal of Agricultural and Food Chemistry 9: 361-365.

Biasazin, T. D., M. F. Karlsson, Y. Hillbur, E. Seyoum, and T. Dekker. 2014. Identification of host blends that attract the African invasive fruit fly, Bactrocera invadens. Journal of chemical ecology 40: 966-976.

Bigiani, A., G. Scalera, R. Crnjar, I. T. Barbarossa, P. C. Magherini, and P. Pietra. 1989. Distribution and function of the antennal olfactory sensilla in Ceratitis capitata Wied.(Diptera, Trypetidae). Italian Journal of zoology 56: 305-311.

Bisotto-de-Oliveira, R., L. Redaelli, and J. Sant'ana. 2011. Morphometry and distribution of sensilla on the antennae of Anastrepha fraterculus (Wiedemann)(Diptera: Tephritidae). Neotropical entomology 40: 212-216.

Blay, S., and B. Yuval. 1997. Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). Animal Behaviour 54: 59-66.

Bo, W., S. Ahmad, T. Dammalage, U. S. Tomas, V. Wornoayporn, I. U. Haq, C. Cáceres, M. Vreysen, J. Hendrichs, and M. Schutze. 2014. Mating compatibility between Bactrocera invadens and Bactrocera dorsalis (Diptera: Tephritidae). Journal of economic entomology 107: 623-629.

Boppré, M. 1984. Redefining "pharmacophagy". Journal of Chemical Ecology 10: 1151-1154.

Boykin, L., M. Schutze, M. Krosch, A. Chomič, T. Chapman, A. Englezou, K. Armstrong, A. Clarke, D. Hailstones, and S. Cameron. 2014. Multi-gene phylogenetic analysis of south-east Asian pest members of the Bactrocera dorsalis species complex (Diptera: Tephritidae) does not support current taxonomy. Journal of applied entomology 138: 235-253.

Briceño, D., W. Eberhard, J. Vilardi, J.-P. Cayol, and T. Shelly. 2007. Courtship behavior of different wild strains of Ceratitis capitata (Diptera: Tephritidae). Florida Entomologist 90: 15-18.

Burk, T. 1984. Male-male interactions in Caribbean fruit flies, Anastrepha suspensa (Loew)(Diptera: Tephritidae): territorial fights and signalling stimulation. Florida Entomologist: 542-547.

Cantrell, B., B. Chadwick, and A. Cahill. 2002. Fruit fly fighters: eradication of the papaya fruit fly, CSIRO PUBLISHING.

Cardé, R. T., and M. A. Willis. 2008. Navigational strategies used by insects to find distant, wind-borne sources of odor. Journal of chemical ecology 34: 854-866.

Castrejón-Gómez, V. R., and J. C. Rojas. 2009. Antennal Sensilla of Anastrepha serpentina (Diptera: Tephritidae). Annals of the Entomological Society of America 102: 310-316.

Christenson, L., and R. H. Foote. 1960. Biology of fruit flies. Annual review of entomology 5: 171-192.

Clarke, A. R., K. S. Powell, C. W. Weldon, and P. W. Taylor. 2011. The ecology of Bactrocera tryoni (Diptera: Tephritidae): what do we know to assist pest management? Annals of Applied Biology 158: 26-54.

Clarke, A. R., K. F. Armstrong, A. E. Carmichael, J. R. Milne, S. Raghu, G. K. Roderick, and D. K. Yeates. 2005. Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the Bactrocera dorsalis complex of fruit flies. Annual Review of Entomology 50: 293-319.

Copeland, R. S., R. A. Wharton, Q. Luke, and M. De Meyer. 2002. Indigenous hosts of Ceratitis capitata (Diptera: Tephritidae) in Kenya. Annals of the Entomological Society of America 95: 672-694.

Cunningham, R. 1989. Parapheromones. World crop pests 3: 221-230.

Cunningham, R., and L. Steiner. 1972. Field Trial of Cue-Lure+ Naled on Saturated Fiberboard Blocks for Control of the Melon Fly| 1 by the Male-Annihilation Technique2, 3. Journal of Economic Entomology 65: 505-507.

De Meyer, M. 2000. Systematic revision of the subgenus Ceratitis MacLeay ss (Diptera, Tephritidae). Zoological Journal of the Linnean Society 128: 439-467.

De Meyer, M., R. S. Copeland, and S. Lux. 2002. Annotated Checklist of Host Plants for Afrotropical Fruit Flies (Diptera: Tephritidae) of the Genus Ceratitis: Liste Commentée Des Plantes Hôtes Des Mouches Des Fruits (Diptera: Tephritidae) Afrotropicales Du Genre Ceratitis, Musée royal de l'Afrique centrale.

De Meyer, M., M. Robertson, A. Peterson, and M. Mansell. 2008. Ecological niches and potential geographical distributions of Mediterranean fruit fly (Ceratitis capitata) and Natal fruit fly (Ceratitis rosa). Journal of Biogeography 35: 270-281.

De Meyer, M., M. P. Robertson, M. W. Mansell, S. Ekesi, K. Tsuruta, W. Mwaiko, J. Vayssieres, and A. T. Peterson. 2010. Ecological niche and potential geographic distribution of the invasive fruit fly Bactrocera invadens (Diptera, Tephritidae). Bulletin of entomological research 100: 35-48.

Dekker, T., I. Ibba, K. Siju, M. C. Stensmyr, and B. S. Hansson. 2006. Olfactory shifts parallel superspecialism for toxic fruit in Drosophila melanogaster sibling, D. sechellia. Current Biology 16: 101-109.

Dickens, J., W. Hart, D. Light, and E. Jang. 1988. Tephritid olfaction: morphology of the antennae of four tropical species of economic importance (Diptera: Tephritidae). Annals of the Entomological Society of America 81: 325-331.

Dowell, R. V., and R. Penrose. 1995. Mediterranean fruit fly eradication in California 1994-1995, pp. 161-185. In G. J. Morse, RL Metcalf, JR Carey, and RV Dowell (ed.), Mediterranean Fruit Fly in California: Defining Critical Research. . Collage of Natural and Agricultural Science University of Califfornia, Riverside.

Drew, D. A. I., and M. Hancock. 2000. Phylogeny of the tribe Dacini (Dacinae) based on morphological, distributional, and biological data, CRC Press, Boca Raton, FL.

Drew, R. 1987. Behavioural strategies of fruit flies of the genus Dacus (Diptera: Tephritidae) significant in mating and host-plant relationships. Bulletin of Entomological Research 77: 73-81.

Drew, R., and G. Hooper. 1981. THE RESPONSES OF FRUIT FLY SPECIES (DIPTERA: TEPHRITIDAE) IN AUSTRALIA TO VARIOUS ATTRACT ANTS. Australian Journal of Entomology 20: 201-205.

Drew, R. A. 1989. The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian regions. Memoirs of the Queensland Museum 26.

Drew, R. A. I. 2004. Biogeography and speciation in the Dacini (Diptera: Tephritidae: Dacinae). Bishop Museum Bulletin in Entomology 12: 165-178.

Drew, R. A. I., K. Tsuruta, and I. White. 2005. A new species of pest fruit fly (Diptera: Tephritidae: Dacinae) from Sri Lanka and Africa. African Entomology 13: p. 149-154.

Duyck, P.-F., P. David, and S. Quilici. 2006. Climatic niche partitioning following successive invasions by fruit flies in La Réunion. Journal of Animal Ecology 75: 518-526.

Duyck, P. F., P. David, and S. Quilici. 2004. A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). Ecol Entomol 29: 511-520.

Ekesi, S., and M. Billah. 2007. A field guide to the management of economically important tephritid fruit flies in Africa, ICIPE Science.

Fabre, F., P. Ryckewaert, P. Duyck, F. Chiroleu, and S. Quilici. 2003. Comparison of the efficacy of different food attractants and their concentration for melon fly (Diptera: Tephritidae). Journal of economic entomology 96: 231-238.

Fay, H. A. 2012. A highly effective and selective male lure for Bactrocera jarvisi (Tryon)(Diptera: Tephritidae). Australian Journal of Entomology 51: 189-197.

Fletcher, B. 1987. The biology of dacine fruit flies. Annual review of entomology 32: 115-144.

Fletcher, B. 1989. Temperature-development rate relationships of the immature stages and adults of tephritid fruit flies, pp. 446, Fruit flies: their biology natural enemies and control. Elsevier Science Publ, New York.

Galizia, C. G., and P.-M. Lledo. 2013. Olfaction, pp. 253-284, Neurosciences-From Molecule to Behavior: a university textbook. Springer.

Gikonyo, N. K., S. Lux, and P. Nemeye. 2005. Variation in Volatiles from Fruits of Mango and Marula Attractive to the Mango Fruit Fly, Ceratitis cosyra (Walker). East and Central African Journal of Pharmaceutical Sciences 6: 3-8.

Gonçalves, G. B., C. E. Silva, J. C. Dos Santos, E. S. Dos Santos, R. R. Do Nascimento, E. L. Da Silva, A. De Lima Mendonça, M. Do Rosário Tenório De Freitas, and A. E. Sant'Ana. 2006. Comparison of the volatile components released by calling males of Ceratitis capitata (Diptera: Tephritidae) with those extractable from the salivary glands. Florida Entomologist 89: 375-379.

Hagen, K. S. 1953. Influence of adult nutrition upon the reproduction of three fruit fly species. Special report on control of the oriental fruit fly: 72-76.

Hagen, K. S., and G. L. Finney. 1950. A food supplement for effectively increasing the fecundity of certain tephritid species. Journal of Economic Entomology 43.

Han, H.-Y., and B. A. McPheron. 1997. Molecular phylogenetic study of Tephritidae (Insecta: Diptera) using partial sequences of the mitochondrial 16S ribosomal DNA. Molecular phylogenetics and evolution 7: 17-32.

Hee, A. K.-W., and K.-H. Tan. 2006. Transport of methyl eugenol-derived sex pheromonal components in the male fruit fly, Bactrocera dorsalis. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology 143: 422-428.

Hu, F., G.-N. Zhang, F.-X. Jia, W. Dou, and J.-J. Wang. 2010. Morphological characterization and distribution of antennal sensilla of six fruit flies (Diptera: Tephritidae). Annals of the Entomological Society of America 103: 661-670.

Hull, C., and B. Cribb. 2001. Olfaction in the Queensland fruit fly, Bactrocera tryoni. I: Identification of olfactory receptor neuron types responding to environmental odors. Journal of chemical ecology 27: 871-887.

Hull, C. D., and B. W. Cribb. 1997. Ultrastructure of the antennal sensilla of Queensland fruit fly, Bactrocera tryoni (Froggatt)(Diptera: Tephritidae). International Journal of Insect Morphology and Embryology 26: 27-34.

IAEA. 2003. Trapping guidelines for area-wide fruit fly programmes.

Iwahashi, O., and T. Majima. 1986. Lek formation and male-male competition in the melon fly, Dacus cucurbitae Coquillett (Diptera: Tephritidae). Applied Entomology and Zoology 21: 70-75.

Jang, E. B., V. Casana-Giner, and J. E. Oliver. 2007. Field captures of wild melon fly (Diptera: Tephritidae) with an improved male attractant, raspberry ketone formate. Journal of economic entomology 100: 1124-1128.

Jayanthi, P. D. K., C. M. Woodcock, J. Caulfield, M. A. Birkett, and T. J. Bruce. 2012. Isolation and identification of host cues from mango, Mangifera indica, that attract gravid female oriental fruit fly, Bactrocera dorsalis. Journal of chemical ecology 38: 361-369.

Katsoyannos, B., N. Kouloussis, and N. Papadopoulos. 1997. Response of Ceratitis capitata to citrus chemicals under semi-natural conditions. Entomologia experimentalis et applicata 82: 181-188.

Keil, T. A. 1999. Morphology and development of the peripheral olfactory organs, pp. 5-47, Insect olfaction. Springer.

Khoo, C. C., and K. H. Tan. 2005. Rectal gland of Bactrocera papayae: ultrastructure, anatomy, and sequestration of autofluorescent compounds upon methyl eugenol consumption by the male fruit fly. Microsc Res Techniq 67: 219-226.

Khoo, C. C. H., and K. H. Tan. 2000. Attraction of both sexes of melon fly, Bactrocera cucurbitae to conspecific males–a comparison after pharmacophagy of cue-lure and a new attractant–zingerone. Entomologia experimentalis et applicata 97: 317-320.

Koyama, J., T. Teruya, and K. Tanaka. 1984. Eradication of the oriental fruit fly (Diptera: Tephritidae) from the Okinawa Islands by a male annihilation method. Journal of Economic Entomology 77: 468-472.

Koyama, J., H. Kakinohana, and T. Miyatake. 2004. Eradication of the melon fly, Bactrocera cucurbitae, in Japan: importance of behavior, ecology, genetics, and evolution. Annual Reviews in Entomology 49: 331-349.

Landolt, P., R. Heath, and D. Chambers. 1992. Oriented flight responses of female Mediterranean fruit flies to calling males, odor of calling males, and a synthetic pheromone blend. Entomologia experimentalis et applicata 65: 259-266.

Leblanc, L., R. I. Vargas, and D. Rubinoff. 2010. Attraction of Ceratitis capitata (Diptera: Tephritidae) and endemic and introduced nontarget insects to Biolure bait and its individual components in Hawaii. Environmental entomology 39: 989-998.

Levinson, H., A. Levinson, and K. Schäfer. 1987. Pheromone biology of the Mediterranean fruit fly (Ceratitis capitata Wied.) with emphasis on the functional anatomy of the pheromone glands and antennae as well as mating behaviour. Journal of Applied Entomology 104: 448-461.

Levinson, H., A. Levinson, and K. Müller. 1990. Influence of some olfactory and optical properties of fruits on host location by the Mediterranean fruit fly (Cera titis capita ta Wied.). Journal of Applied Entomology 109: 44-54.

Liimatainen, J., A. Hoikkala, and T. Shelly. 1997. Courtship behavior in Ceratitis capitata (Diptera: Tephritidae) comparison of wild and mass-reared males. Annals of the Entomological Society of America 90: 836-843.

Linn, C., J. L. Feder, S. Nojima, H. R. Dambroski, S. H. Berlocher, and W. Roelofs. 2003. Fruit odor discrimination and sympatric host race formation in Rhagoletis. Proceedings of the National Academy of Sciences 100: 11490-11493.

Liscia, A., P. Angioni, P. Sacchetti, S. Poddighe, A. Granchietti, M. D. Setzu, and A. Belcari. 2013. Characterization of olfactory sensilla of the olive fly: Behavioral and electrophysiological responses to volatile organic compounds from the host plant and bacterial filtrate. Journal of insect physiology 59: 705-716.

Liu, J. L., X. Y. Chen, and X. N. Zeng. 2015. Classical Olfactory Conditioning in the Oriental Fruit Fly, Bactrocera dorsalis. Plos One 10: e0122155.

Lux, S. A., R. S. Copeland, I. M. White, A. Manrakhan, and M. K. Billah. 2003. A new invasive fruit fly species from the Bactrocera dorsalis (Hendel) group detected in East Africa. Int J Trop Insect Sc 23: 355-361.

Malacrida, A., L. Gomulski, M. Bonizzoni, S. Bertin, G. Gasperi, and C. Guglielmino. 2007. Globalization and fruitfly invasion and expansion: the medfly paradigm. Genetica 131: 1-9.

Manrakhan, A., V. Hattingh, J. Venter, and M. Holtzhausen. 2011. Eradication of Bactrocera invadens (Diptera: Tephritidae) in Limpopo Province, South Africa. African Entomology 19: 650-659.

Marchini, D., G. Del Bene, L. Cappelli, and R. Dallai. 2003. Ultrastructure of the male reproductive accessory glands in the medfly Ceratitis capitata (Diptera: Tephritidae) and preliminary characterization of their secretions. Arthropod structure & development 31: 313-327.

Mayo, I., M. Anderson, J. Burguete, and E. R. Chillida. 1987. Structure of superficial chemoreceptive sensilla on the third antennal segment of Ceratitis capitata (Wiedemann)(Diptera: Tephritidae). International Journal of Insect Morphology and Embryology 16: 131-141.

McGovern, T., R. Cunningham, and B. Leonhardt. 1986. cis-Trimedlure: Attraction for the Mediterranean fruit fly (Diptera: Tephritidae) and isomeric structural assignments. Journal of economic entomology 79: 98-102.

McGovern, T., R. Cunningham, and B. Leonhardt. 1987. Attractiveness of trans-trimedlure and its four isomers in field tests with the Mediterranean fruit fly (Diptera: Tephritidae). Journal of economic entomology 80: 617-620.

McGovern, T. P., and R. T. Cunningham. 1988. Persistent attractants for the mediteranean fruit fly, the method of preparation and method of use. Google Patents.

McInnis, D., and J. Warthen. 1988. Mediterranean fruit fly (Diptera: Tephritidae): Laboratory bioassay for attraction of males to leaf or stem substances from Ficus and Litchi. Journal of economic entomology 81: 1637-1640.

McQuate, G. T., and P. A. Follett. 2006. Use of Attractants to Suppress Oriental Fruit Fly and Cryptophlebia spp. in Litchi. Hawaiian Entomological Society: 27-40.

McQuate, G. T., S. L. Peck, P. G. Barr, and C. D. Sylva. 2005. Comparative evaluation of spinosad and phloxine B as toxicants in protein baits for suppression of three fruit fly (Diptera: Tephritidae) species. Journal of economic entomology 98: 1170-1178.

Metcalf, R. L. 1979. Plants, chemicals, and insects: some aspects of coevolution. Bulletin of the Entomological Society of America 25: 30-35.

Metcalf, R. L. 1990. Chemical ecology of Dacinae fruit flies (Diptera: Tephritidae). Annals of the Entomological Society of America 83: 1017-1030.

Metcalf, R. L., and E. R. Metcalf. 1992. Plant kairomones in insect ecology and control, vol. 1, Springer Science & Business Media.

Mwatawala, M., M. Virgilio, S. Quilici, M. Dominic, and M. Meyer. 2013. Field evaluation of the relative attractiveness of enriched ginger root oil (EGO) lure and trimedlure for African Ceratitis species (Diptera: Tephritidae). Journal of Applied Entomology 137: 392-397.

Namiki, S., M. Takaguchi, Y. Seki, T. Kazawa, R. Fukushima, C. Iwatsuki, and R. Kanzaki. 2013. Concentric zones for pheromone components in the mushroom body calyx of the moth brain. Journal of Comparative Neurology 521: 1073-1092.

Nishida, R., T. E. Shelly, T. S. Whittier, and K. Y. Kaneshiro. 2000. α-Copaene, a potential rendezvous cue for the Mediterranean fruit fly, Ceratitis capitata? Journal of Chemical Ecology 26: 87-100.

Nishida, R., K. Tan, M. Serit, N. Lajis, A. Sukari, S. Takahashi, and H. Fukami. 1988. Accumulation of phenylpropanoids in the rectal glands of males of the Oriental fruit fly, Dacus dorsalis. Experientia 44: 534-536.

Norrbom, A., C. LE, T. FC, W. IM, and F. A. 1999. Fruit Fly Expert Identification System and Biosystematic Information Database. , pp. 65-251. In F. C. Thompson (ed.), Systematic database of names, vol. 9.

Ordax, M., J. E. Piquer-Salcedo, R. D. Santander, B. Sabater-Muñoz, E. G. Biosca, M. M. López, and E. Marco-Noales. 2015. Medfly Ceratitis capitata as Potential Vector for Fire Blight Pathogen Erwinia amylovora: Survival and Transmission. Plos One DOI: 10.1371/journal.pone.0127560.

Papadopoulos, N. T., B. I. Katsoyannos, N. A. Kouloussis, and J. Hendrichs. 2001. Effect of orange peel substances on mating competitiveness of male Ceratitis capitata. Entomologia experimentalis et applicata 99: 253-261.

Park, S.-K., S. Shanbhag, Q. Wang, G. Hasan, R. Steinbrecht, and C. Pikielny. 2000. Expression patterns of two putative odorant-binding proteins in the olfactory organs of Drosophila melanogaster have different implications for their functions. Cell and tissue research 300: 181-192.

Perez‐Staples, D., V. Prabhu, and P. W. Taylor. 2007. Post‐teneral protein feeding enhances sexual performance of Queensland fruit flies. Physiological Entomology 32: 225-232.

Perkins, M., M. Fletcher, W. Kitching, R. Drew, and C. Moore. 1990. Chemical studies of rectal gland secretions of some species ofBactrocera dorsalis complex of fruit flies (diptera: Tephritidae). Journal of chemical ecology 16: 2475-2487.

Piñero, J., M. Aluja, A. Vázquez, M. Equihua, and J. Varón. 2003. Human urine and chicken feces as fruit fly (Diptera: Tephritidae) attractants for resource-poor fruit growers. Journal of economic entomology 96: 334-340.

Prokopy, R., D. Papaj, J. Hendrichs, and T. Wong. 1992. Behavioral responses of Ceratitis capitata flies to bait spray droplets and natural food. Entomologia Experimentalis et Applicata 64: 247-257.

Prokopy, R. J., T. A. Green, and T. T. Wong. 1989. Learning to find fruit in Ceratitis capitata flies. Entomologia experimentalis et applicata 53: 65-72.

Quilici, S., A. Franck, P. Duyck, P. Rousse, F. Fabre, P. Ryckewaert, V. Rioux, I. Litrico, A. Chaboud, and C. Simiand. 2007. Development of Improved Attractants and Their Integration Into Fruit fly SIT Management Programs, pp. 73, Vienna (Austria).

Raghu, S. 2004. Functional significance of phytochemical lures to dacine fruit flies (Diptera : Tephritidae): an ecological and evolutionary synthesis. Bulletin of Entomological Research 94: 385-399.

Raghu, S., and A. R. Clarke. 2003. Spatial and temporal partitioning of behaviour by adult dacines: direct evidence for methyl eugenol as a mate rendezvous cue for Bactrocera cacuminata. Physiological entomology 28: 175-184.

Raghu, S., A. R. Clarke, and B. Yuval. 2002. Investigation of the physiological consequences of feeding on methyl eugenol by Bactrocera cacuminata (Diptera: Tephritidae). Environmental entomology 31: 941-946.

Renou, M., and A. Guerrero. 2000. Insect parapheromones in olfaction research and semiochemical-based pest control strategies. Annual review of entomology 45: 605-630.

Rice, M. 1989. The sensory physiology of pest fruit flies: conspectus and prospectus, pp. 249-272, Fruit Flies, Their Biology, Natural Enemies and Control, vol. 3.

Robacker, D., C. Lauzon, J. Patt, F. Margara, and P. Sacchetti. 2009. Attraction of Mexican fruit flies (Diptera: Tephritidae) to bacteria: effects of culturing medium on odour volatiles. Journal of Applied Entomology 133: 155-163.

Robacker, D. C. 1992. Effects of shape and size of colored traps on attractiveness to irradiated, laboratory-strain Mexican fruit flies (Diptera: Tephritidae). Florida Entomologist: 230-241.

Ross, K., and M. Anderson. 1991. Ultrastructure of the funicular sensilla of the cabbage root fly, Delia radicum L.(Diptera: Anthomyiidae). International Journal of Insect Morphology and Embryology 20: 83-101.

Rwomushana, I., S. Ekesi, I. Gordon, and C. K. Ogol. 2008. Host plants and host plant preference studies for Bactrocera invadens (Diptera: Tephritidae) in Kenya, a new invasive fruit fly species in Africa. Annals of the Entomological Society of America 101: 331-340.

Schutze, M. K., K. Mahmood, A. Pavasovic, W. Bo, J. Newman, A. R. Clarke, M. N. Krosch, and S. L. Cameron. 2014. One and the same: integrative taxonomic evidence that Bactrocera invadens (Diptera: Tephritidae) is the same species as the Oriental fruit fly Bactrocera dorsalis. Systematic Entomology.

Severin, H., and H. C. Severin. 1913. A historical account on the use of kerosene to trap the Mediterranean fruit fly (Ceratitis capitata Wied.). Journal of Economic Entomology 6: 347-351.

Shanbhag, S., B. Müller, and R. Steinbrecht. 2000. Atlas of olfactory organs of Drosophila melanogaster: 2. Internal organization and cellular architecture of olfactory sensilla. Arthropod structure & development 29: 211-229.

Shelly, T. 2010. Effects of methyl eugenol and raspberry ketone/cue lure on the sexual behavior of Bactrocera species (Diptera: Tephritidae). Applied Entomology and Zoology 45: 349-361.

Shelly, T. E. 2001. Lek size and female visitation in two species of tephritid fruit flies. Animal Behaviour 62: 33-40.

Shelly, T. E., and K. Y. Kaneshiro. 1991. Lek behavior of the oriental fruit fly, Dacus dorsalis, in Hawaii (Diptera: Tephritidae). J Insect Behav 4: 235-241.

Shelly, T. E., and E. M. Villalobos. 1995. Cue lure and the mating behavior of male melon flies (Diptera: Tephritidae). Florida Entomologist 78: 473.

Shelly, T. E., and R. Nishida. 2004. Larval and adult feeding on methyl eugenol and the mating success of male oriental fruit flies, Bactrocera dorsalis. Entomologia experimentalis et applicata 112: 155-158.

Siderhurst, M. S., and E. B. Jang. 2006. Female-biased attraction of Oriental fruit fly, bactrocera dorsalis (Hendel), to a blend of host fruit volatiles from Terminalia catappa L. Journal of chemical ecology 32: 2513-2524.

Silva, J. G., M. D. Meixner, B. A. Mcpheron, G. J. Steck, and W. S. Sheppard. 2003. Recent Mediterranean fruit fly (Diptera: Tephritidae) infestations in Florida—a genetic perspective. Journal of economic entomology 96: 1711-1718.

Sivinski, J. M., and C. Calkins. 1986. Pheromones and parapheromones in the control of tephritids. Florida Entomologist: 157-168.

Sookar, P., S. Permalloo, M. Alleck, and S. Seewooruthun. 2006. Development of improved attractants and their integration into fruit fly management programmes. Proceedings of the 7th International Symposium on Fruit Flies of Economic Importance.

Steiner, L. F. 1957. Low-Cost Plastic Fruit Fly Trap1. Journal of Economic Entomology 50: 508-509.

Tan, H. K., and R. Nishida. 1998. Ecological significance of male attractant in the defence and mating strategies of the fruit fly, Bactrocera papayae. Entomologia Experimentalis et Applicata 89: 155-158.

Tan, K.-H., and R. Nishida. 1996a. Sex pheromone and mating competition after methyl eugenol consumption in the Bactrocera dorsalis complex. Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, FL: 147-153.

Tan, K.-H., and R. Nishida. 1996b. Sex pheromone and mating competition after methyl eugenol consumption in the Bactrocera dorsalis complex, pp. 147-153, Fruit fly pests: a world assessment of their biology and management. . St. Lucie Press, Delray Beach, FL.

Tan, K. H., and R. Nishida. 2007. Zingerone in the floral synomone of Bulbophyllum baileyi (Orchidaceae) attracts Bactrocera fruit flies during pollination. Biochemical systematics and ecology 35: 334-341.

Tan, K. H., and R. Nishida. 2012. Methyl eugenol: its occurrence, distribution, and role in nature, especially in relation to insect behavior and pollination. Journal of insect science 12: 56.

Tan, K. H., I. Tokushima, H. Ono, and R. Nishida. 2011. Comparison of phenylpropanoid volatiles in male rectal pheromone gland after methyl eugenol consumption, and molecular phylogenetic relationship of four global pest fruit fly species: Bactrocera invadens, B. dorsalis, B. correcta and B. zonata. Chemoecology 21: 25-33.

Tan, K. H., R. Nishida, E. B. Jang, and T. Shelly. 2014. Pheromones, Male Lures, and Trapping of Tephritid Fruit Flies, pp. 15-74. In T. E. Shelly, N. Epsky, E. Jang, J. REyes-Flores and J. Vargas (eds.), Trapping and the Detection, Control, and Regulation of Tephritid Fruit Flies. Springer Science+Business Media Dordrecht USA.

Taylor, P. W., and B. Yuval. 1999. Postcopulatory sexual selection in Mediterranean fruit flies: advantages for large and protein-fed males. Animal Behaviour 58: 247-254.

Thomas, M., J. Heppner, R. Woodruff, H. Weems, G. Steck, and T. Fasulo. 2001. Featured Creatures: Mediterranean Fruit Fly. Florida Department of Agriculture and Consumer Services, Division of Plant Industry; and University of Florida.

Thomas, M. C., J. Heppner, R. Woodruff, H. Weems, G. Steck, and T. Fasulo. 2010. Mediterranean Fruit Fly, Ceratitis capitata (Wiedemann)(Insecta: Diptera: Tephritidae). University of florida.

Thompson, F. C. 1998. Fruit fly expert identification system and systematic information database: a resource for identification and information on fruit flies and maggots, with information on their classification, distribution and documentation, Backhuys Publ. for the North American Dipterists' Society.

Uchida, G. K., B. E. Mackey, R. I. Vargas, J. W. Beardsley, D. Hardy, M. L. Goff, and J. D. Stark. 2006. Response of nontarget insects to methyl eugenol, cue-lure, trimedlure, and protein bait bucket traps on Kauai island, Hawaii, USA. Hawaiian Entomological Society 38: 61-71.

Van Houdt, J., F. Breman, M. Virgilio, and M. De Meyer. 2010. Recovering full DNA barcodes from natural history collections of Tephritid fruitflies (Tephritidae, Diptera) using mini barcodes. Molecular ecology resources 10: 459-465.

Vargas, R., I,, T. Shelly, E, L. Leblanc, and J. C. Piñero. 2010. Recent Advances in Methyl Eugenol and Cue-Lure Technologies for Fruit Fly Detection, Monitoring, and Control in Hawaii. Vitamins & Hormones 83: 575-595.

Vargas, R. I., N. W. Miller, and R. J. Prokopy. 2002. Attraction and feeding responses of Mediterranean fruit fly and a natural enemy to protein baits laced with two novel toxins, phloxine B and spinosada. Entomologia Experimentalis et Applicata 102: 273-282.

Vargas, R. I., N. W. Miller, and J. D. Stark. 2003. Field trials of spinosad as a replacement for naled, DDVP, and malathion in methyl eugenol and cue-lure bucket traps to attract and kill male oriental fruit flies and melon flies (Diptera: Tephritidae) in Hawaii. Journal of economic entomology 96: 1780-1785.

Vargas, R. I., W. A. Walsh, E. B. Jang, J. W. Armstrong, and D. T. Kanehisa. 1996. Survival and development of immature stages of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. Annals of the Entomological Society of America 89: 64-69.

Vargas, R. I., S. K. Souder, B. Mackey, P. Cook, J. G. Morse, and J. D. Stark. 2012. Field trials of solid triple lure (trimedlure, methyl eugenol, raspberry ketone, and DDVP) dispensers for detection and male annihilation of Ceratitis capitata, Bactrocera dorsalis, and Bactrocera cucurbitae (Diptera: Tephritidae) in Hawaii. Journal of economic entomology 105: 1557-1565.

Vargas, R. I., J. C. Piñero, R. F. Mau, J. D. Stark, M. Hertlein, A. Mafra-Neto, R. Coler, and A. Getchell. 2009. Attraction and mortality of oriental fruit flies to SPLAT-MAT-methyl eugenol with spinosad†. Entomologia experimentalis et applicata 131: 286-293.

Vargas, R. I., S. K. Souder, K. Hoffman, J. Mercogliano, T. R. Smith, J. Hammond, B. J. Davis, M. Brodie, and J. E. Dripps. 2014. Attraction and Mortality of Bactrocera dorsalis (Diptera: Tephritidae) to STATIC Spinosad ME Weathered Under Operational Conditions in California and Florida: A Reduced-Risk Male Annihilation Treatment. Journal of economic entomology 107: 1362-1369.

Varikou, K., N. Garantonakis, and A. Birouraki. 2014. Comparative field studies of Bactrocera oleae baits in olive orchards in Crete. Crop Protection 65: 238-243.

Warthen, J., R. Cunningham, A. DeMilo, and S. Spencer. 1994. Trans-ceralure isomers: differences in attraction for Mediterranean fruit fly, Ceratitis capitata (Wied.)(Diptera: Tephritidae). Journal of chemical ecology 20: 569-578.

Wee, S.-L., and K.-H. Tan. 2007. Temporal accumulation of phenylpropanoids in male fruit flies, Bactrocera dorsalis and B. carambolae (Diptera: Tephritidae) following methyl eugenol consumption. Chemoecology 17: 81-85.

Wee, S.-L., A. K.-W. Hee, and K.-H. Tan. 2002. Comparative sensitivity to and consumption of methyl eugenol in three Bactrocera dorsalis (Diptera: Tephritidae) complex sibling species. Chemoecology 12: 193-197.

Weldon, C. W. 2007. Influence of male aggregation size on female visitation in Bactrocera tryoni (Froggatt)(Diptera: Tephritidae). Australian Journal of Entomology 46: 29-34.

White, I. M., and M. M. Elson-Harris. 1992. Fruit flies of economic significance: their identification and bionomics, CAB International, Wallingford, Oxon.

Wih-Kwasi. 2008. Assessment of Fruit Fly Damage and Implications for the Dissemination of Management Practices for Mango Production in the Upper West Region of Ghana. Journal of Developments in Sustainable Agriculture 3: 117-134.

Zhang, G.-N., H. Hull-Sanders, F. Hu, W. Dou, J.-Z. Niu, and J.-J. Wang. 2011. Morphological Characterization and Distribution of Sensilla on Maxillary

Palpi of Six Bactrocera Fruit Flies (Diptera: Tephritidae). Florida Entomologist: 379-388.