

Review

Plant Chemicals and the Sexual Behavior of Male Tephritid Fruit Flies

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Abstract

Plant compounds affect insects in many different ways. In addition to being a food source, plants also contain secondary metabolites that may have positive and negative impacts on insects. The influence of these compounds on sexual behavior, in particular, has been the focus of many recent studies. Here, we review the existing literature on the effects of plant compounds on the sexual behavior of tephritid fruit fly males. We put special focus on polyphagous species whose males congregate in leks, where females exert strong mate selection. We first summarize the main findings related to plant compounds that increase male signaling behavior and attraction of females and consequently increase mating frequency, a phenomenon that has been recorded mainly for species of *Anastrepha* and *Ceratitis*. In other tephritid species, males are attracted to phenylpropanoids produced by plants (such as methyl eugenol or raspberry ketone) that, upon encounter, are consumed and sequestered by males. These compounds, or metabolic derivatives, which normally have negligible nutritional value, are included in the pheromone and also confer advantages in a sexual context: enhanced female attraction and improved male mating success. These phenomena have been reported for several *Bactrocera* species as well as for *Zeugodacus cucurbitae*. Because many tephritid species are serious pests, the effect of plant compounds on male behavior has been explored for potential incorporation into control strategies such as the sterile insect technique (SIT). We conclude noting several factors, such as age and nutrition during larval and adult stage, that modulate the effect of plant compounds on male mating behavior as well as some prominent gaps that preclude a thorough understanding of the plant-mediated enhancement of male sexual performance and hence limit our ability to effectively utilize phytochemicals in pest control strategies.

Key words: Tephritidae, sexual behavior, phytochemical, male mating enhancement, sex pheromone

Most insects rely on plants to develop during immature stages, survive, and reproduce. Insect–plant interactions are often mediated by plant compounds (phytochemicals) that may affect insects in positive or negative ways (Reddy and Guerrero 2004). Phytochemicals impact insects by two primary modes. They serve as food and directly influence the nutritional status of insects. These so-called primary metabolites include a wide range of lipids, proteins, and carbohydrates (Hounsome et al. 2008). In addition, plants produce a second type of compounds, called secondary metabolites, that primarily benefit the plant, such as anti-herbivore compounds (e.g., insect growth regulators, repellents, or chemicals that recruit natural enemies of herbivores; Nishida 2014). Other compounds benefit

both plants and insects. This is the case for floral compounds that attract pollinators, which in exchange receive a nutritional benefit (Nishida 2014). Secondary metabolites can also favor exclusively, or at least primarily, the insect. For example, phytochemicals may induce oviposition or feeding (both at larval and adult stages) or be sequestered by the insect as chemical defense against predators and parasitoids (e.g., alkaloids) (Nishida 2014).

Secondary plant compounds may also affect the sexual behavior and sexual communication of insects in various ways. First, many plants act as ‘rendezvous’ sites for mating, and plant volatiles often play a key role in attracting insects to these sites (Xu and Turlings 2018). For phytophagous insects in which the sexes meet and mate

principally or exclusively on host plants, host cues have a major influence on mate searching, especially for monophagous species (Landolt and Phillips 1997). Conversely, for polyphagous species with a wide range of potential hosts, the reliability of host cues as indicators of mate presence is low, and pheromones are often used to increase the likelihood of encountering potential mates (Frérot et al. 2017). For these species, phytochemicals may also influence the reproductive physiology and sexual behavior of insects by making one or the two sexes more attractive to the opposite sex (reviewed by Landolt and Phillips 1997, Reddy and Guerrero 2004, Nishida 2014, and Moreau et al. 2017). In some insects, e.g., plant compounds stimulate signaling behavior and may increase the attractiveness of the pheromone to the receiving sex (Jaffe et al. 1993, Landolt et al. 1994). Additionally, plant chemicals are sometimes sequestered by the insect and later incorporated in the sex pheromone (Baker et al. 1981, Krasnoff and Dussourd 1989, Nishida et al. 1996).

Here, we review the existing literature on the effects of plant compounds on the sexual behavior of male fruit flies (Diptera: Tephritidae), with special focus on polyphagous species where male sex pheromone is a key component of the mating system. We put emphasis on the effects of phytochemicals on male signaling behavior, ability to attract females, courtship behavior, and mating success. Although data are limited, we also discuss the physiological mechanisms underlying these sexual behaviors. Because many tephritid species are important fruit pests, we also describe how findings of academic studies have been used in an applied context to improve pest control methods. We conclude the review with two sections dealing, respectively, with other factors that also modulate the sexual behavior of males and might, therefore, interact with the effect of phytochemicals and a non-exhaustive list of information gaps in our understanding of the role of plant compounds on the sexual behavior of tephritid males. The present review builds on several previous studies (Raghu 2004; Papadopoulos et al. 2008; Shelly 2008, 2010; Tan et al. 2014) that have, by and large, focused more sharply on particular tephritid taxa.

Mating Systems of Tephritid Fruit Flies

The Tephritidae comprises approximately 4,600 species (Christenson and Foote 1960, White and Elson-Harris 1992). Larvae of these species feed on diverse plant structures, such as stalks, leaves, buds, and fruit. Among those that feed on fruit, several species have gained the status of pest as they impact commercial fruit species (Norrbom 2004, Liquido et al. 2013). The most economic important genera are *Anastrepha* (native to America), *Bactrocera* (native to Asia and Oceania), *Ceratitidis* (native to Africa) and *Rhagoletis* (native to Eurasia and America) (Fletcher 1987, Aluja 1994, Drew 2004). Other genera, such as *Dacus*, *Zeugodacus*, and *Toxotrypana*, include fruit pests as well, although the number of known species considered pests is lower. Fruit flies are distributed worldwide and have the capacity to establish in temperate and tropical regions (Bateman 1972). Fruit trade contributes to the movement of the pest and establishment of invasive species in new areas. This has been a great challenge for fruit production for more than 150 yr. Given the wide range of hosts and the great economic impact as a result of fruit production losses and trade restrictions, great effort is spent to suppress wild populations.

Mating systems in the Tephritidae vary widely from cases in which copulation is preceded by very brief or almost no courtship to cases where males or females display a complex repertoire of chemical, visual, and acoustical signals (for dedicated reviews see specific chapters in Robinson and Hooper 1989, Aluja and Norrbom 2001, and references therein). Despite this large variation, the mating systems of

many economically important tephritid fruit flies share a common trait, namely the formation of leks (Aluja et al. 2001, Diaz-Fleischer and Aluja 2001, Eberhard 2001). Leks are aggregations of males formed solely for the purpose of mating (Hoglund and Alatalo 1995). Males do not defend resources critical to females and provide only gametes. Females encounter several potential partners at the lek and are free (i.e., not coerced) to select their mate. This results in a marked choosiness in females (Arita and Kaneshiro 1985, 1989). Most lekking tephritids are polyphagous, and, as such, female location is relatively unpredictable (i.e., their location cannot be associated to cues emanating from one [or a few] host species), and males rely on pheromones to attract (i.e., encounter) females. Correspondingly, leks occur on both fruiting and non-fruiting host trees as well as non-host trees. Males occur in the tree canopy and release pheromone while perching on leaf undersides. The sex pheromone, which is released only by sexually mature males, is produced in different structures, such as the salivary glands, the pleural epidermal glands, the rectal glands, and the rectal pouch, depending on the species (Nation 1990).

Mate selection at the lek occurs as follows. Once a female approaches a male, the male performs a series of species-specific, stereotyped, courtship behaviors that typically involve bursts of rapid wing-fanning, which is performed simultaneously with pheromone release, presumably to enhance the dispersion of the pheromone (Kuba and Sokei 1988, White 2001). In the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann) (Diptera: Tephritidae), the courtship is rather complex as it involves head rocking, two distinct types of wing movements and their associated sounds, and positioning by the male and female at particular orientation angles and distances (Feron 1962; Briceño and Eberhard 2000, 2002). In other species, particularly certain *Bactrocera*, courtship is much simpler, and males mount females almost immediately upon their arrival to the male calling site (Shelly and Kaneshiro 1991). In many *Anastrepha* the courtship complexity is intermediate (Gomez Cendra et al. 2011) and also involves wing movements and acoustic signals.

Plant Compounds Affecting Fruit Fly Male Sexual Behavior

Initial work on plant–fruit fly interactions focused on the attraction of fruit flies to certain plants, plant structures, or essential oils (Howlett 1912, Ripley and Hepburn 1935, Steiner et al. 1957, Katsoyannos et al. 1997). The observation that some of these odor sources attracted significantly more males than females pointed to a biological role related to reproduction. The sex-specific nature of the attraction argued against the idea that such odors were associated with food sources, since females, which need to mature eggs, presumably have nutritional needs equal to or greater than males (Shelly 2010). Although plant-derived attractants (or their synthetic analogs) have been used in control efforts for well over 50 yr, data linking plant compounds and male mating behavior have only been collected in the past 25 yr.

Our review of this literature follows taxonomic lines and includes five sections. The first two sections concern the genera *Ceratitidis* and *Anastrepha*, respectively. Species in the large Asian genus *Bactrocera* are discussed in the following two sections based on their lure affiliation. As originally proposed by Drew (1974) and Drew and Hooper (1981), males of *Bactrocera* species may be classified as being 1) responsive to methyl eugenol (ME), 2) responsive to raspberry ketone (RK) (or its synthetic analog cue-lure [CL]), or 3) not responsive to either of these compounds. Accordingly, in discussing *Bactrocera* we consider ME- and RK-responders separately (i.e., in sections ‘*Bactrocera* and ME’ and ‘*Bactrocera* and *Zeugodacus* and

CL/RK', respectively). Males of *Zeugodacus cucurbitae* (Coquillett), from another daceine genera, are also attracted to RK, and this species is included in section 'Bactrocera and *Zeugodacus* and CL/RK'. In the final section, we review data on two other phytochemicals, α -pinene and zingerone (ZG), whose effects on male sexual behavior have received far less study. The information presented in this section has been summarized, species by species, in Table 1 and is presented conceptually in Fig. 1.

Ceratitis

C. capitata— α -Copaene, Ginger Root Oil, and Other Non-Fruit-Derived Essential Oils

Angelica seed oil (*Angelica archangelica* L.) (Apiales: Apiaceae) (ASO) is among the first botanical products known to attract *C. capitata* males (Ripley and Hepburn 1935, Steiner et al. 1957). Additional work by Fornasiero et al. (1969) and Guiotto et al. (1972) further demonstrated that attraction in laboratory bioassays was associated with two compounds, α -copaene and (to a lesser extent) α -ylangene. The former phytochemical is widely distributed among plants, including many hosts of *C. capitata*, such as sweet orange (*Citrus sinensis* L.) Osbeck) (Sapindales: Rutaceae), guava (*Psidium guajava* L.) (Myrtales: Myrtaceae), papaya (*Carica papaya* L.) (Brassicales: Caricaceae), and mango (*Mangifera indica* L.) (Sapindales: Anacardiaceae), and is present in different plant structures, such as fruit, leaves, and other above-ground tissues (Macleod and Gonzalez de Troconis 1982, Buttery et al. 1985, Elzen et al. 1985, Papageorgiou et al. 1985, Teranishi et al. 1987, Macleod et al. 1988, Warthen and McInnis 1989, Koulibaly et al. 1992). Flath et al. (1994a) later demonstrated that 98.6% of the α -copaene in ASO was (+)- α -copaene. Under field conditions, Flath et al. (1994a, 1994b) showed that the (+) enantiomer was more attractive than (-)- α -copaene and structurally related sesquiterpenes, such as α -ylangene and β -copaene. Even though α -copaene is common in nature, it is the (-) enantiomer, which usually predominates in plants (Takeoka et al. 1990), and in those cases where the (+) is the major enantiomer, the total content of α -copaene is low (Flath et al. 1994a).

While male attraction was well documented, the potential effect of α -copaene on male sexual behavior was not investigated until recently. Nishida et al. (2000) showed that *C. capitata* males displayed pheromone calling more frequently on artificial leaves coated with α -copaene than on control, non-treated leaves. Furthermore, when males and females were released in laboratory cages containing leaves treated or not with α -copaene, mating occurred only on treated leaves (Nishida et al. 2000). Based on these results, it was hypothesized that α -copaene acted as a cue of rendezvous sites, where males might congregate to attract females. While perhaps acting as a rendezvous cue, the odor of α -copaene (as well as ASO) was also found to increase the mating ability of *C. capitata* males over control males deprived of aromatic exposure (Shelly 2001a). Under field cage conditions, males that were exposed either to α -copaene or ASO obtained approximately two-thirds of all matings when competing with control (non-exposed males). This finding obviously suggested a more direct role of these chemicals in the mating behavior of male medflies.

Because α -copaene is hard to synthesize and not easily obtained, and ASO is likewise not available in large amounts, Shelly (2001a) evaluated an alternative essential oil, ginger root oil (GRO) that was known to contain α -copaene. In field cage trials, GRO-exposed males achieved 76% of all matings (and control males 24%), which suggested that GRO was as efficient as α -copaene or ASO in boosting mating success. When exposed to GRO, males remain quiescent near the oil and only infrequently contact the source (Nishida et al. 2000, Shelly 2001a, Papadopoulos et al. 2006). Interestingly, male

exposure to the odor of GRO alone (i.e., without physical contact or ingestion) likewise boosted male signaling level and mating success (Shelly 2001a). Males showed an increased mating success even after 8–10 d of exposure to GRO (Shelly 2001a). The effect of GRO on male behavior was found to be independent of the sexual maturation status of males. Male exposure to GRO on day 1 after emergence (sexually immature) yielded the same results as exposure on days 3, 5 or 9–12 post-emergence (sexually mature), i.e., in all cases GRO-exposed males obtained a significantly larger number of matings than non-exposed males (Shelly 2001a, Shelly and McInnis 2001). Correspondingly, tests carried out in field cages showed that 1-d-old males and 9- to 13-d-old males were equally attracted to traps baited with GRO (Shelly and Pahio 2002). Exposure at pupal stage, however, did not affect male mating success (Shelly 2001a). Other studies, conducted in Hawaii (United States) as well as in Central and South America, subsequently confirmed the mating enhancement effect of GRO on *C. capitata* males (McInnis et al. 2002, Shelly et al. 2002, Barry et al. 2003, Briceño et al. 2007, Shelly et al. 2007f, Juan-Blasco et al. 2013, Paranhos et al. 2013).

Enhanced mating success appears to result from enhanced sexual signaling. Males exposed to GRO spent 20–25% more time pheromone calling than non-exposed males (Shelly 2001a, Papadopoulos et al. 2006). In a study conducted in large field cages that housed >15 guava trees, Shelly (2001a) evaluated the attraction of sexually mature females to groups of five GRO-exposed or non-exposed males that were confined in transparent, plastic cups and then hung in the guava trees. Cups containing GRO-exposed males attracted approximately 30% more females than cups containing non-exposed males. Interestingly, when the number of female arrivals was expressed on a per signaling male basis, the rate of female visits was similar between aggregations of GRO-exposed and non-exposed males. This led the authors to suggest that exposure to GRO did not affect either the amount of pheromone released per male or its quality and that the differences in attraction were related to the higher collective calling effort of exposed males (Papadopoulos et al. 2006). Nonetheless, there are no studies in which the composition or amount of the male sex pheromone emitted were compared between GRO-exposed and non-exposed males.

While GRO-mediated mating enhancement has now been widely documented, possible mechanisms responsible for this phenomenon, other than heightened pheromone calling, are largely unknown. Male courtship behavior is relatively elaborate in *C. capitata* and includes three distinct behavioral components all performed while the male faces the female: continuous wing vibration (or fanning), wing buzzing (rapid and rhythmic back and forward movement of the wings), and fast rotations (or oscillations) of the head (Feron 1962). Briceño et al. (2007) investigated whether GRO affected the expression of these behaviors by videotaping male–female pairs involving a GRO-exposed male or a non-exposed male. Analysis of these recordings showed that, not only did the two types of males perform the same courtship behaviors, but also that the duration of each was similar between GRO-exposed and non-exposed males (Briceño et al. 2007). Focusing on close-range signals as well, (Shelly et al. 2007d) examined the potential role of cuticular compounds in GRO-enhanced copulatory success. In an experiment undertaken to eliminate possible behavioral differences, female medflies were presented with dead males (killed by freezing) that had or had not been exposed to GRO just prior to being killed. Females showed greater attraction to the GRO-exposed males, indicating that, in addition to boosting signaling rate, chemical exposure changed the aroma of the exoskeleton, similar to a perfume, which elicited higher acceptance by females (Shelly et al. 2007d). These authors also showed

Table 1. Continued

Species	Source or compound	Delivery method	Sexually related parameter	Effect	Persistence	Reference
	Orange fruit	Contact precluded	Male mating success	No effect ^{1,2}		¹ Papadopoulos et al. 2001 ² Shelly et al. 2004
		Contact allowed	Male mating success	Increase ^{1,3}	10 DPE ²	¹ Kouloussis et al. 2013 ² Papadopoulos et al. 2001 ³ Shelly et al. 2004
	Grapefruit fruit	Contact precluded	Male mating success	Increase ²		¹ Kouloussis et al. 2013 ² Shelly 2009
		Contact allowed	Male mating success	No effect ¹ Increase ²	At least 3 DPE ²	
	Mandarin fruit	Contact allowed	Male mating success	Increase		Kouloussis et al. 2013
	Lemon fruit	Contact allowed	Male mating success	Increase		Kouloussis et al. 2013
	Bitter orange fruit	Contact allowed	Male mating success	No effect		Kouloussis et al. 2013
	Guava tree	Contact precluded	Mating success	No effect		Shelly and Villalobos 2004
		Contact allowed	Male signaling	Increase		
			Female attraction	Increase		
	Guava leaves	Contact allowed	Male mating success	Increase	At least 3 DPE	Shelly and Villalobos 2004
	Guava fruit	Contact allowed	Male mating success	No effect		Shelly and Villalobos 2004
	Ginger root oil	Contact precluded	Male mating success	Increase	At least 3 DPE	Quilici et al. 2013
		Contact allowed	Male mating success	Increase		
	Orange oil	Contact precluded	Male mating success	No effect		Quilici et al. 2013
		Contact allowed	Male mating success	Increase		
	Guava fruit	Contact precluded	Male signaling	Increase (P, WF, GE) ¹		¹ Bachmann et al. 2015 ² Bachmann et al. submitted ³ Vera et al. (2013)
			Male mating success	Increase ¹⁻³		
			Female fecundity (F) or fertility (f)	Increase (F) ² No effect (f) ²		
	Lemon fruit	Contact allowed	Male mating success	Increase		Vera et al. 2013
		Contact precluded	Male mating success	Increase		Vera et al. 2013
		Contact allowed	Male mating success	Increase		Vera et al. 2013
	Selected guava aroma compounds	Contact precluded	Male mating success	Increase		Bachmann et al. 2015
	Grapefruit oil	Contact precluded	Male mating success	Increase		Morató et al. 2015
	Ginger root oil	Contact precluded	Male mating success	Increase		Flores et al. 2011
	Methyl eugenol	Feed on source	Male signaling	Increase (P) ^{1,3} Increase (WF) ^{6,9}	At least 35 DPF ⁹	¹ Hee and Tan 2006 ² Ji et al. 2013 ³ Nishida et al. 1988
			Female attraction	Increase ^{6,9,12}	At least 35 DPF ⁹	⁴ Orankanok et al. 2013 ⁵ Shelly 2000a ⁶ Shelly 2001b
			Male mating success	Increase ^{2,4,7-12}	At least 35 DPF ^{4,9,10}	⁷ Shelly and Nishida 2004 ⁸ Shelly et al. 2008 ⁹ Shelly and Dewire 1994 ¹⁰ Shelly 1995

Table 1. Continued

Species	Source or compound	Delivery method	Sexually related parameter	Effect	Persistence	Reference
			Female fecundity (F) or fertility (f)	No effect (F/f) ⁵		¹¹ Shelly et al. 2007b
	<i>Terminalia catappa</i> fruits	Feed on source	Male mating success	Increase		¹² Tan and Nishida 1996
	<i>Cassia fistula</i> flowers	Feed on source	Male signaling	No effect (WF)		Shelly and Edu 2007
			Female attraction	Increase		Shelly 2000a
			Male mating success	Increase	At least 21 DPF	
	<i>Fragaria berteriana</i> flowers	Feed on source	Male signaling	Increase (P) ¹		¹ Nishida et al. 1997
			Female attraction	Increase (WF) ²		² Shelly 2001b
			Male attraction	Increase ²		
	<i>Carrica papaya</i> flowers	Feed on source	Male mating success	Increase ¹		Shelly 2001c
			Male signaling	Increase (WF)		
			Female attraction	Increase		
			Male mating success	Increase	At least 7 DPF	
<i>Bactrocera papayae</i>	Methyl eugenol	Feed on source	Male mating success	Increase (P) ²		¹ Hee and Tan 1998
			Male signaling	Increase ¹		² Hee and Tan 2004
			Female attraction	Increase ¹		³ Tan and Nishida 1996
			Male attraction	Increase ^{3,4}		⁴ Tan and Nishida 1998
			Male mating success	Increase		Raghu and Clarke 2003
<i>Bactrocera cacuminata</i>	Methyl eugenol	Feed on source	Male mating success	Increase (small lab cages)	At least 32 DPF (but not before 16 DPF)	
<i>Bactrocera carambolae</i>	Methyl eugenol	Feed on source	Male signaling	No effect (large field cages)		¹ Haq et al. 2015
			Female attraction	Increase (P) ^{2,3}		² Tan and Nishida 1996
			Male mating success	Increase ³		³ Wee et al. 2007
			Male mating success	Increase ^{1,3}	At least 3 DPF (but not before 2 DPF) ^{1,3}	
		Contact precluded	Male mating success	Increase ^{1,2}	At least 3 DPE ²	¹ Haq et al. 2014
<i>Bactrocera correcta</i>	Methyl eugenol	Feed on source	Male signaling	Increase (P) ²		² Haq et al. 2015
			Male mating success	Increase ¹		¹ Orankanok et al. 2013
			Male signaling	Increase (WF) ²	At least 16–18 DPF ¹	² Tokushima et al. 2010
<i>Bactrocera philippinensis</i>	Methyl eugenol	Feed on source	Female attraction	Increase ²		¹ Obra and Resiva 2013
			Male mating success	Increase ^{1,2}	At least 5 DPF (but not before 3 DPF) ²	² Shelly et al. 1996
<i>Bactrocera umbrosa</i>	Methyl eugenol	Feed on source	Female attraction	Increase		Wee et al. 2018
			Male mating success	Increase		
<i>Bactrocera tryoni</i>	Raspberry ketone	Feed on source	Male signaling	Increase (ARG) ³		¹ Akter and Taylor 2018
			Male mating success	Increase ²		² Akter et al. 2017
			Female remating propensity	No effect ¹		³ Tan and Nishida 1995
	Cue lure	Feed on source	Male signaling	Increase (P) ²		¹ Kumaran et al. 2013
			Female attraction	Increase ^{2,3}		² Kumaran et al. 2014a
			Male mating success	Increase ^{1,3}	At least 3 DPF ¹	³ Kumaran et al. 2014b
			Female remating propensity	Decrease ¹		

Table 1. Continued

Species	Source or compound	Delivery method	Sexually related parameter	Effect	Persistence	Reference
	Zingerone	Feed on source	Female fecundity (F) or fertility (f) Male signaling Female attraction Male mating success Female remating propensity	Increase (F and f) ¹ Increase (P) ² No effect ² Increase ¹ No effect ¹	At least 1 DPF ¹	¹ Kumaran et al. 2013 ² Kumaran et al. 2014
<i>Zeugodacus cucurbitae</i>	Raspberry ketone Cue lure	Feed on source Feed on source	Female fecundity (F) or fertility (f) Male mating success Male signaling Female attraction Male mating success	Increase (F) ¹ No effect (f) ¹ Increase Increase (WF) ² Increase ^{1,2} Increase ^{2,3}	At least 1 DPF	Shelly 2000b ¹ Khoo and Tan 2000 ² Shelly and Villalobos 1995 ³ Shelly and Nishimoto 2016
	Zingerone	Feed on source	Female fecundity (F) or fertility (f) Female attraction Male mating success	No effect (F) ³ Decrease (f) ³ Increase ¹ No effect ²		¹ Khoo and Tan 2000 ² Shelly 2017a ³ Gerofotis et al. 2013
<i>Bactrocera oleae</i>	α -pinene	Contact precluded	Male mating success	Increase		

Delivery method: males were allowed to contact the source (contact allowed), and in some cases they feed on it (feed from source) or they impeded to contact the source by a physical barrier (contact precluded). Signaling was measured through different parameters: P: released pheromone; WF: wing fanning; GE: salivary glands exposure; ARG: accumulation of compounds or its derivatives in the rectal gland. DPF: days post-feedings; DPE: days post-exposure

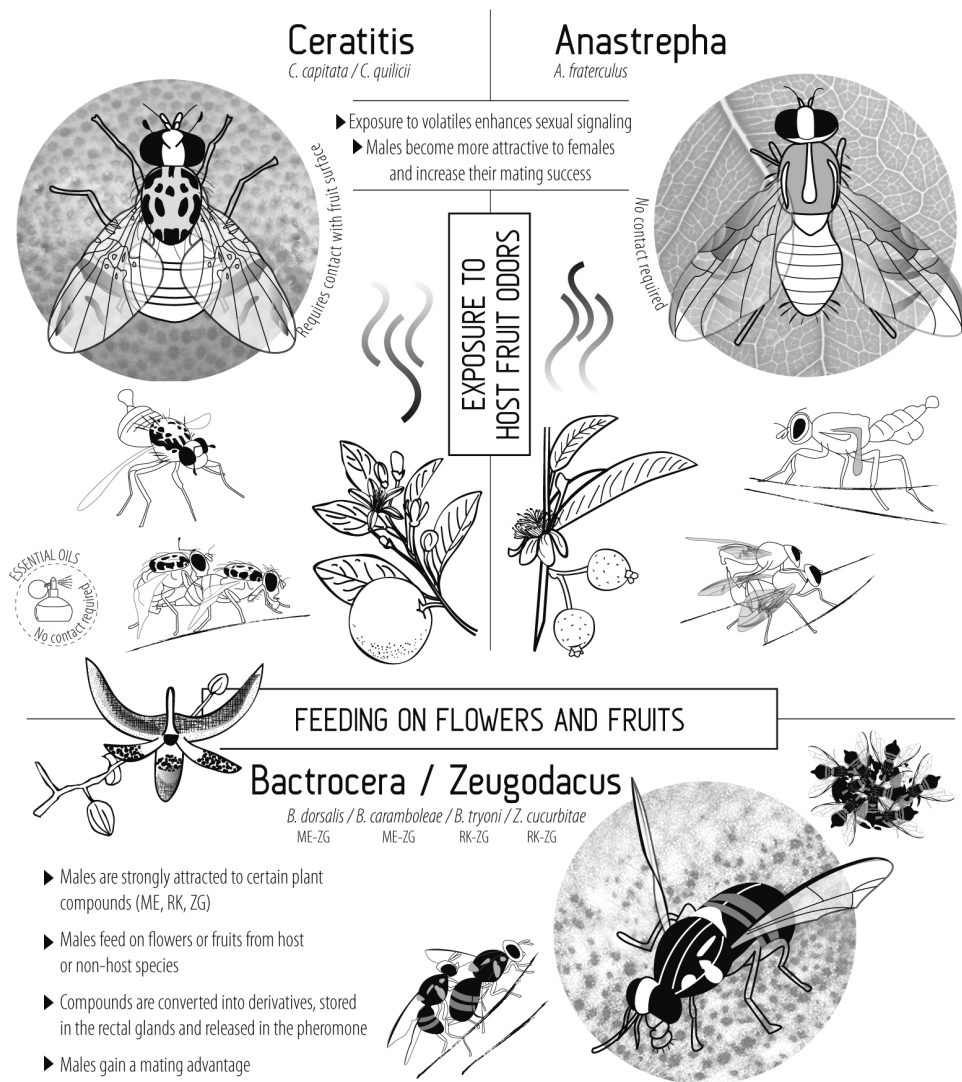


Fig. 1. Effect of plant compounds on the sexual behavior of male fruit flies after volatile exposure, fruit contact, or phytochemical ingestion. Details for each fruit fly species and plant compound are presented in section 'Plant Compounds Affecting Fruit Fly Male Sexual Behavior'.

that males whose antennae were excised before exposure nonetheless displayed mating enhancement, which suggests that GRO acts through an external phenomenon (rather than internal processing, like pheromone synthesis), consistent with the proposed alteration of the cuticular scent (Shelly et al. 2007d). Although strong evidence was provided to support the perfume effect, no chemical analysis of the cuticle was carried out to confirm this hypothesis. Interestingly, in diethyl ether extracts of wild males caught using traps in orchards of host and non-host trees, Mavraganis et al. (2008) found detectable (well above trace values) levels of α -copaene in the cuticle of wild *C. capitata* males, which could be considered as evidence supporting the perfume effect.

There are, however, two additional aspects that might explain these results without the need to invoke the perfume effect. First, Mavraganis et al. (2008) found that the cuticle of male medflies contained several compounds that were previously described as part of the male sex pheromone (Jang et al. 1989), such as linalool, indole, dihydro-3-methyl-2(3H)-furanone, and (E,E)- α -farnesene, among others. A similar result was also reported for another tephritid species, *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae) (Bachmann, 2016). As noted above, *C. capitata* males exposed to

GRO perform pheromone calling more frequently than non-exposed males. If pheromonal compounds are retained by their cuticle, exposed dead males could still attract more females than dead non-exposed males without needing to invoke a GRO-mediated perfume effect. Furthermore, Gonçalves (2005) and Gonçalves et al. (2006) found α -copaene in the pheromone of wild *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) and *C. capitata* males that were not exposed to oils or fruits, which, in turn, could also be retained in the cuticle. Second, Hughes (1974) and Byers (1982) found that host plant-derived compounds can be internalized through the cuticle and affect the physiology of beetles. So, even though male medflies whose antennae were excised gained a mating boost via GRO treatment, this effect still could have been attained through an internal, physiological phenomenon. Additionally, the fact that GRO exposure results in a significant increase in signaling activity, strongly suggests that GRO does not act exclusively through an external mechanism.

Work on GRO and ASO prompted further research on the effect of other oils on the sexual behavior of *C. capitata* males. For example, Shelly et al. (2008a) tested manuka oil (*Leptospermum scoparium* J.R. Forst. & G. Forst.) (Myrtales: Myrtaceae), which contains about 10 times the amount of α -copaene as GRO. Under

field cage conditions, traps containing manuka oil attracted almost three times the number of males collected by traps that contained only water (control). Concurrently, in mating tests conducted in field cages, males exposed to manuka oil obtained significantly more matings than control males (Shelly et al. 2008a). Furthermore, male mating success was increased to levels similar to those induced by GRO. As with GRO and orange oil (OO) (*C. capitata* - Host Fruits and Derived Essential Oils) (see *C. capitata*—Host Fruits and Derived Essential Oils), there was no need for males to contact the oil to gain a mating advantage. The finding that male mating enhancement was similar after exposure to manuka oil and GRO, despite the large difference in α -copaene concentration between these oils, indicates an ‘all or nothing’ effect. In a recent study, Jofré-Barud et al. (2014) evaluated the effect of exposure to the aroma of two essential oils extracted from plant species native to South America, which were known to synthesize a large variety of monoterpenes and sesquiterpenes, on the attraction and mating success of *C. capitata* males. The essential oil of *Baccharis spartoides* (Cav.) Cabrera (Asterales: Asteraceae) did not attract male medflies in Y-tube olfactometer trials, and although exposure to the oil’s aroma significantly increased male mating success, this effect was weak (approximately 56% of the matings involved oil-exposed males). On the other hand, the essential oil of *Schinus polygama* (Hook. & Arn. ex DC.) (Sapindales: Anacardiaceae) was efficient in attracting males and induced a larger increase in male mating success (i.e., exposed males obtained 63% of all matings). The chemical composition of the tested oils differed greatly, but it is noteworthy that α -copaene was detected only in *S. polygama* (Jofré-Barud et al. 2014).

The selection of manuka oil and ASO for testing was based on the presence of α -copaene in these substances. However, Shelly and Epsky (2015) recently found that exposure to tea tree oil (*Melaleuca alternifolia*) (Maiden & Betche) Cheel (Myrtales: Myrtaceae) (TTO), which was reported to lack α -copaene (Swords and Hunter 1978, Butcher et al. 1994, Keszei et al. 2010), generated results similar to those obtained with other oils, namely 1) exposed males increased their mating success (56–59% of total matings under field cage conditions where exposed and non-exposed males competed for females); 2) no contact was needed for the enhancement to occur; and 3) exposed males performed pheromone calling more frequently than non-exposed males. These results led Shelly and Epsky (2015) to propose that compounds other than α -copaene may also enhance male sexual signaling and mating success. In fact, the effect of TTO was similar to that recorded by Jofré-Barud et al. (2014) using oils that did not contain α -copaene. Moreover, TTO-mediated increase in male mating success was not detected when mating trials were carried out 5 d after exposure, whereas GRO-mediated effects lasted up to 8–10 d after exposure (Shelly 2001a). However, a recent study (Niogret et al. 2017) calls this proposal into question as it reported detectable amounts of α -copaene in TTO. What is more, α -copaene concentrations in TTO were very similar to those found in GRO, which strongly suggests a role for this compound in producing the TTO-mediated boost in male mating success.

C. capitata—Host Fruits and Derived Essential Oils

Initial work on the interaction between fruit aroma and *C. capitata* suggested that males, like females, detected fruit volatiles with their antennae (Light et al. 1988) and were attracted by these odors (Prokopy and Vargas 1996). In both studies, the authors proposed that host odors might act as olfactory cues of suitable lekking or mating sites. However, Hendrichs and Hendrichs (1990) found that mating in *C. capitata* frequently occurs in the vicinity of host plants, and not on the host plant itself, so the attraction of males to host fruit

odors may not be related to locating leks. Subsequently, Katsoyannos et al. (1997) observed that *C. capitata* males, but not females, were strongly attracted to *Citrus* fruit that were wounded in the flavedo region. Males remained motionless on the fruit surface and contacted the fruit with their proboscis. This led to the suggestion that attraction to fruits represented more than a response to possible locations for encountering females and that males ingested substances that were later used as precursors in the synthesis of the sex pheromone. These seminal studies triggered a series of papers that focused on the effects of host fruit, host leaves, and essential oils on the sexual behavior of Mediterranean fruit fly males. Such studies have been particularly centered, but not restricted to, *Citrus* species. The fact that sweet orange essential oils contain α -copaene (Teranishi et al. 1987) fostered the idea that this compound might be responsible for attraction, followed by arrestment, to orange peel. Papadopoulos et al. (2001) presented the first evidence on the positive effect of host fruit-derived compounds on the mating success of *C. capitata* males. In a series of laboratory trials, these authors first confirmed that males were attracted by sweet oranges that were superficially wounded in the flavedo region and about 50% of the males that were attracted were seen lowering their head and touching the peel with their mouthparts, apparently ingesting exudates from the fruit (Papadopoulos et al. 2001). Exposure to wounded fruit resulted in increased mating success, which, depending on the experimental arena, allowed exposed males to obtain 65–74% of all matings. Contact with fruit surface was needed in order for male enhancement to occur (Papadopoulos et al. 2001). Exposure to wounded oranges for 24 h on adult day 1, 5, and 9 enhanced male mating success, which indicates that, as with GRO, the orange peel effect is not affected by the sexual maturation status of the male (Papadopoulos et al. 2001). As with GRO, the effect of increased mating success lasted at least 10 d after exposure to wounded oranges.

Subsequent research demonstrated that exposure to orange leaves and fruits of other citrus species, namely grapefruit (*Citrus paradisi* Macfad.) (Shelly 2009) and oranges, mandarin (*Citrus reticulata* Blanco), and lemon (*Citrus limon* (L.) Burm. F.) (Sapindales: Rutaceae) (Kouloussis et al. 2013) also increased the mating performance of male medflies, which obtained 70–75% of matings when exposed and non-exposed competed for non-exposed females. In all cases, males needed to contact the fruit to gain a mating boost, with the exception of grapefruit (Shelly 2009), which represents the only known case where volatile compounds released by a plant structure increased the mating ability of *C. capitata* males. There are currently no data available regarding the effect of exposure to citrus fruit on the rate of sexual signaling or the sex pheromone quality and quantity.

The results obtained with citrus fruits prompted the study of citrus essential oils. Shelly et al. (2004) compared the mating success of *C. capitata* males exposed to OO and control males, under field cage conditions and found that treated males accounted for 70% of all matings, showing that OO was also able to enhance male mating success. As reported for orange fruit, the mating enhancement effect of OO was recorded even after 5 d from the exposure (Shelly et al. 2004). In this case, contact with the odor source was not needed, and males exposed only to the aroma of OO gained a mating advantage, similar to the phenomena mediated by GRO (Shelly 2001a). The effect of OO on male mating success was later confirmed by Papadopoulos et al. (2006) and Kouloussis et al. (2013) and also extended to other citrus essential oils, such as those extracted from grapefruit (Shelly 2009, Kouloussis et al. 2013), mandarin, lemon, and bitter orange (*Citrus aurantium* L.) (Sapindales: Rutaceae) (Kouloussis et al. 2013). In most cases, mating enhancement was independent of the contact with the oil (Shelly et al. 2004, Papadopoulos et al. 2006, Shelly 2009).

As shown for GRO, OO affected the rate of sexual signaling in *C. capitata* males. Exposure to OO increased male signaling activity by approximately 25%, an increase that is similar to that recorded for GRO-exposed males (Papadopoulos et al. 2006). In wind tunnel experiments, the pheromone released by exposed males did not attract more females (over a distance of 2.61 m) than pheromone released by non-exposed males. However, females exhibited a higher degree of behavioral arrestment after they approached OO-exposed calling males (Papadopoulos et al. 2006). Such arrestment might contribute to the elevated mating success of OO-exposed males because these males would have more chances to court and mount females. Indirect evidence suggests that OO exposure does not affect the cuticular chemical profiles as was suggested for GRO (Shelly et al. 2007d). Papadopoulos et al. (2006) compared the effect of treating males with OO topically on the abdomen and the wings on their mating performance against non-treated males. OO increased male mating success only when applied to the abdomen, which suggests that it is unlikely that an OO effect on male behavior is mediated through changes in their scent, because otherwise it should have also worked when it was applied into the wings. In a related study, Shelly (2009) found that females displayed similar attraction to dead males that had been exposed or not exposed to grapefruit oil, further suggesting that modifications in cuticular scent following exposure to citrus oil volatiles were unlikely to account for the increased mating success of oil-exposed males (in contrast to GRO; Shelly et al. 2007d). The fact that abdominal treatment with OO boosted male mating success led Papadopoulos et al. (2006) to propose that specific components of OO are internalized and used to synthesize a pheromone with higher attractant potential to females, at least at close ranges. However, the pheromones of OO-exposed and non-exposed males have not yet been compared, and consequently this hypothesis remains speculative.

In addition to *Citrus* species, two other host fruits have been tested for their potential role on *C. capitata* sexual behavior. Exposure of males to mango fruits (which contain α -copaene) showed no effect on male mating success, even when they were able to contact the fruit surface (Shelly et al. 2008a). On the other hand, in an extensive study on the interaction of *C. capitata* males and guava trees and fruit, Shelly and Villalobos (2004) observed clusters of males on specific sections of the trunk and branches of guava trees, where α -copaene presumably occurs in high concentrations. Interestingly, these clusters, so-called hotspots, appeared associated to specific guava trees, while other trees were never chosen by males. In the hotspots, males were largely motionless and videotaping using macro lens showed that males moved their mouthparts up and down, which suggested they were feeding on the bark. Males confined to hotspots (using net-bags) had higher mating success than males held in randomly chosen, non-hotspot areas (Shelly and Villalobos 2004). Exposure to guava fruit also enhanced male mating success. In both cases (hotspots and fruit) the enhancement effect lasted at least 3 d after exposure, but the effect of hotspots was much stronger than exposure to guava fruit since approximately 80% of the matings involved males exposed to hotspots (with the remaining 20% involving non-exposed males), whereas this percentage reached ca. 62% for males exposed to the fruit (Shelly and Villalobos 2004). Contact with hotspots was needed in order for the male mating enhancement to take place. Shelly and Villalobos (2004) also measured calling activity and female visitation for groups of hotspot-exposed or not exposed males and found that exposed males called ca. 1.7 times more frequently than non-exposed males. This increased rate of sexual signaling was accompanied by higher female attraction. However, the attraction rate per signaling male was similar between the two types of males, which was interpreted as evidence of no

differences in the pheromonal composition as suggested earlier for GRO (Shelly 2001a).

Across the many papers in which host fruit and essential oils were found to attract and boost the mating success of *C. capitata* males, α -copaene was considered the compound most likely responsible for these effects. Shelly (2001a) provided evidence that this compound is able, on its own, to increase male mating success. Furthermore, practically all fruit species and essential oils tested contain α -copaene. Nonetheless, there are several lines of evidence that suggest chemicals other than α -copaene might influence male mating performance. Kouloussis et al. (2013) found that a mixture of five compounds, all of which are constituents of citrus oils (geraniol, α -pinene, limonene, β -myrcene, and linalool), mimicked the effect of exposure to citrus oil, which led the authors to conclude that α -copaene is not a necessary component ingredient for mating enhancement. Similarly, Juan-Blasco et al. (2013) compared the effects of GRO- and linalool-exposure on male mating competitiveness and found that the two treatments were equally effective in enhancing mating success. More recently, Niogret et al. (2017) studied the attraction of male medflies to traps baited with six different essential oils (ASO, GRO, OO, manuka oil, cubeb oil, and TTO) both under laboratory and field cage conditions. Although all the tested oils contained α -copaene, the level of male attraction was not correlated to the amount of this compound. In fact, attraction was better explained by the quantity of other compounds, such as β -myrcene, linalool, geraniol, camphene, and α -terpineol (Niogret et al. 2017). Interestingly, three of these compounds were part of the experimental mixture created by Kouloussis et al. (2013). Niogret et al. (2017) acknowledged the key role that α -copaene might have on *C. capitata* reproduction but suggested that other volatile chemicals act synergistically with α -copaene in attracting males. The fact that four precursors of *C. capitata* sex pheromone were released from the essential oils tested by Niogret et al. (2017) (i.e., β -myrcene, limonene, linalool, and geraniol; Heath et al. 1991, Howse and Knapp 1996, Kouloussis et al. 2013) provides additional evidence for the importance of compounds other than α -copaene.

Research in two unexplored fields might clarify the role of fruit or essential oil on the mating behavior of male medflies. First, possible physiological changes experienced by males after fruit or oil exposure, including the chemical characterization of the sex pheromone and gene expression profiles, will provide information on male responses to different odor sources and thus shed light on whether the mechanisms triggered by different volatiles are the same or not. Second, most host plants (or oils derived from them) studied thus far do not share an evolutionary history with *C. capitata*. The claim that males respond to certain compounds, because this increases their mating success, and therefore their overall fitness, requires an evolutionary framework in which the plants native to the original area of distribution of *C. capitata* (i.e., the Afrotropical region; de Meyer et al. 2004) should have a key role. However, none of the aforementioned studies used plants native to Africa. Chemical characterization of the main host species of *C. capitata* in its geographic origin and the assessment of their impact on male sexual behavior and physiology will help to unravel the well-recorded male enhancement phenomenon and the evolutionary forces that have shaped it.

Ceratitis quilicii

Quilici et al. (2013) extended studies of GRO and OO to another *Ceratitis* species, namely *Ceratitis quilicii* (de Meyer, Mwtawala, Copeland & Virgilio) (Diptera: Tephritidae) (formerly known as *Ceratitis rosa* Karsch). This species showed a very similar response to that recorded for *C. capitata*. Under field cage conditions, *C. quilicii*

males were attracted to cotton discs impregnated with these oils but were never seen landing on the discs. Attraction to OO was not affected by the age of males, whereas attraction to GRO increased with age over the interval considered (i.e., between 5 and 20 d post-emergence). Exposure (without contact) to GRO and OO improved *C. quilicii* male mating success, and exposed males obtained ca. 70% of the matings, competing with control males, under field cage conditions (Quilici et al. 2013). However, OO was able to enhance male competitiveness only when the adults were deprived of protein in the adult diet, whereas for *C. capitata* males fed on sugar and protein as adults, the effect of OO was quite evident.

Anastrepha

In comparison to *C. capitata* or *Bactrocera* species, there are relatively few studies on the potential effect of plant compounds on the sexual behavior of *Anastrepha* species. As for *C. capitata*, initial studies focused on the attraction of males to host fruit odors. Robacker et al. (1990a, 1990b, 1992) reported that fermented fruit of chapote (*Sargentia greggii* S. Watson) (Sapindales: Rutaceae) attracted males, as well as females, of the Mexican fruit fly *Anastrepha ludens* (Loew) (Diptera: Tephritidae). Subsequent studies on this species showed male attraction to other fruit species, such as grapefruit, oranges and guava (Robacker and Fraser 2002a, 2002b, 2003; Malo et al. 2005). Male attraction to fruits was also demonstrated for the congeneric species *Anastrepha suspensa* (Loew) (Diptera: Tephritidae) (Nigg et al. 1994) and *A. obliqua* (Cruz-López et al. 2006, Malo et al. 2012). Most of these studies did not consider male attraction in a sexual context but as a means of finding food sources. Robacker and Fraser (2002b) and Cruz-López et al. (2006) proposed that males respond to host fruit odor, because this increases the probability of finding females.

Inspired by the research on *C. capitata* and orange fruits, López-Guillén et al. (2008) compared the amounts of four volatile compounds released by *A. obliqua* males [(Z)-3-nonenol; (Z,E)- α -farnesene; (E,E)- α -farnesene; and a fourth, not identified, compound] between males that had been exposed or not exposed to *Spondias mombin* L. (Sapindales: Anacardiaceae) fruit. No detectable effect of fruit exposure was found for any of the four compounds measured, but this may have resulted from an insufficient exposure interval to the fruits [*C. capitata* males were exposed to orange fruit for 1–3 d and assessed 24 h later (Shelly et al. 2004); whereas *A. obliqua* were exposed for 6 h and assessed 24 h later (López-Guillén et al. 2008)].

Vera et al. (2013) directly tested the role of exposure to host fruit on male mating success in *A. fraterculus*. In this study, males were exposed to fruits of different species, which were previously wounded. Exposure to mango had no effect even when the flies could access the fruit, but exposure to fruits of guava and lemon, or just their aroma, caused an increase in the mating success of males. In both cases, males exposed to the fruit odor obtained around 75% of the matings, but the duration of exposure required for mating enhancement differed greatly between the fruit types. In the case of guava, 7 or more days of exposure were required compared to a single day for lemon (Vera et al. 2013). The authors postulated that, as proposed for *C. capitata*, α -copaene, which occurs in detectable concentrations in citrus and guava, could be responsible, at least in part, for the response in *A. fraterculus* as well. In support of this idea, Morató et al. (2015) found that exposure to grapefruit oil increased mating success of *A. ludens* males as reported for *C. capitata* males (Shelly 2009, Kouloussis et al. 2013), although the effect seems weaker as exposed *A. ludens* males accounted for ca. 56% matings compared to nearly 70% in *C. capitata* (Shelly 2009). However, the idea that α -copaene alone is responsible for

these responses in *Anastrepha* species is difficult to reconcile with the finding that GRO exposure failed to enhance mating ability in *A. fraterculus*, *A. ludens*, or *A. obliqua* (Mendoza 2010, Flores et al. 2011). At present, GRO has been found to increase male mating ability in only one *Anastrepha* species, namely *Anastrepha serpentina* (Wiedemann) (Diptera: Tephritidae) (Flores et al. 2011). Also, the fact that mango did not affect male mating success in *A. fraterculus* even when it contains detectable amounts of α -copaene (see references in Shelly et al. 2008a) allows questioning the role of this compound on the response of this species to citrus and guava. It is worth mentioning that *C. capitata* males likewise did not respond to mango exposure. Shelly et al. (2008a) proposed that this may have reflected low amounts of α -copaene in the fruit or the occurrence of other compounds that blocked α -copaene's effect on the male medflies. The role of pure α -copaene on *Anastrepha* males mating success has not yet been tested.

More recently, Bachmann et al. (2015) confirmed that guava odor increases mating success in *A. fraterculus* and further showed that exposure increased male signaling rate by 30–40% (measured through wing fanning and salivary gland exposure) above that of non-exposed males. The enhanced signaling activity of exposed males resulted in the release of more sex pheromone, at least for three (anastrephin, epianastrephin, suspensolide) of the four constituent compounds that were measured (Bachmann et al. 2015). However, no differences were found in the chemical profile of the cuticle of guava exposed and non-exposed males (Bachmann 2016). Furthermore, EAG studies showed that females have the exact same response towards cuticular extracts from exposed and non-exposed males. Together, these results suggest that a 'perfume effect' is not responsible for the increased mating success of guava-exposed *A. fraterculus* males.

Based on the compounds identified in the aroma of guavas, Bachmann et al. (2015) designed a mixture of seven compounds from different chemical families [aldehydes ((E)-2-hexenal), esters (ethyl butanoate and ethyl hexanoate), monoterpenes (β -myrcene, limonene, (E)- β -ocimene) and sesquiterpenes (α -humulene)] and used this blend in exposing treated males. Males exposed to the mixture obtained approximately 60% of the matings, a proportion well below the 70–75% enhancement recorded by Vera et al. (2013) and Bachmann et al. (2015). Interestingly, this mixture lacked α -copaene, suggesting this compound plays a minor role, if any, in the guava-mediated changes in the sexual behavior of *A. fraterculus* males. Alternatively, however, the smaller effect of the mixture (compared to guava exposure) suggests that one or more important compounds were absent, including, perhaps, α -copaene.

Bactrocera and ME

While testing new attractants for tephritid flies, Howlett (1912) observed that oil of citronella *Cymbopogon nardus* (L.) Rendle (Poales: Poaceae) attracted males of genus *Dacus*, which upon arrival consumed the oil. According to this author, several phenylpropanoid compounds were responsible for that attraction, but ME was the most attractive for *Dacus diversus* Coquillett and *Dacus zonatus* Saunders (Diptera: Tephritidae). Additional work showed that males of these species fed voraciously on pure ME, and Howlett (1912, 1915) hypothesized that this behavior was related to reproduction, since ME has no nutritional value and attracted only males. Later studies showed that attraction of males from various species of *Bactrocera*, as well as *Dacus*, is higher when males approach sexual maturity (Steiner 1952; Fitt 1981; Tan et al. 1987; Metcalf 1990; Iwahashi et al. 1996; Wee and Tan 2000, 2001; Shelly 2008), which further supported the notion that feeding on ME is related to reproduction.

Furthermore, [Raghu and Clarke \(2003\)](#) found that sexually mature males of *Bactrocera cacuminata* (Hering) (Diptera: Tephritidae) were most commonly collected in traps baited with ME at dusk, the time at which sexual activity peaks in this species.

The strong attraction to, and subsequent ingestion of, ME triggered questions related to the fate of this compound after ingestion. [Fitt \(1981\)](#) was the first to propose that ME or ME-derived compounds were released by males as part of their sex pheromone. This was confirmed a few years later for *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), as males that ingested ME produced a pheromone that contained metabolites of this compound ([Nishida et al. 1988](#), [Hee and Tan 2004](#)). These authors were able to demonstrate that after ingestion, ME is converted to two derivatives, 2-allyl-4,5-dimethoxyphenol and (E)-coniferyl alcohol, that were stored in the rectal glands. Similarly, males of *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae) and *Bactrocera correcta* (Bezzi) (Diptera: Tephritidae) convert ME into derivatives before storing them in the rectal glands. In the case of *B. carambolae*, ME is converted only to (E)-coniferyl alcohol ([Tan and Nishida 1996](#), [Wee and Tan 2005](#)), whereas in *B. correcta* ME is transformed to (Z)-coniferyl alcohol and (Z)-3,4-dimethoxycinnamyl alcohol ([Tokushima et al. 2010](#)). So, even when males from different species respond similarly to ME, biotransformation of ME into derivated compounds varies according to the species, but all the studied species convert ME before storage. Phenylpropanoids were found to be stored in the rectal gland, the site of pheromone production and storage of male flies ([Shelly 2010](#)). For males offered access to pure ME, accumulation of ME or its derivatives in the rectal gland starts as early as 15 min after ingestion and gradually increases until the day 1 or 6 after feeding in *B. carambolae* and *B. dorsalis*, respectively ([Wee and Tan 2007](#)), after which phenylpropanoid titers decline progressively. Phenylpropanoid levels reach values similar to those found in unfed males 12 and 20 d after ME feeding for *B. carambolae* and *B. dorsalis*, respectively ([Wee and Tan 2007](#)).

Despite widespread awareness of the powerful attractiveness of ME to males of certain *Bactrocera* species ([Shelly 2010](#), [Vargas et al. 2010](#), [Tan et al. 2014](#)), evidence that ME consumption influenced male mating behavior has been gathered only over the past 25 yr. Working with *B. dorsalis*, [Shelly and Dewire \(1994\)](#) evaluated the mating competitiveness of males that had been given unrestricted access to a cotton wick treated with ME at different intervals after ME exposure. ME treated males obtained a significantly higher number of matings (63–75%) than control males even after 35 d of ME exposure. A mating advantage was observed only after feeding on ME, and males prevented from contacting the chemical displayed no mating enhancement. Later research confirmed that *B. dorsalis* males are able to exploit natural sources of ME, such as flowers of *Fagraea berteriana* A. Gray ex Benth. (Gentianales: Gentianaceae), *Cassia fistula* L. (Fabales: Fabaceae), and *C. papaya*, as well as fruits of *Terminalia catappa* L. (Myrtales: Combretaceae), to gain a mating advantage as originally noted after ingestion of pure ME ([Nishida et al. 1997](#); [Shelly 2000a, 2001b,c](#); [Shelly and Edu 2007](#)). ME-mediated male mating enhancement was later documented for other *Bactrocera* species, including *Bactrocera philippinensis* Drew & Hancock (later synonymized with *B. dorsalis*) ([Shelly et al. 1996](#)), *B. cacuminata* ([Raghu and Clarke 2003](#)), *B. carambolae* ([Wee et al. 2007](#)), *B. correcta* ([Orankanok et al. 2013](#)) and *Bactrocera umbrosa* (Fabricius) (Diptera: Tephritidae) ([Wee et al. 2018](#)). The effect of ME ingestion on mating success is not immediate and a time window of 2–3 d is needed ([Shelly and Dewire 1994](#), [Wee et al. 2007](#)) at least when pure sources of ME were studied. This may be related to the fact that ME is toxic at certain levels, so males need a recovery time

after feeding on pure ME. In fact, male mating success enhancement after exposure to ME-containing flowers (which contain lower doses of ME) occurs on the same day for *B. dorsalis* ([Shelly 2000a](#)).

The mating boost conferred by ME appears to derive from increases in both the quantity and quality of sex pheromone released. [Shelly and Dewire \(1994\)](#) observed the response of *B. dorsalis* females to ME treated and control males that were placed singly in mini-cages, which were hung on potted guava plants within a larger cage ([Poramarcom and Boake 1991](#)). Treated males were found to both wing-fan more frequently and attract more females than control males even after 35 d of exposure. Female visitation was positively correlated to male calling within treated and control groups, but the rate at which female visits increased with calling effort was much higher for treated males. This result suggests that ME feeding improves the quality of the pheromone, an interpretation consistent with findings that ME and its derivatives are stored in the rectal gland and released afterwards as part of the pheromone ([Nishida et al. 1988](#), [Tan and Nishida 1998](#), [Hee and Tan 2004](#), [Wee et al. 2007](#)). In a related study, [Hee and Tan \(1998\)](#) found that *B. dorsalis* (formerly known as *Bactrocera papayae*) females were 2.3 times more attracted to ME-fed males than control males within a wind tunnel, but because male signaling activity was not monitored, it is not clear whether female attraction reflected changes in pheromone quantity or quality. The same relationship between ME feeding and male signaling effort and female visits was later observed following male feeding on flowers of *F. berteriana*, which contain ME ([Shelly 2001b](#)), again indicating increases in both pheromone production and attractiveness after ME feeding. However, in another study involving ME-bearing flowers, feeding on *C. fistula* flowers increased male mating success and female visitation but did so without a concomitant increase in wing-fanning levels, indicating that floral feeding enhanced the attractive quality, but not the quantity, of the sex pheromone ([Shelly 2000a](#)).

In addition to intersexual communication, limited data suggest that pheromone-containing ME metabolites may serve as an aggregation pheromone that attracts conspecific males. In wind tunnel trials, ME-fed males attracted significantly more males than control, non-fed males for *B. dorsalis* ([Hee and Tan 1998](#)), *B. carambolae* ([Wee et al. 2007](#)) and *B. umbrosa* ([Wee et al. 2018](#)). Furthermore, while running mating tests with ME-fed and ME-deprived males of *B. carambolae*, [Wee et al. \(2007\)](#) observed control males aggregating around ME-fed males, who were calling or mating, and feeding on the anal region of ME-fed males, which contained derivatives of ME. [Wee et al. \(2018\)](#) recorded the same behavior for *B. umbrosa* males also in field cage mating tests where ME fed and unfed males were released together. This suggests that ME derivatives influence, not only lek formation via long-range attraction of other males, but they also affect behavioral interactions of males within leks. The nature and consequences of such interactions remain unknown.

In contrast to the above species, males of *B. cacuminata*, which likewise are attracted to ME, do not gain mating benefits until weeks after feeding on the lure. In this species, feeding on ME had no effect on male mating success 24 h after feeding but did increase mating success 16 and 32 d after exposure ([Raghu and Clarke 2003](#)). If ME acted as a precursor of male sex pheromone in *B. cacuminata*, then the effect of mating enhancement should arise sooner, at least if ME is processed as in other *Bactrocera* where its transformation and storage takes 1 to 3 d ([Nishida et al. 1988](#)). [Raghu and Clarke \(2003\)](#) suggested that this delay in the response to ME indicates the existence of other benefits from ME consumption, perhaps related to improving their nutritional status. However, in a related study [Raghu et al. \(2002\)](#) compared the energetic reserves between ME fed and unfed

B. cacuminata males and found no effect of ME feeding on overall weight or lipid, carbohydrate and protein reserves (Raghu et al. 2002), suggesting that ME-responsiveness in this species is not related to their nutritional status. Although the reasons for the delayed effect of ME remain unknown, it does seem likely that the mechanism is different from that reported for other *Bactrocera* species.

Bactrocera and *Zeugodacus* and CL/RK

As noted above, another assemblage of lure-responding *Bactrocera* and *Zeugodacus* species are attracted, not to ME, but to CL and its hydrolysis product RK (Tan et al. 2014). RK occurs in a diversity of plant species in nature (Hirvi et al. 1981, Hirvi and Honkenen 1984, Marco et al. 1988, Nishida et al. 1993, Tan and Nishida 1995, Tan 2009), and males of CL/RK-responsive species have been observed visiting the flowers of orchids that produce and release RK (Nishida et al. 1993, Clarke et al. 2002, Tan and Nishida 2005). Until recently, CL was considered a synthetic compound, but Tan et al. (2014) report detection of CL in certain *Bulbophyllum* orchids. As with ME-responders, in RK/CL responsive species the males show far greater attraction to RK or CL than females (Wong et al. 1991, Tan and Nishida 1995, Weldon et al. 2008). Likewise, attraction of males increases after attaining sexual maturation (Fitt 1981, Wong et al. 1991, Weldon et al. 2008).

Attraction to natural sources of RK (orchids) leads to ingestion of this compound by males of *Z. cucurbitae* and *Bactrocera caudata* (Fabricius) (Diptera: Tephritidae) which, in turn, leads to accumulation of RK in their rectal glands (Nishida et al. 1993, Tan and Nishida 2005). Accumulation of RK was also reported for *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) males that were fed either pure RK (Tan and Nishida 1995) or CL (Kumaran et al. 2014a) that is rapidly hydrolyzed and stored. A recent study by Kumaran et al. (2014a) compared the chemical composition of droplets of excretions (presumed to be male pheromone volatiles) left by *B. tryoni* males fed on CL during the peak of calling activity (at dusk) with that left by the same type of males but at noon. Results showed that *B. tryoni* males released RK together with other pheromonal compounds exclusively during pheromone release phase. Interestingly, RK is incorporated into the pheromone without modifications, as opposed to ME which is converted to two metabolites after ingestion (Nishida 2014). Because RK is stored in the rectal glands and released with other pheromonal compounds and because female attraction to CL fed males gradually increased with decreasing light intensity (Khoo and Tan 2000), these phytochemicals are strongly suggested to be involved in attraction of females, their courtship, or both.

Both CL and RK have been shown to influence male mating success. In *Z. cucurbitae*, the effect of CL is short-lived: CL-fed males enjoyed a mating advantage over unfed males in laboratory tests performed the same day or 1 d after CL feeding but not 3 d after CL feeding (Shelly and Villalobos 1995). This relatively brief interval contrasts markedly from the long-lasting effects of ME and essential oils on *Bactrocera* and *Ceratitis* males, respectively. Shelly and Nishimoto (2016) found similar results under field cage conditions; however, the CL-mediated mating enhancement lasted longer as CL-fed males achieved significantly more matings than control males 3 d (but not 5 d) after feeding. Similar findings have been reported for RK-fed males of *Z. cucurbitae* (Shelly 2000b). More recently, CL has been shown to increase mating success of *B. tryoni* males under laboratory conditions (Kumaran et al. 2013). Interestingly, the advantage is relatively brief for this species as well, and CL feeding conferred an advantage to *B. tryoni* males that lasted only 3 d post-feeding.

CL-mediated mating enhancement seems to be related to an increase in sexual signaling, which in turn is associated to enhanced female attraction. Using mini-cages within larger flight cages, Shelly and Villalobos (1995) compared signaling rate and female attraction for CL-fed and unfed males of *Z. cucurbitae*. Wing-fanning was recorded 70 times of a total of 135 observations (52%) for CL-fed males, whereas control males were observed wing-fanning 54 times (40%). These differences in male signaling translated into higher arrival rates to mini-cages that contained CL-fed males (Shelly and Villalobos 1995). However, the increase in female arrivals was similar to the increase in male signaling activity which, as noted above, suggests that increased pheromone release alone could account for increased female visitation without need to invoke qualitative (compositional) changes in the pheromone. Similarly, wind tunnel experiments recorded increased attraction of *Z. cucurbitae* females to CL fed males (Khoo and Tan 2000), although in this case male signaling activity was not monitored. On the other hand, Kumaran et al. (2014a) found differences in the composition of pheromone released by CL-fed and unfed males in *B. tryoni*. RK was found only in the pheromone of CL-fed males, and the abundance of some endogenous pheromone components (*N*-(3-methylbutylacetamide), *N*-hexylpropanamide and *N*-propylbutylamide) was higher in CL-fed males. In addition, they demonstrated that females are more attracted to isolated glands of CL-fed males than control (non-CL-fed) males, strongly suggesting that the greater attractiveness of CL-fed males is related to the quality of the olfactory signal. However, Kumaran et al. (2014a) did not measure either the level of pheromone calling or pheromone release rate and were thus unable to tease apart the impacts of pheromone quantity and quality on female attraction. As reported for ME-fed *B. carambolae* and *B. dorsalis* males, *Z. cucurbitae* males that ingest CL were also attractive to conspecific males in flight tunnel assays (Khoo and Tan 2000), suggesting again a potential role of CL (and perhaps also RK) in promoting male aggregation.

Even though RK can remain in the rectal glands up to 6 d (Nishida et al. 1993), the positive effects of CL and RK on *Z. cucurbitae* male mating success were no longer evident after 3 d from feeding (Shelly and Villalobos 1995, Shelly 2000b, Shelly and Nishimoto 2016). This suggests that the effect of these phytochemicals cannot be entirely explained on the basis of their own contribution to the pheromone composition and that other mechanisms may also be involved. For instance, Shelly and Villalobos (1995) showed that CL ingestion increases male calling frequency and Kumaran et al. (2013) and Kumaran (2014) found that CL feeding increases male locomotor activity and successful mating rate after mounting. Altogether, these results point to a general increase in activity after contact with a CL or RK source, a similar phenomenon to that described for *A. fraterculus* after males are exposed to guava fruit aroma (Bachmann et al. 2015).

Ingestion of RK or CL may also confer a non-sexual benefit to males, i.e., reduced predation risk. Using houseflies as prey and geckos as predators, Tan (2000) found that geckos avoided eating flies topically treated with RK (at a biologically meaningful dose; Tan and Nishida 2005). Therefore, while recent attention has focused on the sexual context, consumption of these phytochemicals may confer selective advantages via increased survivorship.

Recent Findings on Other Phytochemicals

The Olive Fruit Fly and α -Pinene

Bactrocera oleae (Rossi) (Diptera: Tephritidae) is a monophagous species that lay eggs on ripe olives. The mating system of *B. oleae* is quite different from other fruit fly species, as in this species it is the

female that attracts males by releasing sex pheromones (Mazomenos and Haniotakis 1985), although recent studies showed that males also release small amounts of specific pheromonal compounds (Carpita et al. 2012). α -pinene, a terpene that forms part of the female sex pheromone (Mazomenos and Haniotakis 1981), was found to attract *B. oleae* males (Mazomenos and Haniotakis 1985) but only weakly attract females (Scarpati et al. 1993). This compound is among the most common plant volatiles in nature (Mercier et al. 2009) and is present in olives (Scarpati et al. 1993). Based on the response of males to α -pinene, Gerofotis et al. (2013) evaluated its effect on male sexual behavior. Exposure to α -pinene was carried out with mature males that were prevented from contacting the source. Under these conditions, Gerofotis et al. (2013) found that α -pinene increased mating success in *B. oleae* males, but the physiological and behavioral basis of this phenomenon was not investigated. Recently, Kokkari et al. (2017) evaluated the effect of exposing *B. oleae* males to the aroma of olive fruit on their mating propensity and mating duration by caging either exposed or non-exposed males with non-exposed virgin females. Exposed males mated more frequently and for longer durations than non-exposed males (Kokkari et al. 2017). As both *B. oleae* females and olive fruits release α -pinene, it is not clear whether these results reflect the response of males to fruit compounds (as shown for *C. capitata*, *A. fraterculus*, and *A. ludens*) or whether male mating enhancement occurs as a response to sensing one of the components of the female sex pheromone. Further studies are needed in order to identify the biological meaning of the response of *B. oleae* males to α -pinene.

Zingerone

Tan (1998) found that males of both ME- and CL/RK-responding species were attracted to flowers of *Bulbophyllum patens* King (Asparagales: Orchidaceae), which led Tan and Nishida (2000) to hypothesize that these flowers produce both ME and RK. However, these authors did not detect these compounds but instead found that flowers were releasing large amounts of a different compound, which was identified as ZG [4-(4-hydroxy-3-methoxyphenyl)-2-butanone] and was accompanied by a small amount of a related compound, identified as zingerol (ZGol) [4-(4-hydroxy-3-methoxyphenyl)-2-butanol]. As happens with ME and RK, males ingest ZG, which is subsequently stored in the rectal glands. The form in which ZG is stored varies among species, with cases in which ZG is not altered (*B. tryoni*, Kumaran et al. 2014a), ZG is completely transformed to ZGol (*B. carambolae*, Tan and Nishida 2000), or where a mixture of ZG and ZGol is stored at varying ratios (*Z. cucurbitae* and *B. dorsalis*, Tan and Nishida 2000, 2007). *Z. cucurbitae* males store much larger amounts of ZG than ZGol, at ratios that are similar to those found in the flowers of *B. patens* (Tan and Nishida 2000). Conversely, *B. dorsalis* was found to store larger amounts of ZGol than ZG, in ratios that markedly differ from those found in flowers, suggesting that males are preferentially incorporating ZGol, or they convert ZG to ZGol, or both (Tan and Nishida 2007).

These interesting findings prompted a study of the potential effects of ZG on male sexual behavior. Khoo and Tan (2000) reported that *Z. cucurbitae* males that ingested ZG attracted more males and females than control, unfed males, which led the authors to postulate that ZG might enable males to court female flies more successfully than males that do not consume ZG. Nonetheless, because neither male signaling rate nor pheromone composition were compared between ZG-fed males and ZG-unfed males, it is not possible to determine whether increased female attraction was due to enhanced pheromone calling, altered pheromone composition, or both. However, a recent study by Shelly (2017a) found no evidence of male mating enhancement in *Z. cucurbitae* after ZG feeding. Conversely, males of *B. tryoni*, which are attracted to both CL and ZG (Fay

2012), have been shown to increase their mating success in response to ZG ingestion (Kumaran et al. 2013), an effect that lasts only one day after feeding. Surprisingly, and differently from *Z. cucurbitae*, the pheromone of ZG-fed *B. tryoni* males attracts females at the same level as control, unfed males (Kumaran et al. 2014a). Thus, males of both *Z. cucurbitae* and *B. tryoni* are attracted to and fed on ZG, preferentially store this compound without alterations, and release it as part of the sex pheromone. However, in *Z. cucurbitae*, male pheromone is more attractive to females after ZG feeding, although male mating success remains unchanged, whereas in *B. tryoni*, males increase their mating success after ZG feeding but their pheromone was no more attractive than control males. These discrepancies might be explained by consistent differences in the fate of ingested ZG. In *Z. cucurbitae* small amounts of ZG are converted to ZGol, whereas in *B. tryoni* small amounts of ZG are converted to RK and b-(4-hydroxy-3-methoxyphenyl)-propionic acid. RK is known to boost male mating success; however, the potential role of ZGol has not been evaluated. If ZGol has no effect on male mating success, then the conversion of a fraction of ZG into ZGol might account for the lack of effect of ZG on *Z. cucurbitae* males.

Applications of Plant Compounds in the Framework of the Sterile Insect Technique

Improving the Mating Competitiveness of Sterile Males

Plant-derived semiochemicals have long played an important role in the management of tephritid pests as attractants in traps deployed for detection or population suppression via attract-and-kill. Tan et al. (2014) provide an extensive review of these applications, and these uses will not be treated here. In addition to trapping, the fact that semiochemicals may boost the mating success of males offers a promising tool to increase the efficacy of the sterile insect technique (SIT). This control method requires that released, sterile males compete effectively with wild males and induce sterility in wild females. The sexual competitiveness of sterile males reflects the cumulative effects of adaptation of the strain to mass rearing conditions as well as sterilization and release procedures (Robinson et al. 2002). Unfortunately, evidence from many fruit fly species indicates that these processes may all negatively affect the sexual performance of released, sterile males (Calkins and Parker 2005). Furthermore, while the development of genetic sexing strains (GSS) that allow for early sex sorting and the release of only males improves the efficacy of the SIT (Robinson 2002), the translocation induced to stabilize a GSS may also adversely affect male sexual competitiveness (Munhenga et al. 2016, Rempoulakis et al. 2016).

For any one semiochemical-fruit fly interaction, initial work was conducted in an academic context, with emphasis on the role of plant chemistry on female mate choice and sexual selection. These early experiments were typically performed under laboratory conditions using wild flies. Once chemical enhancement of male mating success was documented, possible use of such enhancement in the context of SIT programs was examined. Below, we describe work that expanded upon early findings with wild males in small laboratory cages to sterile males in field situations. Methods used to expose large numbers (i.e., millions) of males to pre-release chemical treatment are noted, as these are critical for successful implementation in SIT.

Phenylpropanoids

Following studies on wild flies, ME-mediated enhancement of male mating success was confirmed under laboratory conditions for sterile (irradiated) *B. dorsalis* males (Shelly 1995). Subsequent research under semi-natural conditions of field cages (where one tree served

as mating arena) corroborated this finding for bisexual strains of *B. philippinensis*, *B. dorsalis* and *B. correcta* (Shelly et al. 1996, Shelly and Nishida 2004, Orankanok et al. 2013). Additional trials (Shelly et al. 2010a, Ji et al. 2013) using field cages further demonstrated an ME-mediated boost in mating competitiveness for sterile males of GSS (translocation) strains of *B. dorsalis* (McCombs and Saul 1995).

Because the final goal of SIT is the induction of sterility in wild females under open field conditions, Shelly et al. (2010a) mimicked these conditions by releasing sterile, ME-fed or control (non-ME-fed) *B. dorsalis* males along with wild males and females at different sterile:wild male ratios (5:1 to 60:1) in large field enclosures (16 m long × 6 m wide × 2.5 m high) that contained 10–15 guava trees. After 4 d, flies were provided apples (*Malus domestica* Borkh.) (Rosales: Rosaceae) for 24 h for oviposition. Deposited eggs were removed from the fruit and incubated for 72 h to allow hatching. At all overflowing ratios, egg hatch was lower in enclosures containing ME-fed sterile males than control sterile males. Furthermore, results suggested that pre-release feeding on ME allows for a reduction in the number of sterile flies required for release, which would increase the cost-effectiveness of the SIT (Shelly et al. 2010a). McInnis et al. (2011) repeated this basic protocol, but releases were made in citrus orchards, with one orchard receiving sterile, ME-fed males and another receiving sterile, control males (all released males were from a GSS strain of *B. dorsalis*). Eggs were dissected from field-collected fruit and, consistent with the results from the large field enclosures, induced sterility was higher in the orchard where sterile, ME-fed males had been released than in the orchard where sterile, control males had been released (McInnis et al. 2011).

Altogether, the above evidence strongly suggests that ME treatment increases the mating success of irradiated *B. dorsalis* males under natural conditions, even when they derive from a GSS. Nonetheless, there is still a major issue regarding the use of ME as a prerelease treatment in SIT, i.e., how might ME be delivered to millions of males simultaneously. The initial report (Shelly and Dewire 1994) on the ME-mediated mating enhancement showed that feeding on the phytochemical was required and that exposure to the odor of ME alone (without physical contact) did not increase male mating competitiveness. This finding implied that the operational challenge would involve the design of a feeding system, such that males held in high density would all have access to the ME source. This is not a trivial problem, as males are so strongly attracted to ME that any source would quickly be covered with males, thus greatly restricting access to the chemical. As an alternative solution, Shelly and Nishida (2004) tested whether feeding larvae on a diet containing ME would have a similar impact on their mating competitiveness as ME feeding at adult stage. However, adults that fed on ME as larvae showed no increase in their mating success, apparently because larvae failed to convert ME to its metabolites or to sequester its metabolites in the rectal gland (Shelly and Nishida 2004). Realizing the necessity of adult feeding, Tan and Tan (2013) designed an automated ME feeding structure in which males are exposed to a belt impregnated with ME and allowed to feed for a certain period of time after which they are brushed off and collected. A prototype based on this design was tested and shown to deliver ME efficiently to males under high-density conditions. To our knowledge, however, this machine is not being used in any SIT facility. Haq et al. (2014) acknowledged this innovative design but argued that it is not suitable for treating sterile males on an industrial scale (i.e., millions of males per day). Based on progress regarding large-scale application of GRO for Mediterranean fruit fly (see below), Haq et al. (2014) assessed the potential of exposing *B. carambolae* males to the volatiles emitted

by dispensers impregnated with ME ('ME aromatherapy') to deliver ME through inhalation or impregnation of the cuticle and subsequent internalization. Under field cage conditions, Haq et al. (2014) showed that ME aromatherapy enhanced the mating competitiveness of *B. carambolae* males. Haq et al. (2015) also showed that ME aromatherapy produced a mating boost as early as 1 d after exposure compared to 3 d required by ME feeding (Wee et al. 2007). This shorter interval allows earlier release of sterile, ME-exposed males, which could reduce costs of SIT substantially. Even though ME aromatherapy seems to work for *B. carambolae*, it does not have the same effect on *B. dorsalis* (Shelly and Dewire 1994), and because the conditions of exposure to ME were similar [in *B. carambolae* 100 males were exposed for 3 h to 0.5 ml of ME (Haq et al. 2014); whereas in *B. dorsalis* 5–10 males were exposed for 2 h to 1.5 ml of ME (Shelly and Dewire 1994)], the reason for such differences remains unknown.

While plant compounds clearly improve male mating performance, it is imperative to assess any negative effects on male longevity. ME, as happens with essential oils, is known to have insecticidal activity (Tan and Nishida 2012). However, Raghu et al. (2002) and Shelly et al. (2010a) found no evidence that ME feeding affected survival of *B. cacuminata* and *B. dorsalis* males, respectively. Nonetheless, when mating competitiveness tests for ME-fed *B. dorsalis* males were carried out on the same day that males were exposed to the phytochemical, ME-fed males were outcompeted by unfed males, suggesting that males needed a recovery time after feeding. In *B. carambolae*, Wee et al. (2007) found that males fed on ME exhibited more than 90% mortality 2 wk after feeding, but the reason for this high mortality was not investigated. For CL or RK, the results seem contradictory. On the one hand, Kumaran et al. (2013) observed that *B. tryoni* males that fed CL showed higher mortality about 4 wk after CL intake. Conversely, Shelly and Nishimoto (2016) and Akter et al. (2017) found no effect of CL feeding on male survival in *Z. cucurbitae*. These differences could be explained on the basis of species-specific effects and by the different doses used in the two studies: *B. tryoni* males had access to CL for several days throughout the trial assay (Kumaran 2014), whereas *Z. cucurbitae* males were only exposed for 2 and 48 h, respectively (Shelly and Nishimoto 2016, Akter et al. 2017). In any case, if ME, CL, or RK have a negative impact on survival, according to (Kumaran 2014), this effect would not be detrimental to the SIT, because it is expressed late in life, most likely after sterile males have already mated. Thus, while evidence is not particularly abundant, it seems that ME and CL/RK exposure may be safe in the context of the SIT.

Essential Oils

Studies on potential applications of GRO and OO have gone farther than those focused on ME, and this is particularly true for GRO. This reflects the fact that feeding is not necessary for any of the oil-mediated mating boost documented so far, which simplifies its use in the context of a mass release facility. The first studies focused on testing the effect of GRO exposure in outdoor enclosures, with males from different strains (GSS and bisexual strains) and different ratios of sterile:wild males. Shelly and McInnis (2001) reported that, in competition with wild males for wild females, GRO-treated sterile, mass-reared males (from a bisexual strain) obtained 75% of all matings compared to only 25% for non-exposed males. Paranhos et al. (2008) and Silva et al. (2013) obtained similar results, under field cage conditions, when the effect of GRO was investigated for *tsl*-based, GSS (Franz et al. 1996). McInnis et al. (2002) combined artificial selection for mating competitiveness and GRO aromatherapy and identified a potential approach for greatly improving Mediterranean

fruit fly SIT. The selection scheme was based on the ability of mass-reared males to procure matings with wild females in competition with wild males under field cage conditions. The laboratory male × wild female crosses formed the basis of a selected high mating line (Stud strain). In this line, selection for male mating competitiveness was carried out every other generation through 30 generations. Mating tests performed at the 20th and 30th generations showed that Stud males obtained three times as many matings as control (unselected) males from the mass-reared strain and almost two times the number of matings obtained by wild males (McInnis et al. 2002). To test whether the male mating success of Stud strain could be further increased, Stud males were exposed to GRO and released in field cages together with wild males and females. After GRO treatment, Stud males accounted for 92% of all matings compared to 63% for non-exposed Stud males (McInnis et al. 2002). When GRO treatment was applied to irradiated Stud males, this increase was reduced to 79%, which still represents a significant contribution of GRO to male mating success. Barry et al. (2003) compared the mating success of GRO-treated or control (non-treated) sterile males at different sterile:wild male ratios and found that GRO-treated sterile males released at a 1:1 ratio with wild males achieved 62% of all matings, a level similar to that achieved by non-exposed sterile males at ratios of 5:1 (69%) or 10:1 (73%). Thus, GRO exposure would allow for reduction in the released numbers of sterile males, which means huge savings in SIT programs (Barry et al. 2003).

These promising results prompted further research focused on testing GRO exposure at larger scales and under more natural conditions. Using large field enclosures that contained 10–15 guava trees, Shelly et al. (2005) released wild flies and irradiated *tsl* males that were or not exposed to GRO and measured hatch rates of eggs laid in provided fruit. Results revealed that, at all four of the sterile:wild male ratios tested, induced sterility was greater in enclosures containing GRO-exposed males than control males. A field study was subsequently performed in which GRO-exposed or non-exposed sterile *tsl* males were released in different plots of Hawaiian coffee, *Coffea arabica* L. (Gentianales: Rubiaceae) (Shelly et al. 2007f). Coffee berries were collected from these plots and dissected to compare the induced sterility, which was significantly higher in the plot that received GRO-exposed males than the plot that received control males, providing strong support to the use of GRO as part of the pre-release treatments used in Mediterranean fruit fly SIT programs (Shelly et al. 2007f).

In addition to switching from laboratory to field conditions, GRO exposure was attempted for larger numbers of sterile males. In initial studies, males were exposed to GRO in groups of 25 individuals in small cups (400 ml) (Shelly 2001a, Shelly and McInnis 2001, Shelly et al. 2002). Exposure was then conducted using larger plastic boxes (so-called PARC boxes) that held ca. 36,000 males, and once again GRO-exposed males had a mating advantage over non-exposed males (Shelly et al. 2004). Following this work, GRO exposure was expanded to entire rooms holding millions of sterile males for release. In one study, approximately 14 million sterile males from the *tsl* strain were exposed to GRO simultaneously and used in subsequent mating trials (Shelly et al. 2007e). When *tsl* males competed against males from Guatemala and Hawaii, they obtained 29–36% and 38–43% of all matings, respectively. However, when *tsl* males were exposed to GRO, these percentages significantly increased to 51–55% and 52–64% when they competed with Guatemalan and Hawaiian strains, respectively (Shelly et al. 2007e). A second study (Shelly et al. 2010b) was conducted at the largest Mediterranean fruit fly eclosion and release facility in the world (Retalhuleu, Guatemala) where 83 to 179 million of sterile *tsl* males were exposed to GRO. In this case *tsl* sterile males obtained

19–26% of all matings, a percentage that significantly increased to 34–41% when they were exposed to GRO. Based on these findings, and the relatively low costs associated with GRO exposure, eclosion and emergence centers in California (United States), Florida (United States), and Guatemala adopted GRO exposure as standard protocol in their SIT programs.

Applied research has also focused on the use of OO to boost sterile Mediterranean fruit fly male mating success. Shelly et al. (2006) essentially repeated the protocols used for GRO and increased the scale of OO exposure first to PARC boxes (36,000 *tsl* males) and then entire holding rooms (ca. 14 million *tsl* males). In both cases, OO exposure increased the mating success of sterile males. Interestingly, the enhancement effect of OO was similar to that recorded for GRO. Because OO is less expensive than GRO, Shelly et al. (2008a) proposed that OO would reduce costs associated with aromatherapy as a pre-release method in the context of SIT. For that reason, the sterile fly release center in Chiapas (Mexico) has implemented the use of OO.

Essential oils have been extensively studied as potential bio-insecticides (Tripathi et al. 2009, Buentello-Wong et al. 2016, Pavela and Benelli 2016). Furthermore, Jofer-Barud et al. (2014) showed that the same essential oils that enhance the mating success of Mediterranean fruit fly males can be toxic when applied topically. Similarly, extracts from citrus oils that enhance mating success in *C. capitata* males (Shelly et al. 2004, Shelly 2009, Kouloussis et al. 2013) were shown to be toxic for *C. capitata*, both for immature and mature stages (Salvatore et al. 2004, Siskos et al. 2009, Ruiz et al. 2014). Therefore, it is important to rule out any detrimental effect of GRO or OO exposure at least for the required doses to enhance male competitiveness. This prompted additional studies on the ability of exposed males to survive and disperse under open field conditions. Shelly et al. (2004) found no evidence of a detrimental effect of GRO exposure carried out at a massive level, when comparing survival of treated and control *tsl* males under field cages conditions. In a related study, Shelly et al. (2006) performed a mark-release-recapture experiment, which compared the survival and dispersal ability of *tsl* males that were or not exposed to GRO in PARC boxes. Release-recapture data did not suggest any detrimental effect of GRO exposure. Furthermore, the results from the trapping arrangement suggested similar dispersal ability between exposed and non-exposed males (Shelly et al. 2006). These results were confirmed in a thorough assessment of the survival and dispersal abilities of *tsl* males in Brazil and Spain (Andrés et al. 2009, Paranhos et al. 2010, Juan-Blasco et al. 2013). In a recent study, Kouloussis et al. (2017) analyzed the effect of exposure to OO on the longevity of sterile *tsl* males. Similarly to GRO, OO exposure did not affect longevity in flies that were fed sugar and protein. Furthermore, Kouloussis et al. (2017) found that if males were fed only sugar, OO exposure was associated with a longer lifespan, which in turn could increase the effectiveness of the SIT. In sum, evidence from the two most studied essential oils with respect to male mating suggests that exposure to volatiles from these oils has no detrimental effect on male survival. Nonetheless, attention should be paid to the method in which these oils are delivered to the flies, as topical applications of three of the main constituents of OO (i.e., limonene, linalool and α -pinene) induced high toxicity on medflies, particularly in males (Papanastasiou et al. 2017).

Phytochemicals and the Joint Use of the SIT and the Male Annihilation Technique

As mentioned before, phytochemicals have been used effectively as lures in the control of fruit fly pests. In particular, ME and CL have been extensively used as part of the male annihilation technique

(MAT), which involves large-scale deployment of male-specific lures plus insecticide to reduce males to such a low level that eradication or suppression is achieved (Vargas et al. 2014). SIT and MAT were considered incompatible control methods, because the release of sterile males in an area where traps baited with lures would result in huge losses of sterile males, reducing the effectiveness of SIT. Furthermore, because traps would be full of sterile males, their efficiency to attract wild male would also be reduced. Therefore, MAT and SIT have been often used sequentially. MAT is first used to reduce wild male population, allowing higher sterile:wild male overflooding ratios, thus improving the effectiveness of SIT. In this scenario, the exposure of laboratory, sterile males to phytochemicals before they are released, seems to have opened a door to explore the joint use of SIT and MAT. Several studies have shown that after feeding on lures (ME, CL, TML), males show lower attraction to these lures (Chambers et al. 1972, Shelly 1994, Shelly and Villalobos 1995). Likewise, *C. capitata* males exposed to GRO showed a lower response to trimedlure-baited traps (Shelly et al. 2007a). Therefore, exposure to phytochemicals before release allows the release of sterile males in areas in which wild males are been attracted and killed in traps. However, in most studies lures were provided to males that were already sexually mature, and under an SIT approach flies are released soon after emergence while still immature. This potential limitation was recently overcome in a study by Akter et al. (2017). In this work, immature *B. tryoni* males were fed RK for 2 d after emergence, after which its attraction to CL-baited traps was studied until the males were 35 d-old. Both laboratory and field tests revealed that RK fed males showed a lower attraction to CL-baited traps even after 16–20 d from RK feeding. These results provide support to the idea of using phytochemicals as a pre-release treatment that allows simultaneous application of MAT and SIT. Regrettably, the possibility of mating enhancement as a consequence of RK feeding by immature males of *B. tryoni* was not assessed.

Interaction Between Plant Compounds and Other Factors That Modulate Male Sexual Behavior

Male mating success and related behaviors (i.e., calling and courting) have been shown to be modulated by a large number of factors, other than exposure to, or ingestion of, phytochemicals. The acquisition of nutrients during the adult stage, as well as male age, have received the most consideration, but other factors, such as the gut bacterial community and the quantity and quality of larval food, may affect the competitive skills of tephritid males (Pereira et al. 2013, Benelli et al. 2014). Despite their importance, the way these factors interact with phytochemicals in affecting male sexual behavior has been insufficiently addressed.

Access to protein sources by adult males is probably the most frequently studied external modulator of male mating success, showing in general a positive association with male mating success in species from the genera *Anastrepha*, *Ceratitis*, *Bactrocera*, *Zeugodacus* (Shelly et al. 2005, Yuval et al. 2007, Pereira et al. 2009, Pérez-Staples et al. 2009, Haq et al. 2013, Liendo et al. 2013). This might explain why several studies have investigated the interaction between protein intake and exposure to phytochemicals. In the case of GRO, studies carried out on *C. capitata* and *C. quilibii* suggested that the enhancement effect caused by GRO exposure is independent of protein intake (Shelly et al. 2003, Quilici et al. 2013). Conversely, OO exposure increased mating success of *C. quilibii* males only when protein was provided (Quilici et al. 2013). More recently, Kouloussis

et al. (2017) evaluated the effect of exposure to OO, limonene and a mixture of 5 compounds found in the citrus oil (Kouloussis et al. 2013) on the pheromone calling rate of *C. capitata* males that were fed or deprived of proteins. Higher calling activity of *C. capitata* males exposed to OO was found only when males were fed protein and sugar (no effect was evident for sugar-fed males), whereas diet had no effect when males were exposed to a mixture of five compounds present in OO. In the case of ME, RK, and CL, protein intake has been found to always condition the effect of phytochemical ingestion. For *B. dorsalis*, *B. philippiniensis* and *B. correcta*, ME failed to increase mating success in males that were deprived of protein during the adult stage (Shelly et al. 2005, Obra and Resilva 2013, Orankanok et al. 2013). Nonetheless, in *B. dorsalis*, Shelly et al. (2007b) showed that ME can delay the negative effects of a shortage of protein during the adult stage on male mating success. In this study, males were fed on protein for a period of 20–23 d after emergence after which they were fed only sugar. This dietary switch produced a drop in their mating competitiveness as soon as 3 d after protein deprivation, when compared to males that fed continuously on protein. However, if protein-deprived males were fed ME on the day before the mating test, they still competed with protein-fed males, and the negative impact of protein deprivation arose later, after 7 d (Shelly et al. 2007b). Similarly, CL ingestion also interacts with protein intake to determine the mating success of *Z. cucurbitae* males (Shelly 2017b). As with ME and *B. dorsalis*, *Z. cucurbitae* males deprived of protein experience a huge drop in mating competitiveness, which is buffered by CL and RK feeding. Akter et al. (2017) showed that even when RK intake increases mating success in *B. tryoni* males, this effect requires that males feed on protein. Based on the few studies that addressed the interaction between protein intake and phytochemical exposure (e.g., essential oils) or ingestion (e.g., ME, CL, RK), it seems that the influence of those phytochemicals whose effects do not require ingestion is often independent of the adult diet, whereas those that are ingested are strongly affected by the nutritional status, or at least the consumption of protein, by the adults. This hypothesis is nonetheless challenged by the fact that OO exposure requires protein intake in order to affect male mating behavior (Quilici et al. 2013, Kouloussis et al. 2017), which suggests a more complex scenario in which potential interactions between diet and plant compounds are not only species-specific but also depend on the phytochemical under study.

The mating success of tephritid males varies with age. Males (as well as females) are anautogenous (Hendrichs and Prokopy 1994), i.e., they emerge with undeveloped gonads and rely on protein intake to fully develop their testes and accessory glands (Drew and Yuval 2001). Therefore, most species go through a maturation or immature phase during which males do not mate or release pheromone. After sexual maturation is attained, male behaviors, such as calling, courting, and mating, are still modulated by age in ways that vary greatly among species (Papadopoulos et al. 1998, Liedo et al. 2002, Shelly et al. 2007c, Diamantidis et al. 2008). However, there are only a handful of published papers that focused on the interaction between age and the exposure to, or consumption of, phytochemicals. Shelly and McInnis (2001) found that, in the case of the Mediterranean fruit fly and GRO, the increase in male mating success occurred regardless of whether males were exposed to the oil before or after they were sexually mature. Age after sexual maturation does not seem to modulate the effect of GRO on male mating competitiveness (Shelly 2001a). Similarly, the increase in male signaling rate mediated by exposure to OO (and related compounds) was independent of age in the Mediterranean fruit fly (Kouloussis et al. 2017). Based

on the currently available data, it seems that neither age at exposure nor time since the exposure influence the effect of GRO and OO on male mating success in *C. capitata*.

On the other hand, ME feeding confers a mating advantage to males of *B. dorsalis* and *B. correcta* only when it occurs after maturation has been attained (Shelly et al. 2008b, Orankanok et al. 2013). Interestingly, a small number of young *B. dorsalis* males were attracted to and fed upon ME but were apparently unable to produce the associated metabolites, which, in mature males, are released as pheromone components. Thus, the immature males that feed on ME did not, upon achieving maturity, display a mating advantage over ME-deprived males (Shelly et al. 2008b). Regarding the interaction between male age and exposure to phytochemicals after sexual maturation has been attained, ME seems to have a long-lasting effect on *B. dorsalis* male mating success [up to 35 d after feeding from pure ME (Shelly and Dewire 1994) and 21 d when males feed on flowers containing ME (Shelly 2000a)]. Conversely, CL and RK provided a mating advantage for only one day following feeding in *Z. cucurbitae* (Shelly and Villalobos 1995, Shelly 2000a). Similarly, *B. tryoni* males feeding on ZG, CL, and RK increased mating success for 1, 3, and 10 d, respectively (Kumaran et al. 2013, Akter et al. 2017). In any case, as ME, CL, RK, and ZG, are consumed and released by the fly, the duration of the effect might be related more to the biochemistry of this process than to the actual age of the fly.

If plant compounds are to be used as a pre-release treatment of sterile males, the way in which ‘phytochemical therapy’ interacts with other proposed, pre-release treatments should be addressed (Pereira et al. 2013). Besides the addition of protein into the diet of released males, pre-release treatments may include the enrichment of artificial diets with beneficial bacterial symbionts (Yuval et al. 2013), application of juvenile hormone analogues to accelerate the onset of sexual maturation (reviewed by Teal et al. 2013), and different holding regimes where light, temperature, and other abiotic factors can affect male physiology and behavior (Pereira et al. 2013).

Gaps in Our Knowledge

Chemical Composition of the Sources

One of the main constraints on our understanding of chemically mediated male mating enhancement is the limited knowledge on the identity and relative abundance of compounds produced or emitted by those plant structures, or their extract or essential oils that increase male mating success. In many cases, males have been exposed to oils or fruits that release an unknown set of compounds. Some studies relied upon previously published information on the chemistry of a particular source to interpret their findings and suggest potential bioactive compounds. However, because plant chemistry may vary among cultivars and/or growing conditions, using such information could lead to the mischaracterization of the relative abundances of potentially relevant compounds as well as the misidentification of the actual behavior-mediating compounds. Furthermore, when the sources are fruits, other factors such as the ripening stage, the time elapsed since removal from the tree, and the holding conditions, may also affect their chemistry. Therefore, the best approach would be to collect volatiles from the actual source used to expose flies for behavioral assays. In the case of essential oils, the repeatability is higher, especially when the oils are commercially available, however, storage conditions (i.e., exposure to light, temperature, oxygen, etc.) can affect the integrity of the oils (Turek and Stintzing 2012), again potentially leading to inconsistent results or misleading attempts to replicate results with synthetic blends. This

lack of knowledge confounds possible comparisons among experiments. For example, if male exposure to two different fruit species boosts their mating ability, is this the result of males responding to the same ‘generic’ chemicals or response to fruit-specific volatiles? Where males respond to a complex mixture of volatiles, such as fruits or essential oils, is there more than one bioactive compound? If so, do their ratios matter? At present, we do not have answers to such questions.

One compound that is normally present in many of the essential oils evaluated as potential enhancers of the mating success of *C. capitata* males is α -humulene (also α -caryophyllene). This phytochemical is present in GRO, OO, ASO, manuka oil, and TTO (Niogret et al. 2017). α -humulene elicited very high electroantennogram response in *C. capitata* males (Niogret et al. 2011) but not in females (Cossé et al. 1995). However, field studies showed that traps baited with this chemical did not attract male or female medflies (Casaña-Giner et al. 2001). Shelly and Nishimoto (2015) evaluated the effect of α -humulene on *C. capitata* mating behavior. In laboratory tests, these authors first confirmed the lack of attraction of males and females to α -humulene and then showed that exposure to this compound had no effect on females but significantly reduced mating success in males. Males exposed to the phytochemical obtained approximately 35% of all mating, whereas non-exposed males obtained the remaining 65% (Shelly and Nishimoto 2015). Preventing direct contact with the chemical did not modify this result. Lower mating competitiveness was correlated with a reduction on pheromone calling behavior. Recordings of male behavior in field caged showed that 61% of the calling males were non-exposed males, whereas 39% were males that had been exposed to α -humulene (Shelly and Nishimoto 2015). This example illustrates that without a good knowledge of the chemical composition of the oils or plant structures tested as sexual enhancers, there is always the possibility that certain co-occurring compounds may inhibit other stimulatory chemicals from effectively increasing male signaling and mating.

Physiological Effect

Several studies showed that, for *Bactrocera* and *Z. cucurbitae* males, ingested phenylpropanoids are either converted to related compounds or left intact and then released as part of the sex pheromone. In the particular case of *B. dorsalis*, several studies have successfully identified genes which expression is associated to ME detection (Zheng et al. 2012; Wu et al. 2015, 2016; Liu et al. 2017). Beyond this, however, the physiological changes that males experience after exposure to fruit and essential oils, and that ultimately increase their mating success, remain largely unknown in *Ceratitis* and *Anastrepha*. In these genera, treated males typically show increased signaling rate, but few studies addressed changes in pheromonal emission rate and chemical composition. In most cases, contact with the volatile source is not required, which suggests that some volatiles could be retained by the insect cuticle and released slowly as a perfume, but this hypothesis has not been fully tested. Whatever mechanism underlies male enhancement, it should be accompanied by a specific gene expression pattern. Kumaran et al. (2014b) followed a RNA-seq-based approach to compare gene expression pattern between *B. tryoni* males that were fed ZG and males that did not feed on this compound. Results showed that several genes potentially associated with pheromone production, courtship interactions and mating were expressed differently in ZG-fed and unfed males, such as the *takeout* and *white eye protein* genes (which possibly regulate courtship); the *Obp*, *Obp3* and *Obp99c* genes (associated with pheromone production); and the gene *Timeless* (which regulates mating activity rhythm

in *Drosophila*) (Kumaran et al. 2014b). This information supports the idea that ZG was not affecting *B. tryoni* male mating success by increasing pheromone production (Kumaran et al. 2014a) as happened in other fruit fly-phenylpropanoids systems, but that a more complex scenario mediated this effect, including potential changes in inter-male aggression, courtship, and mating behavior. To our knowledge, this is the only published paper that analyzed the transcriptome of males treated with a phytochemical that boost their mating success. This approach would significantly improve our understanding of the changes induced by the exposure to plant compounds and provide a needed complement to behavioral and physiological studies.

Ecological and Evolutionary Implications

Detecting and feeding on specific phytochemicals has obvious benefits for male tephritids. However, the evolution of these interactions requires that females develop the ability to discriminate between fed/exposed and unfed/non-exposed males, which further suggests that there should be a fitness benefit to females in mating with fed/exposed males. Somewhat surprisingly, among more than 100 papers focusing on the effect of phytochemicals on the sexual behavior of tephritids, we identified only five papers that addressed potential benefits to females, and the evidence reported so far is not conclusive. No evidence of direct benefits for females in terms of fertility, fecundity or survival was found for *B. dorsalis* females mated to ME-fed males or *C. capitata* females mated to GRO-exposed males (Shelly 2000a, 2005). Kumaran et al. (2013) reported that *B. tryoni* females mated with CL-fed males exhibited higher fecundity (a clear indicator of a direct fitness benefit) but lower longevity than females mated with males that did not feed on CL. Later, Kumaran and Clarke (2014) found that male offspring of CL-fed males were better able to locate CL sources than sons of CL-deprived males. According to these authors, females that mate with CL-fed males could obtain, besides a direct benefit associated to increased lifetime fecundity, an indirect benefit because their sons would exploit RK/CL sources more effectively, which would increase their mating success, a proposed case of the ‘sexy son hypothesis’ (Fisher 1930). However, CL seems not to have the same effect in all species. In fact, Shelly and Nishimoto (2016) found that *Z. cucurbitae* females that mated with CL-fed males exhibited lower fertility than females mated with control (CL-unfed) males. For *Anastrepha*, Bachmann et al. (in review) reported that *A. fraterculus* females that mated with males exposed to guava volatile compounds showed higher fecundity than females mated to non-exposed males, with no effect on their fertility. In sum, results from five different species show contrasting results, even when, as for *B. tryoni* and *Z. cucurbitae*, the same phytochemical is involved. At present, limited data and apparent inconsistencies hinder understanding of the ecological and evolutionary forces that shape female mate preferences. Practical uses of such information, e.g., for increasing the fecundity, fertility, and longevity of females for mass rearing purposes (Bachmann et al., in review), are likewise constrained by the limited data available.

Effect of Larval Host

Many insect species spend their immature stages in confined microhabitats that are selected by their mothers and from which larvae cannot leave. Under this scenario, female choice of oviposition sites should be under strong selective pressure, because laying eggs in a low-quality substrate will negatively affect offspring survival and reproduction, therefore affecting the female’s own fitness. Natural selection should, therefore, favor females that preferentially oviposit in hosts that are nutritionally superior, a concept known as the preference–performance hypothesis, or the ‘mother knows best’ hypothesis

(Mayhew 1998, Gripenberg et al. 2010). This hypothesis has been widely studied both in herbivorous species feeding in confined plant structures and parasitoids (see Gripenberg et al. 2010 and references therein; van Alphen and Vet 1986, Rivero 2000). However, most studies, whether they support the preference-performance hypothesis or not, have focused on the development of the immature stages and far less attention has been given to the impact of host choice on the behavior of adult insects, and these studies are biased towards females (Shelly 2018 and references therein). However, in some cases, larval host has been shown to affect male sexual behavior (Conner et al. 1990, Forister and Scholl 2012, Muller et al. 2014). Furthermore, larval diet has been shown to affect male pheromone composition (Edde et al. 2007), epicuticular hydrocarbons that act as contact pheromone potentially involved in mate recognition (Etges et al. 2006, Edde et al. 2007, Etges and Tripodi 2008) and even male mating success in several insect families, including many examples in Diptera (Delisle and Bouchard 1995, Hurtado et al. 2012, Havens and Etges 2013), including tephritid fruit flies (Shelly 2018). Nonetheless, the effect of the host fruit on the response of males to phytochemicals that enhance their mating success has not been thoroughly addressed. In a recent study, Manoukis et al. (2018) investigated the effect of the rearing substrate on the attraction of *B. dorsalis* males to ME. Males that developed in fruits of *T. catappa* showed a lower response to ME than those that developed in guava fruit. Interestingly, *T. catappa* fruit has higher content of ME than guava fruit, which prompted Manoukis et al. (2018) to compare the response to ME between males reared on artificial diets containing or lacking this chemical. Results confirmed that ingestion of ME during larval stage reduced the response of adults to this phytochemical. This research area merits more attention, since the possibility that a larval host reduces the response of adult males to a particular attractant has obvious implications regarding the reliability of detection programs that use this attractant in baiting traps.

Similarly, female mate choice could depend on the substrate where they develop. Thorpe and Jones (1937) proposed that larval experience could affect behavioral preferences, a phenomenon known as preimaginary conditioning. Morató et al. (2015) found that wild *A. ludens* females reared on grapefruit preferentially mate with males that were exposed to grapefruit essential oils over non-exposed males; however when these same females (reared on grapefruit) had to choose between males that were exposed to bitter OOs and control, non-treated males, they showed no preference. Even though this result could be explained by differences between oils in their effect on males (i.e., grapefruit oil enhances male mating behavior, but OO does not), the finding hints that the larval substrate of females may predispose them to more readily accept males from the same host over males from different hosts, a possible instance of preimaginary conditioning. To our knowledge, there are no published studies that address the potential importance of female larval rearing substrate on their response to males treated or exposed to plant compounds. Furthermore, while reviewing published papers that were included in section ‘Plant Compounds Affecting Fruit Fly Male Sexual Behavior’, we found that well over 50% of the experiments were carried out with flies that developed in artificial larval media. Common use of this protocol adds a cautionary note to data interpretation and calls for more studies on flies reared from natural larval hosts.

Wider Ecological Perspective of Potential Effect of Phytochemical Ingestion and Exposure

Several lines of evidence suggest that phytochemicals benefit male tephritids beyond increasing their mating success. Both Gerofotis

et al. (2016) and Kouloussis et al. (2017) reported longer lifespan in *B. oleae* and *C. capitata* males, respectively, after exposure to plant compounds that increase their mating success. Another potential benefit induced by phytochemical exposure/ingestion is related to the ability of exposed/fed males to induce longer refractory periods in females and therefore increase the odds that their own sperm are used to fertilize eggs. This possibility has been studied in *C. capitata* females mated with males exposed or not exposed to GRO, with contrasting results. Shelly et al. (2002) found that females that initially mated to GRO-exposed, *tsl* males showed a similar propensity to remate as females that mated to non-exposed males (in both cases, remating propensity was ca. 10%). On the other hand, Morelli et al. (2013) found that females reduced their remating propensity from 64 to 33% when *tsl* males had been previously exposed to GRO. Contrasting results were also found for *B. tryoni* females. On one hand, Kumaran et al. (2013) reported a significantly lower remating propensity among *B. tryoni* females mated with ZG- or CL-fed males than those mated with unfed males. However, in a recent study, Akter and Taylor (2018) found no such effects on remating propensity when males of *B. tryoni* were fed RK, which is, as mentioned before, very similar to CL. Akter and Taylor (2018) proposed that these differences could be related to the fact that they provided RK when males were still sexually immature, whereas Kumaran et al. (2013) fed ZG and CL to males that already attained sexual maturity. While remating in tephritids has been extensively studied, there is a considerable gap in our understanding of the effect of phytochemicals on the ability of males to modulate female sexual behavior (Pérez-Staples et al. 2013). Furthermore, phytochemicals could affect other ecological aspects. In those cases where the plant compounds are consumed by the insects (CL, RK, ZG, and ME), ingestion might lead to reduced predation risks by geckos (Tan and Nishida 1998; Tan 2000; Wee and Tan 2001, 2005). Such alternative effects may be a key part of the evolution of the response of fruit fly to phytochemicals and may allow a more comprehensive understanding of this phenomenon.

Concluding Remarks

That plant chemicals may strongly influence the sexual behavior of male tephritids is a recent discovery. Once demonstrated for the ME–*B. dorsalis* system, work expanded to include a larger set of plant species, structures, and chemicals and a broader range of fruit fly species. This work has identified a fairly consistent outcome: whether ingested or inhaled, certain plant-borne chemicals uniformly increase the production of male sexual signals and in certain instances increase the attractiveness of those signals, which collectively boost male mating success. Despite emergence of this behavioral pattern, at least three major gaps in our knowledge limit our understanding of it. First, in many cases, particularly when exposure involves whole plant structures or oils, we do not yet know which compounds are responsible for the change in male behavior. Second, aside from information on the metabolic fate of ingested phytochemicals, we do not know the physiological basis for increased male activity following exposure to plant compounds. Finally, in most studies, the plant and fly species studied do not share a common evolutionary history (e.g., *Ceratitis* and *Anastrepha* and *Citrus* species). Presumably, the plants tested act as surrogates for other (as yet unidentified) plant species that evolved in the native range of the fly species. Still, in our view, complete understanding of the evolution of the plant–insect interactions discussed here awaits information from species with a shared evolutionary history.

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