

## Chapter 2

# Pheromones, Male Lures, and Trapping of Tephritid Fruit Flies

Keng Hong Tan, Ritsuo Nishida, Eric B. Jang, and Todd E. Shelly

**Abstract** Both sex pheromones and male lures appear to play an important role in the mating systems of many species of economically important tephritid species. Typically, stationary males emit pheromone attractive to searching females, and recent evidence indicates that naturally occurring male lures may function as precursors in pheromone synthesis. Here, we review (i) the basic biology of sex pheromones and the importance of naturally occurring male lures as pheromone components or precursors and (ii) the use of sex pheromones and male lures as trap baits, primarily in fruit fly detection programs, for the major genera of *Anastrepha*, *Bactrocera*, *Ceratitis*, *Dacus*, *Rhagoletis*, and *Toxotrypana*. Relatively few studies have examined the effectiveness of pheromone-based trapping, and most of these have involved only three species, the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), the Mexican fruit fly, *Anastrepha ludens* (Loew), and the Caribbean fruit fly, *A. suspensa* (Loew). In general, the results have been inconsistent, with traps baited with live males or male pheromone extracts or components attracting more females than blanks or food-baited traps in some studies but not in others. This inconsistency, along with the chemical complexity of pheromones and the

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multimodal nature of sexual communication (where olfaction is but one of several sensory channels used in male signaling and courtship), has limited research on the development of pheromone baits. Male lures, on the other hand, have proven incredibly useful and consistently effective trap baits. The major male lures – methyl eugenol, cue-lure/raspberry ketone, and trimedlure – are discussed as are possible replacements/modifications, such as fluorinated analogues of methyl eugenol, raspberry ketone formate, zingerone, ceralure, and enriched ginger root oil. In addition, we discuss various factors influencing the efficacy of male lures, including fly age, prior lure ingestion, selection for non-responsiveness, interspecific differences in responsiveness, and the use of liquid versus solid dispensers.

**Keywords** Aggregation • Anisylacetone • Attractant •  $\alpha$ -copaene • Cuelure • Electroantennogram • Floral volatile • Kairomone • Male lure • Methyl eugenol • Orchid • Phenylbutanoid • Phenylpropanoid • Pheromone • Raspberry ketone • Rectal gland • Sesquiterpene • Synomone • Trimedlure

## 1 Introduction

Chemical cues and signals influence the behavior, physiology, and ecology of insects in a remarkably large number of ways. It is hardly surprising, then, that strategies designed to protect agricultural systems are often based on chemical stimuli and cues important to pestiferous insects. These strategies are themselves diverse and may involve the elimination, modification, disruption, imitation, or circumvention of chemical information important to the target insect. Tephritid fruit flies are trapped for a variety of reasons – surveillance, suppression, and ecological study among others – and chemical baits have played a central role in these efforts. The existence of male lures was reported approximately 100 years ago (Howlett 1912, 1915), and such lures have been among the most widely used in programs to detect and manage tephritid fruit fly pests. Likewise, the presence of sex pheromones in economically important Tephritidae has been recognized for over 50 years (Féron 1959), and though not yet as effective as male lures, they have received considerable attention as possible tools in fruit fly surveillance and control.

This chapter provides an overview of the use of pheromones and male lures in trapping economically important fruit flies of the genera *Anastrepha*, *Bactrocera*, *Ceratitis*, *Dacus*, *Rhagoletis*, and *Toxotrypana*. Given the broad scope of this topic and the accompanying rich body of literature, our review is not exhaustive. Though somewhat idiosyncratic, reflecting invariably our own research experiences, we nonetheless believe we have highlighted main themes and introduced some new ideas or perspectives as well.

As evidenced by the chapter title, we have decided to describe compounds, such as methyl eugenol, cue-lure, raspberry ketone, trimedlure, and others, as male lures or male attractants and to avoid the oft-used term ‘parapheromone’. We do so for three main reasons: (i) Payne et al. (1973) originally defined parapheromones as

“compounds which are not naturally used in intraspecific insect communication”. However, several studies (Nishida et al. 1988a, b, 1993; Tan and Nishida 1995, 2007; Tan et al. 2011) have demonstrated that certain male lures (e.g., methyl eugenol, raspberry ketone, and zingerone) are used in synthesizing male sex pheromones, and so the original definition of parapheromone does not apply to tephritids; (ii) in a recent review of insect parapheromones, Renou and Guerrero (2000) restrict parapheromones to “chemical compounds of anthropogenic origin not known to exist in nature”. Once again, this criterion does not apply to methyl eugenol and raspberry ketone, which occur in many different plant species (Tan and Nishida 1995, 2012), and so excludes these two important tephritid male attractants (indeed, Renou and Guerrero’s review does not even include discussion of the Tephritidae), and (iii) the very use of the root ‘pheromone’ implies that male lures produce behavioral and/or physiological effects that resemble those of natural pheromones. There is evidence that male-produced sex pheromones may attract conspecific males and so act as aggregation pheromones (Nishida et al. 1988b; Tan and Nishida 1996; Hee and Tan 1998; Khoo and Tan 2000; Wee and Tan 2005a; Wee et al. 2007). Because male lures may (upon ingestion) be used in pheromone synthesis (references above), the idea that the male lures mimic the male sex pheromone appears reasonable and may eventually be shown to be valid. However, the available data regarding male-male olfactory attraction derive exclusively from laboratory studies (with a single exception, Nishida et al. 1988b). With few field data available, we consider it premature to conclude that male lures resemble pheromones in function. That said, we also recognize that the term male lure is not completely accurate, since the lures are known to occasionally attract females (Steiner et al. 1965; Nakagawa et al. 1970; Fitt 1981a; Verghese 1998). While not dismissing the importance of these observations, our collective field experience (except for a female *Bactrocera umbrosa* (Fabricius) captured by Tan in 2014) is that males comprise the vast majority of all individuals observed at point sources (traps, flowers, etc.) of known male lures, and hence the terms male lure or male attractant are generally, if not always, appropriate.

## 2 Tephritid Pheromones and Trapping

The family Tephritidae contains several genera, namely *Anastrepha*, *Bactrocera*, *Ceratitis*, *Dacus*, *Rhagoletis* and *Toxotrypana*, with species that are major agricultural pests of fruits and vegetables. Information on the identification of pheromones and their possible use in trapping programs is summarized below for each of these genera.

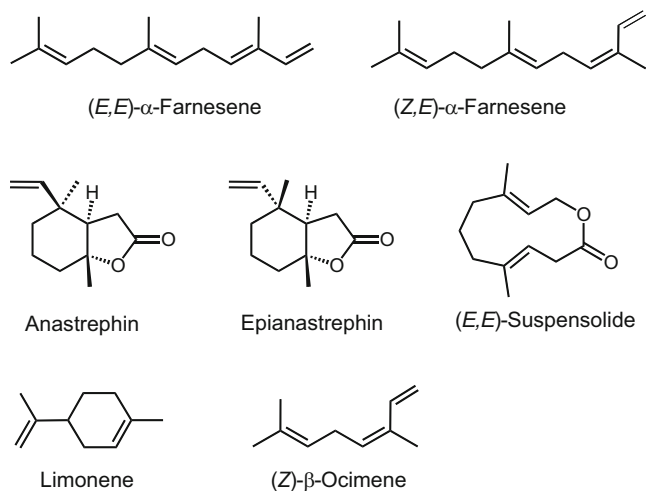
## 2.1 *Anastrepha Pheromones*

The genus *Anastrepha* contains approximately 200 species distributed in tropical and subtropical areas of the New World (Norrbon et al. 2000) of which eight (*A. distincta* Greene – Inga fruit fly, *A. fraterculus* (Wiedemann) – South American fruit fly, *A. grandis* (Macquart) – South American cucurbit fruit fly, *A. ludens* (Loew) – Mexican fruit fly, *A. obliqua* (Macquart) – West Indian fruit fly, *A. serpentina* (Macquart) – sapote fruit fly, *A. striata* Schiner – guava fruit fly, and *A. suspensa* (Loew) – Carribean fruit fly) are major agricultural pests, attacking a wide variety of fruits and vegetables (Aluja 1994; Norrbom et al. 2012). Although field observations are incomplete, many of the polyphagous and economically important species appear to display a lek mating system in which males occupy mating territories on leaves and attract females to the territory via a complex suite of visual, acoustic, and olfactory signals (Aluja et al. 2000). Regarding the latter, pheromone-calling males emit volatiles from everted pleural pouches and anal membranes, with aerial dispersion aided by intense bouts of rapid wing vibrations (Nation 1972). Volatile components are also released via the mouth (Nation 1990), and abdominal dipping of the evaginated anal membranes to the leaf surface may amplify pheromone attractiveness by increasing the evaporative surface area of the volatile components (Sivinski et al. 1994). Pheromone calling has been observed for a small number of *Anastrepha* species, and chemical analysis and identification of pheromonal components has been undertaken for only a subset of these species (Fig. 2.1 and Table 2.1).

Measurements of female attraction to male sex pheromone, or components thereof, have been made for an even smaller subset of all species, with nearly all of the research conducted on *A. suspensa* (Table 2.2) or *A. ludens* (Table 2.3). The biological activity of male pheromones has been studied in only four other species, with only one study undertaken for each. In both *A. fraterculus* and *A. obliqua*, freshly dissected salivary glands of males were found to attract mature and virgin females in laboratory cage tests (Lima et al. 2001; Ibañez-López and Cruz-López 2001). However, in *A. serpentina*, three putative pheromonal components were examined, with no strong female response observed for any of them (Robacker et al. 2009a, b). In *Anastrepha sororcula* Zucchi, field tests found no difference in female captures in traps baited with live calling males versus blank control traps (Santos Felix et al. 2009).

Despite the large amount of research conducted on *A. suspensa* and *A. ludens*, trapping and detection efforts for these two species still rely primarily on food-based lures (e.g., Robacker and Thomas 2007; Epsky et al. 2011), and an effective pheromone-based trap has not been developed. Several authors (Landolt and Heath 1996; Landolt and Averill 1999) have enumerated the reasons for this, and these generally include:

First, the long-range attractiveness of the male sex pheromone has weak empirical support, since the majority of research has been conducted in the small, laboratory cages and thus measures only short-range attractiveness or arrestant



**Fig. 2.1** Some sex pheromonal components of *Anastrepha* (Adapted from Rocca et al. 1992)

properties of the test chemicals. The widely used cage-top bioassay, for example, has generally been used in cubical cages only (0.2–0.3 m per side). Moreover, although the cage-top assay has generally indicated female response to male-derived chemicals, other laboratory tests involving slightly larger cages have failed to demonstrate long-range attraction of females to male pheromone. For example, arrivals of *A. ludens* females did not differ significantly between citrus trees having chemically-treated (with male pheromone extract or pheromonal components) or control (blank) leaves (Robacker and Hart 1986; Robacker 1988). However, using a 1.2 m long wind tunnel and a videotape system, Heath et al. (1993) found that *A. suspensa* females land more frequently on male-baited traps than control traps but spent equal amounts of time on the two trap types after landing. These data clearly indicate that the male volatiles are an attractant and not a simple arrestant. In sum, then, use of small cages does not allow rigorous identification of long-range attraction of *Anastrepha* females, and other laboratory results from slightly larger cages are inconsistent in this regard.

Second, field tests have yielded inconsistent results regarding female attraction to male-produced odors. In an early study, sticky traps baited with aggregations of 20 or 40 males captured significantly more released virgin females of *A. suspensa* than McPhail traps baited with an aqueous solution of yeast hydrolysate (Perdomo et al. 1975). A follow-up study on the same species (Perdomo et al. 1976) generated the same result and also documented attraction of released males to the male-baited traps. In contrast, although the difference was not statistically significant, Robacker and Wolfenbarger (1988) found that food-baited McPhail traps captured three times as many *A. ludens* females as pheromonal traps (baited with extracts of male abdomens). Similarly, and as noted previously, field tests involving *A. sororcula* found no difference in female captures in traps baited with live calling males versus

**Table 2.1** *Anastrepha* species for which male pheromone calling has been observed and the incidence of chemical analyses of pheromonal components in these species

Species	Pheromone calling	References	Pheromone Chemistry	References
<i>A. bistrigata</i> Bezzi	+	Da Silva et al. (1985)	–	–
<i>A. fraterculus</i> (Wiedemann)	+	Malavasi et al. (1983), Morgante et al. (1983), Lima et al. (1994), Segura et al. (2007)	+	Cáceres et al. (2009), Lima et al. (1996), (2001)
<i>A. ludens</i> (Loew)	+	Aluja et al. (1983), (1989), Moreno et al. (1991), Robacker et al. (1991), (2003), Robacker and Hart (1985a), Aluja et al. (2008)	+	Battiste et al. (1983), Stokes et al. (1983), Robacker and Hart (1985b), Rocca et al. (1992), Baker and Heath (1993)
<i>A. obliqua</i> (Macquart)	+	Aluja et al. (1983), (1989) Da Silva et al. (1985), Meza-Hernández et al. (2002), López Guillén et al. (2008), Henning and Matioli (2006)	+	Meza-Hernández et al. (2002), Ibañez-López and Cruz-López (2001), López-Guillén et al. (2008)
<i>A. pseudoparallela</i> (Loew)	+	Da Silva et al. (1985), Polloni and Da Silva (1986)	–	–
<i>A. robusta</i> Greene	+	Aluja (1993)	–	–
<i>A. serpentina</i> (Macquart)	+	Aluja et al. (1989), Castrejón -Gómez et al. (2007), Robacker et al. (2009a)	+	Robacker et al. (2009a)
<i>A. sororcula</i> Zucchi	+	Da Silva et al. (1985)	–	–
<i>A. striata</i> Schiner	+	Aluja et al. (1993), (2008)	–	–
<i>A. suspensa</i> (Loew)	+	Nation (1972), (1989), (1990), Dodson (1982), Burk (1983), (1984), Landolt and Sivinski (1992),	+	Nation (1975), (1989), (1990), (1991)), Battiste et al. (1983), Chuman et al. (1988), Mori and Nakazono (1988), Tumlinson

**Table 2.1** (continued)

Species	Pheromone calling	References	Pheromone Chemistry	References
		Epsky and Heath (1993a, b), Sivinski et al. (1994)		(1988), Rocca et al. (1992), Epsky and Heath (1993a, b), Baker and Heath (1993), Heath et al. (1993), Lu and Teal (2001)
<i>A. zenildae</i> (Zucchi)	+	De Almeida et al. (2011)	–	–

**Table 2.2** Published accounts for *Anastrepha suspensa* regarding the behavioral response of females to the sex pheromones of conspecific males

Odor source	Bioassay arena	Positive response		Reference
		Identified	Observed	
Live males	Wind tunnel (0.45 m long)	Move 25 cm toward source	Yes	Nation (1972)
Pheromonal components <sup>a</sup>	Screen cage (0.45 m per side)	Enter trap	Yes	Nation (1975)
Live males	Avocado grove	Capture in male-baited sticky traps <sup>b</sup>	Yes	Webb et al. (1983)
Pheromone extract	Field cage	Capture in sticky traps	Yes	Webb et al. (1983)
Filter paper treated with volatiles	Screen cage (0.20 m per side)	Aggregation near treated paper <sup>c</sup>	Yes	Sivinski and Heath (1988)
Filter paper treated with major pheromone components <sup>d</sup>	Screen cage (0.2 × 0.12 × 0.10 m)	Aggregation near treated paper <sup>c</sup>	Yes	Nation (1991)
Filter paper treated with minor pheromonal components <sup>e</sup>	Screen cage (0.2 × 0.12 × 0.10 m)	Aggregation near treated paper <sup>c</sup>	No <sup>f</sup>	Nation (1991)
Live males	Flight tunnel (0.3 × 0.3 × 1.22 m)	Enter trap	Yes	Heath et al. (1993)

<sup>a</sup>Later identified (Nation 1983) as (Z)-3-nonenol, (Z,Z)-3; 6-nonadienol; anastrephin; epianastrephin; attraction was observed for individual compounds as well as pairs and trios, with greatest attraction observed for a combination of all four components

<sup>b</sup>Released 13 m from any trap

<sup>c</sup>A so-called cage-top test, where control and treated papers were placed, one per quadrant, placed on top of cage, and distribution of females in four quadrants was measured

<sup>d</sup>Same four as in footnote a

<sup>e</sup>Bisabolene, ocimime, suspensolide

<sup>f</sup>No response was observed when these compounds tested individually, but each increased female response when added to blend containing the major components (listed in footnote a)

**Table 2.3** Published accounts for *Anastrepha ludens* regarding the behavioral response of females to the sex pheromones of conspecific males

Odor source	Bioassay Arena	Positive response		Reference
		Identified	Observed?	
Filter paper treated with pheromone extract <sup>a</sup>	Screen cage (0.3 m per side)	Aggregation near treated paper <sup>b</sup>	Yes <sup>c</sup>	Robacker and Hart (1984), Robacker et al. (1990), Moreno et al. (1991)
Filter paper treated with pheromonal components <sup>d</sup>	Screen cage (0.3 m per side)	Aggregation near treated paper <sup>b</sup>	Y <sup>e</sup>	Robacker and Hart (1985b)
Citrus leaf treated with pheromonal components <sup>f</sup>	Wind tunnel (2 × 0.7 × 1.3 m)	Arrivals to treated leaves	No <sup>g</sup>	Robacker (1988)
Citrus leaf treated with combinations of pheromonal components <sup>h</sup>	Wind tunnel (2 × 0.7 × 1.3 m)	Arrivals to treated leaves	Yes	Robacker (1988)
Citrus leaf treated With pheromone extract <sup>a</sup>	Wind tunnel (2 × 0.7 × 1.3 m)	Arrivals to treated leaves	Yes	Robacker (1988)
Citrus leaf treated with pheromone extract <sup>a</sup>	Screen cage (0.7 × 1.6 × 1.0 m)	Arrivals to treated leaves	Yes <sup>i</sup>	Robacker and Hart (1986)
Cigarette filter treated with pheromone extract <sup>a</sup>	Citrus grove	Capture in treated McPhail traps	Yes <sup>j</sup>	Robacker and Wolfenbarger (1988)
Filter paper treated with pheromone extract <sup>a</sup>	Hallway (30.0 × 2.5 × 2.0 m)	Upwind movement; flight <sup>k</sup>	Yes	Robacker and Moreno (1988)



Table 2.3 (continued)

Odor source	Bioassay Arena	Positive response		Reference
		Identified	Observed?	
Pheromone extract <sup>l</sup>	Screen cage (0.3 m per side)	Aggregation near treated paper <sup>b</sup>	Yes <sup>m</sup>	Robacker and Garcia (1990)
Live males	Flight tunnel (30 × 30 × 122 cm)	Enter trap	Yes	Heath et al. (1993)

<sup>a</sup>Obtained from filtering and concentrating extract obtained from grinding abdomens of adult males

<sup>b</sup>A so-called cage-top test, where control and treated papers were placed, one per quadrant, placed on top of cage, and distribution of females in four quadrants was measure

<sup>c</sup>Attraction much stronger for mature virgin females than immature or recently mated females

<sup>d</sup>Six components were tested individually and in various combinations: (Z)-3-nonenol, (Z,Z)-3,6-nonadienol, (R,R)-(+)-anastrephin, (S,S)-(-)-anastrephin, (R,R)-(+)-epianastrephin, (S,S)-(-)-epianastrephin

<sup>e</sup>Only three components (the two alcohols plus epianastrephin) elicited female responses individually. Both synergistic and inhibitory effects were reported among the 15 combinations of paired components

<sup>f</sup>The six components listed in footnote d were tested individually

<sup>g</sup>With a single exception: (Z,Z)-3,6-nonadienol attracted more females than control (untreated) leaves

<sup>h</sup>Three combinations involving pheromonal components listed in footnote d were tested: (Z)-3-nonenol + (S,S)-(-)-epianastrephin; (Z,Z)-3,6-nonadienol + (S,S)-(-)-epianastrephin; all 6 components

<sup>i</sup>Females did not distinguish between treated and control trees but within trees were more attracted to treated than control leaves

<sup>j</sup>Highest dose did not attract more females than control suggesting an overdose effect; male attraction also observed

<sup>k</sup>Females behavior monitored in screen cages placed at different distances from odor source, with upwind movement scored as the number of females on upwind versus downwind sides of cages

<sup>l</sup>Obtained from crushing whole males

<sup>m</sup>Host fruit odor inhibited attraction of mature virgin females

blank control traps (Santos Felix et al. 2009). A field trial on the attractiveness of a pheromonal blend likewise yielded negative results. In laboratory tests conducted in small cages, *A. suspensa* females responded to four major components of the male pheromone as well as various mixtures of these chemicals (Nation 1975; see also Robacker and Hart 1985b for similar findings for *A. ludens*). However, a synthetic blend of these same four components placed in the field failed to attract flies of either sex over a 5-day period in Florida (Nation 1989). The uneven performance of pheromone-baited traps in the field, coupled with data showing that host fruit odors are equally or more attractive to females than male odors alone (Robacker and Garcia 1990), has been an important constraint on further research on the development of pheromone-based traps for *Anastrepha*.

Third, the pheromones of different *Anastrepha* males are complex and contain multiple chemicals with different isomers (Heath et al. 2000). This complexity has several important implications. It appears, for example, that the component ratios

affect the attractiveness of the blend. Differences in the attractiveness of two dispensers to *A. ludens* females, for example, apparently reflected differential release of pheromone components, which resulted in the emission of abnormal component ratios for one of the dispensers (Robacker and Wolfenbarger 1988). In general, data support the conclusion that individual pheromonal components stimulate little behavioral response but instead function as an integrated unit to elicit behavior (Robacker 1988), and identifying the specific nature of this complex signal is seen as a daunting challenge. Moreover, the composition of male pheromone may vary with time of day (Tumlinson 1988; Nation 1990), social context (calling singly or in a group, Nation 1990), and food availability (Epsky and Heath 1993a), making it even more difficult to identify the particular blend most attractive to females. Analogously, variability in pheromone release rate (Epsky and Heath 1993b; Meza-Hernández et al. 2002) confounds identification of those rates that may be maximally attractive to females. In addition, the different components have different volatilities (Landolt and Averill 1999) and liabilities (Robacker et al. 2009b), which render production of synthetic pheromones difficult from a methodological perspective and imprecise from a biological one.

Finally, the importance of male pheromone to female mate searching remains uncertain, and it appears likely that a combination of visual, auditory, and olfactory cues may be involved. The pheromone appears to attract females to the vicinity of calling males but not to point sources (Robacker 1988), and after approach, females may rely on acoustic and/or visual signals to locate males (Webb et al. 1983; Sivinski and Calkins 1986). As with the complex pheromonal blend, the multifaceted nature of mate location appears to have lessened the impetus to develop pheromone-based traps for *Anastrepha*.

## 2.2 *Bactrocera* Pheromones

The genus *Bactrocera* consists of over 500 species distributed in the tropical and subtropical regions of Asia (Smith et al. 2003) and includes many serious and/or highly invasive polyphagous pest species, namely *B. correcta* (Bezzi) – guava fruit fly, *B. cucurbitae* (Coquillett) – melon fly, *B. carambolae* Drew & Hancock – carambola fruit fly, *B. dorsalis sensu stricto* (Hendel) – oriental fruit fly, *B. invadens* Drew, Tsuruta & White, *B. papayae* Drew & Hancock – Asian papaya fruit fly, *B. philippinensis* Drew & Hancock – Philippines fruit fly, *B. latifrons* (Hendel) – solanaceous fruit fly, *B. tryoni* (Froggatt) – Queensland fruit fly, *B. umbrosa* (Fabricius) – *Artocarpus* or jack-fruit fly, and *B. zonata* (Saunders) – peach fruit fly. Males of these species, with the exception of *B. cucurbitae* and *B. tryoni* (both attracted to cue-lure (CL)/raspberry ketone (RK)) and *B. latifrons* (not attracted to either CL/RK or methyl eugenol (ME)), are attracted to ME, a compound found in a wide diversity of plant species (Tan and Nishida 2012) and now known to be a pheromonal precursor. As discussed below, the strong attraction of males to ME has, to some degree, limited impetus to explore sex pheromones as a

trapping tool for *Bactrocera* species. Here, we summarize the chemistry of *Bactrocera* pheromones and note studies that have monitored male or female attraction to pheromonal emissions.

As true for most of the economically important tephritid species examined thus far, sexual signaling in *Bactrocera* typically involves the production and broadcast of sex pheromone by males (a behavior termed “calling”) while resting on vegetation and detection and subsequent mate searching by receptive females. Most accounts of male calling and mating derive from laboratory or field cage observations (e.g., Tychsen 1977; Ohinata et al. 1982; Arakaki et al. 1984; Kuba and Koyama 1985), and the few field studies conducted – all on *B. dorsalis*– indicate plasticity in that species’ mating system. Working in Hawaii, Shelly and Kaneshiro (1991) observed calling males and matings in the canopy of a single fruiting tree within a citrus orchard, suggestive of a lek mating system. In contrast, Stark (1995), also working in Hawaii, observed *B. dorsalis* females moving from papaya trees to non-host (*Panax*) trees in the late afternoon followed by males 30–60 min later. Although their incidence was not quantified, Stark (1995) observed matings on this nonhost plant. Finally, working in Thailand, Prokopy et al. (1996) released *B. dorsalis* within a non-fruiting orchard and experimentally added food, water, and host fruits to the trees. In this case, and in contrast to the aforementioned studies, all sexual behavior and all matings were recorded on trees with fruits and on the fruit itself, leading the authors to suggest that the importance of host fruits as foci for sexual activity may vary with microclimatic conditions. The behavioral variability described for *B. dorsalis*, along with the lack of field studies on *Bactrocera* species in general, serves as a cautionary prelude to the following discussion: little is known about the importance of male pheromones in sexual selection in the genus, and consequently evaluation of male pheromones as potential trap attractants is necessarily preliminary and inconclusive.

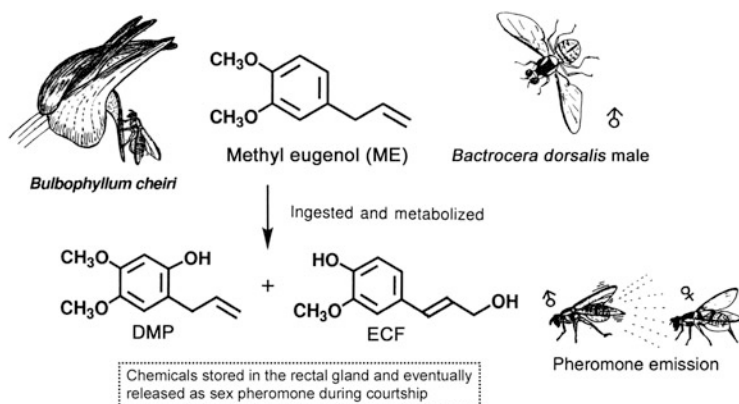
### 2.2.1 Sex Pheromone of *B. dorsalis* Complex Species

The *B. dorsalis* species complex comprises over 70 recognized species (White and Elson-Harris 1992), several of which, namely *B. dorsalis*, *B. invadens*, *B. papayae*, *B. philippinensis*, and *B. carambolae*, are serious agricultural pests. Recent molecular (Tan et al. 2011, 2013; Schutze et al. 2012; Krosch et al. 2013), morphological (Mahmood 1999, 2004; Schutze et al. 2012; Krosch et al. 2013), behavioral (i.e., mating compatibility; McInnis et al. 1999; Tan 2000, 2003; Wee and Tan 2005b; Schutze et al. 2013), and pheromone chemistry (Tan and Nishida 1996, 1998; Tan et al. 2011, 2013) data have raised doubts regarding the validity of species status for these sibling taxa (except *B. carambolae* – see below). Below, we retain the names as originally used but recognize that results obtained for one species may, if taxonomic synonymies are eventually recognized (Schutze et al. 2014), apply to other currently recognized species in the complex.

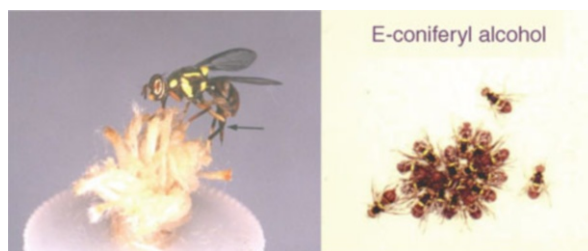
In the first published description on the pheromone chemistry of male *Bactrocera*, Ohinata et al. (1982) analyzed “smoke” produced by male *B. dorsalis* and found that

trisodium phosphate was the major component (90 %) with much smaller amounts of N-(2-methylbutyl)propanamide and heptacosane. Perkins et al. (1990a) examined an acetate extract of rectal glands of sexually mature male *B. dorsalis* from a colony maintained in Hawaii and detected the trimethyl ester of citric acid (a major component), the trimethyl ester of phosphoric acid, and dimethyl succinate along with methyl esters of fatty acids and two spiroacetals. The males sampled in this study had not fed on ME, and no biological activity was demonstrated for the compounds identified. However, Nishida et al. (1988a, b) and Tan and Nishida (1996) demonstrated that males of *B. dorsalis* and *B. papayae* transformed consumed synthetic ME to two major pheromonal components – *E*-coniferyl alcohol (ECF) and 2-allyl-4,5-dimethoxy phenol (DMP), with trace quantity of *Z*-3,4-dimethoxycinnamyl alcohol (detected in some males). Nishida et al. (1988a) also detected these compounds in wild *B. papayae* males, indicating the males had fed on ME-bearing plants in the field, and a later study (Tan et al. 2002) showed that *B. papayae* males that fed on an ME-bearing orchid flower contained ECF and DMP in the rectal gland (Fig. 2.2). In laboratory tests, males deprived of ME did not have ECF or DMP in the rectal gland. As an aside, *B. papayae* males visiting an orchid whose floral fragrance contained zingerone (a compound structurally similar to ME) were found to have zingerol in the rectal gland, suggesting a role in pheromone synthesis for this compound as well (Tan and Nishida 2000, 2007). More recently, Tan et al. (2011, 2013) found ECF and DMP in the rectal sac of ME-fed males of *B. invadens* and *B. philippinensis*. Males of *B. carambolae* differ from the aforementioned species in that they produce only ECF after ingesting ME (Tan and Nishida 1996; Wee and Tan 2005a). Moreover, the sex pheromone of *B. carambolae* contains larger amounts of endogenously produced compounds, including 6-oxo-1-nonanol (a major component that is also detected in a closely related sibling species, *Bactrocera occipitalis* (Bezzi) and a distant species, *B. umbrosa* (Perkins et al. 1990b)) and three minor components, *N*-3-methylbutyl acetamide, ethyl benzoate, and 1,6-nonanediol (Wee and Tan 2005a).

Since Nishida et al.'s reporting, a number of studies have demonstrated that ME consumption increases male mating success in several species in the *B. dorsalis* complex (Shelly and Dewire 1994; Shelly et al. 1996; Shelly 2010a; Tan and Nishida 1996, 1998; Wee et al. 2007; Orankanok et al. 2013; Obra and Resilva 2013). However, the role of pheromone composition in determining this outcome is not known with certainty. In laboratory cage assays, Kobayashi et al. (1978) demonstrated attraction of *B. dorsalis* females to both live males and male rectal gland extract even when males were not previously fed ME. Wee and Tan (2005a) likewise reported zigzag anemotaxis by *B. carambolae* females to live males and endogenously produced rectal gland substances. Thus, the breakdown products of ME are not necessary to elicit female response. Nonetheless, using a wind tunnel or laboratory cages, several studies on *B. dorsalis* complex species (Shelly and Dewire 1994; Hee and Tan 1998; Wee et al. 2007) have reported greater female attraction to males that had previously fed on ME than to unfed males, and Hee and Tan (1998) and Khoo et al. (2000) showed female attraction to ECF and DMP individually (with greater attraction to ECF than DMP in these tests) and in combination (Fig. 2.3). Importantly, greater female response to ME-fed males has been



**Fig. 2.2** Acquisition and biotransformation of methyl eugenol to sex pheromone by *Bactrocera dorsalis* males



**Fig. 2.3** *Bactrocera dorsalis* females and males attracted to E-coniferyl alcohol. A An attracted female with ovipositor extruded (arrow), B Aggregation of males and an attracted female with extruded ovipositor at bottom left

documented, not only using synthetic ME, but also after male feeding on natural floral (Shelly 2000a, 2001a) or fruit (Shelly and Edu 2007) sources of ME. Several studies (Hee and Tan 1998; Wee and Tan 2005a; Wee et al. 2007) have documented maximum female attraction to male sex pheromone at dusk, the time of peak sexual activity in *B. dorsalis* species complex.

To our knowledge, only two studies have examined the long-range attractiveness of male pheromone to females in the field. In a study examining female attraction to groups (leks) of varying size, Shelly (2001b) placed *B. dorsalis* males (none of which had fed on ME) in screen-covered cups, which were in turn placed on trees situated in a circular (10 m radius) array around a central female release point. Approximately 10 % of released females were sighted near male-containing cups over all groups. In a second study also conducted on *B. dorsalis* in Hawaii, Shelly (2001c) performed two experiments in which groups of (i) ME-fed or ME-deprived males or (ii) flower-fed or flower deprived males (where the flower used

[puakenikeni, *Fagraea berteriana* A. Gray ex Benth] was known to contain ME-like compounds [Nishida et al. 1997]) were placed in cups suspended in host trees (one male type [i.e., fed or non-fed] per tree) situated in a circle (12 m radius), and females were released from the center. Compared to non-fed males, both ME- and flower-fed males were found to signal more frequently and attract greater total numbers of females as well as greater numbers of females per signaling male. These studies were not designed to test explicitly the function of pheromone signaling (since blank controls were not run in either study), but they nevertheless hint at long-range attraction mediated by male pheromone and thus suggest the potential for male pheromone as a trap bait for species in the *B. dorsalis* complex.

Data on pheromonally-mediated male-male attraction are inconsistent. In laboratory cages, *B. dorsalis* males showed no attraction to conspecific males (non-ME-fed, Kobayashi et al. 1978). In contrast, Nishida et al. (1988b) found that traps baited with DMP captured as many wild males as traps baited with ME. In wind tunnel tests, Hee and Tan (1998) found that *B. papayae* males were attracted to both ME-fed and control (unfed) conspecific males but showed greater attraction to the treated males. Also using a wind tunnel, Wee et al. (2007) found non-ME-fed males of *B. carambolae* were attracted to ME-fed conspecific males at a much higher level than observed in the converse situation (i.e., ME-fed males responding to non-ME-fed males). Moreover, field cage observations showed that unfed males aggregated around ME-fed males and fed on anal secretions of ME-fed males (see also Tan and Nishida 1996). Results for *B. papayae* and *B. carambolae* thus suggest that male sex pheromone may also serve as an aggregation pheromone. However, this function implies an evolutionary advantage to aggregation per se (e.g., increased mating success), whereas the possibility remains that male-male attraction simply represents a special case of male attraction to ME (or ME-like compounds), where the ME source is a male rather than a plant.

## 2.2.2 Presumed Sex Pheromone of Two Sibling Species of *B. zonata* Complex

ME also acts as a pheromone precursor for both *B. correcta* and *B. zonata*. In *B. zonata*, it is transformed to two male sex pheromonal components, DMP and Z-coniferyl alcohol (ZCF), although final confirmation awaits tests of biological activity on female response (Tan et al. 2011). In *B. correcta*, however, ME is converted to ZCF and (Z)-3,4-dimethoxycinnamyl alcohol (ZDMC) (Tokushima et al. 2010). Furthermore, wild *B. correcta* males also accumulate large quantities of sesquiterpene hydrocarbons, namely  $\beta$ -caryophyllene,  $\alpha$ -humulene, and alloaromadendrene, in the rectal gland in addition to, or instead of, ZCF and ZDMC (Tokushima et al. 2010). The distinct difference in sex pheromonal profiles, albeit having a common ZCF component, between the two sibling species, most likely, plays an important role in maintaining reproductive isolation.

Interestingly, recent comparative field tests conducted in Thailand during 2012–2013 and based on average flies/trap/day using a similar lure dosage per trap

showed that  $\beta$ -caryophyllene caught on average 7 (range 3–16) times more *B. correcta* wild males than ME during the first 3 days of trapping (Tan, Chinvinijkul, Wee & Nishida, unpublished data). This is the first case of a lure being more attractive than the very potent ME to a ME-sensitive *Bactrocera* species. Therefore, further behavioral/ecological studies, especially related to the role of the sesquiterpene and its possible replacement of ME in the trapping of *B. correcta*, are warranted.

### 2.2.3 Sex Pheromone of *B. umbrosa*

Rectal gland extracts showed the presence of (*E*)- and (*Z*)-2-methyl-1,6-dioxaspiro [4.5]decanes, 3-methylbutanol, 1,7-dioxaspiro [5.5]undecane, and 6-oxononan-ol (Perkins et al. 1990b). In addition, some unidentified ME metabolites (identities currently being evaluated) were detected in the rectal gland after consumption of ME by males (Nishida and Tan, unpublished data). In Malaysia, *B. umbrosa* and *B. papayae* are endemic and sympatric species as well as serious pests of jackfruit, *Artocarpus heterophyllus* Lam., but they do not interbreed. Apparent reproductive isolation was observed between the two species even when both males and females of both the species were kept together in a cage for approximately 2 months; intraspecific but no interspecific matings were observed (Tan, unpublished observations).

### 2.2.4 Sex Pheromone of *B. cucurbitae* and *B. tryoni*

Males of these species are attracted to RK/CL. Rectal gland secretions of *B. cucurbitae* contain *N*-3-methylbutyl acetamide, two spiroacetals, and three pyrazines (Baker et al. 1982a; Baker and Bacon 1985). Later, ethyl 4-hydroxybenzoate (a major component) and propyl 4-hydroxybenzoate (a minor component) were also detected in the rectal gland of the melon fly (Perkins et al. 1990b). Nishida et al. (1990) showed that sexually mature male melon flies produce, endogenously in the rectal gland, relatively small quantities of *N*-3-methylbutyl acetamide, methoxy-acetamide, methyl, ethyl, and propyl 4-hydroxybenzoate, and a large quantity of 1,3-nonanediol, which was not detected in the previous studies. The amounts of 1,3-nonanediol and ethyl 4-hydroxybenzoate stored in the rectal gland increased with age, starting 2 weeks after adult eclosion, thus coinciding with attainment of sexual maturity (Nishida et al. 1990). Additionally, at sexual maturity males of *B. cucurbitae* consume and sequester RK from anthropogenic (Nishida et al. 1990) and natural (Nishida et al. 1993; Tan and Nishida 2005) sources into the rectal gland. As noted above for *B. papayae*, males of *B. cucurbitae* are also attracted to and feed on zingerone, an orchid floral volatile, and store it unmodified in the rectal gland (Tan and Nishida 2000).

Males of *B. tryoni* produce endogenously six amides as major sex pheromonal components, and three of the six, namely, *N*-3-methylbutyl acetamide (MBA), *N*-3-methylbutyl propanamide (MBP), and *N*-3-methylbutyl-2-methylpropanamide,



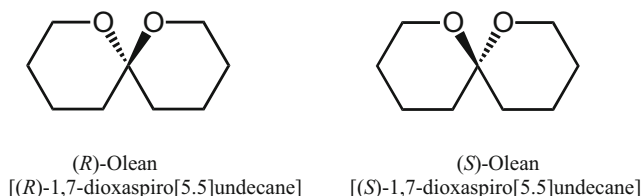
are frequently detected in the rectal gland (Bellás and Fletcher 1979). Furthermore, MBA and MBP increase significantly from 14 to 17 day-old males corresponding with attaining sexual maturity (Tan and Nishida 1995). This suggests that the two chemicals may act as close range sex pheromone. Males consume plant-borne RK or RK from spontaneous hydrolysis of CL and sequester it in the rectal gland as a major pheromonal component (Tan and Nishida 1995).

Analogous to the *B. dorsalis* complex, ingestion of CL/RK has been shown to enhance male mating success, though the effect appears short-lasting both for *B. cucurbitae* (1 day after feeding, Shelly and Villalobos 1995; Shelly 2000b) and *B. tryoni* (1–3 days after feeding, Kumaran et al. 2013). More recently, *B. tryoni* males fed zingerone were also found to have a mating advantage over control males deprived this compound (Kumaran et al. 2013). The role of the sex pheromone in influencing male mating success is unknown. Kobayashi et al. (1978) found that *B. cucurbitae* females were attracted to male rectal glands as well as live males (in neither case were males fed CL/RK) but that the attraction was far weaker than that observed for *B. dorsalis* females to conspecific males. In wind tunnel trials, Khoo and Tan (2000) demonstrated that CL-fed and zingerone-fed males of *B. cucurbitae* attracted more females compared to males deprived these compounds, which strongly suggests a sex pheromonal role for these exogenous phenylbutanoids. To our knowledge, there are no laboratory or field data available investigating the effect of the male sex pheromone on female attraction or male mating success in *B. tryoni*.

### 2.2.5 Sex Pheromone of *Bactrocera oleae*

*Bactrocera oleae* (Rossi) [formerly *Dacus oleae* (Gmelin)], the olive fruit fly, unlike the other major pest *Bactrocera* species mentioned above, is a monophagous pest species. Additionally, the species differs from other *Bactrocera* in that the *B. oleae* females attract males for mating and not vice versa (Haniotakis 1974; but see below). Baker et al. (1980) identified the major component of the female sex pheromone as (1,7-dioxaspiro[5.5]undecane (also known as olean; as noted above, this compound was also identified from the pheromone of *B. umbrosa*). Additional studies (Mazomenos and Haniotakis 1981) confirmed this finding and also identified three minor components, o-pinene, n-nonanal, and ethyl dodecanoate, in the female pheromone (see also Baker et al. 1982b, who identified two hydroxyspiroacetals from *B. oleae* females). Other components of the female sex pheromone were reported (Gariboldi et al. 1982), but their isolation and biological activity (tested with synthetic products) was not corroborated (Jones et al. 1983; Mazomenos 1989). Interestingly, olean was also isolated from the rectal gland of male *B. oleae* along with other components (Mazomenos and Pomonis 1983). Canale et al. (2012) reported that, among males, olean production is greatest among young males (5–8 days old) and then ceases by 11 day of age. Also, in a recent finding, Carpita et al. (2012) identified (Z)-9-tricosene from male rectal gland extracts and reported female attraction to this compound in synthetic form.





**Fig. 2.4** Stereo enantiomers of (*R*)- and (*S*)-olean found in *B. oleae* sex pheromone

Several studies (Haniotakis 1974; Mazomenos and Haniotakis 1981, 1985) have demonstrated male attraction to natural or synthetic components or whole blends of the female pheromone in *B. oleae*. Laboratory and field experiments demonstrated that olean was more attractive than the remaining three components but that the combination of all four components was more attractive than olean alone. More detailed chemical analysis (Haniotakis et al. 1986a) revealed that olean exists as (*R*) and (*S*) mirror (stereo) image enantiomers, (*R*)-olean and (*S*)-olean (Fig. 2.4) and that (i) males are more strongly attracted to (*R*)-(–)-oleanthan(*S*)-(+)-olean, (ii) the converse was true for females, and (iii) overall, males showed greater attraction to response to the compound than did females. Haniotakis et al. (1986a) suggest olean may serve an aggregation or aphrodisiac function for females. Relative to the strong evidence gathered for male attraction to the female sex pheromone, data regarding female attraction to male olfactory signals are less conclusive. Mazomenos and Pomonis (1983) reported negligible female response in laboratory tests to extracts of rectal glands of mature males. More recently, however, Mavraganis et al. (2010) demonstrated that whole body extracts of *B. oleae* males were highly attractive to females and suggest that the previous negative results may have reflected low pheromone concentrations in the rectal gland extracts compared to those of whole body. Benelli et al. (2013) found that young males, which, as noted above, produce olean at higher levels than old males, did not have a mating advantage over older individuals.

In contrast to the other economically important species discussed here, several studies have demonstrated the usefulness of olean in baiting traps. In general, because olean is primarily a male attractant, the most effective traps appear to be those that combine the pheromone with ammonium or some other food bait that targets females (Haniotakis and Vassiliou-Waite 1987; Broumas and Haniotakis 1994). Traps baited with this combination have been used both in detection (Rice et al. 2003; Yokoyama et al. 2006) and in mass-trapping efforts to lower olive infestation (Haniotakis et al. 1986b, 1991; Iannotta et al. 1994; Petacchi et al. 2003; Noce et al. 2009; see also Navarro-Llopis and Vacas, Chap. 15, this volume).

### 2.2.6 Synthesis

Because males of many economically important *Bactrocera* species are strongly attracted to male lures (see below), the development of pheromone-based trapping for this genus would target females primarily. The important finding that ME and CL/RK are used in pheromone synthesis and that their incorporation in this process enhances the attractiveness of the male olfactory signal could facilitate the production of effective pheromone baits. Nonetheless, many of the obstacles noted above for *Anastrepha* apply to *Bactrocera* as well, namely the lack of data on (i) the long-range attractiveness of the male pheromone, (ii) the optimal blend (relative amounts) and release rate of pheromonal components that produce maximal attractiveness, and (iii) the importance of olfactory signals relative to other modalities (i.e., visual, acoustic) in the mating behavior of *Bactrocera* species

## 2.3 *Ceratitis* Pheromones

The genus *Ceratitis* contains approximately 80 species, most of which are found in tropical Africa, although *C. rosa* Karsch (Natal fruit fly) has invaded Mauritius and Réunion and *C. capitata* (Wiedemann) (Mediterranean fruit fly or medfly) has spread globally (South and Central America, Western Australia, and Hawaii) (De Meyer 2000). The medfly is, of course, one of the most harmful agricultural pests worldwide, with females ovipositing in soft fruits of more than 300 plant species (Liquidó et al. 1990). Other major economic pests in the genus include *C. rosa*, *C. cosyra* (Walker) – mango fruit fly, and *C. catovirii* Guérin-Méneville (White and Elson-Harris 1992). Because of its economic importance, the medfly has been studied far more intensively than its congeners, and this review will necessarily focus on this species.

Féron (1959, 1962) provided the first detailed description of calling behavior in *C. capitata* males, which he associated with the emission of volatiles attractive to females. While the notion of male-produced olfactory stimuli had been proposed decades earlier (Martelli 1910; Back and Pemberton 1918, both cited in Jones 1989), Féron supplied empirical evidence by reporting female attraction to a cotton wick previously exposed to calling males. Quilici et al. (2002) and Briceño et al. (2005) report similar pheromone-calling behavior in *C. rosa* and *C. catovirii*, but data showing female attraction to calling males are not yet available for these species. For the medfly, Ohinata et al. (1977) and Nakagawa et al. (1981a) provided the first quantitative demonstration of the long-range, female attraction to calling male in the field by recording female captures in male-baited traps. Female attraction to live, calling medfly males (or their odor) was reported in further laboratory (Landolt et al. 1992a; Jang 1995; Jang and Light 1996; Jang et al. 1994, 1998) and field (Shelly 2000c) studies. The importance of olfaction to females has been demonstrated conclusively via antennal ablation: in existing studies, females with

antennae removed either mated not at all (Nakagawa et al. 1973; Levinson et al. 1987) or at very low levels (Shelly et al. 2007).

Research aimed at characterizing the chemical composition of the male sex pheromone in *C. capitata* and identifying the biologically active components was undertaken even before female attraction to calling males was demonstrated in the field. Jacobson et al. (1973) identified two putative pheromonal components – methyl (*E*)-6-nonenoate and (*E*)-6-nonen-1-ol – and indicated that females were attracted to both compounds in assays performed in small cages. Ohinata et al. (1977, 1979) identified the same two components as well as 15 carboxylic acids, which were presumed to ‘activate’ the two main components. However, contrary to Jacobson et al. (1973), various blends of these different chemicals were found to attract males but not females. Delrio and Ortu (1987, cited in Millar 1995) likewise reported no female attraction to methyl (*E*)-6-nonenoate. Jacobson and Ohinata (1980) also reported (–)- $\beta$ -fenchol in the medfly sex pheromone, but subsequent analyses failed to detect this compound.

In fact, it appears that, due to inadequate analytical methods, initial efforts to identify pheromonal components led to inaccurate results, which could not be confirmed by later studies. Despite the potential usefulness of pheromone-based lures in medfly surveillance programs, relatively few studies have further investigated pheromonal composition and/or the role of particular components as female attractants. Baker et al. (1985) identified nine components in male medfly emissions, with the three most abundant being ethyl (*E*)-3-octenoate, geranyl acetate, and (*E*, *E*)- $\alpha$ -farnesene. They further proposed that another component, 3,4-dihydro-2-*H*-pyrrole (1-pyrroline), functioned as the key attractive element to females (although no data on its purported biological activity were provided). In a follow-up study, Baker et al. (1990) tested the attractiveness of four compounds (linalool, two pyrazines, and geranyl acetate) in field trials in Mexico. Both individually and in various blends, these chemicals attracted both sexes of *C. capitata*, although the olfactory stimuli used bore little resemblance to the emissions of calling males.

More thorough chemical analyses (Jang et al. 1989a; Flath et al. 1993) confirmed the presence of the nine components reported by Baker et al. (1985), with one exception, and revealed a pheromonal complexity far greater than previously documented. Jang et al. (1989a) identified a total of 56 compounds from the odor of calling males, and Flath et al. (1993) identified four additional compounds, thus revealing that the sex pheromone of *C. capitata* males consists of approximately 60 different compounds. Jang et al. (1989b) established four abundance categories for the pheromonal constituents, with five considered major components (ethyl acetate, 1-pyrroline, ethyl (*E*)-3-octenoate, geranyl acetate, and (*E,E*)- $\alpha$ -farnesene). Based on electroantennogram (EAG) recordings, ethyl acetate, 1-pyrroline, and (*E*, *E*)- $\alpha$ -farnesene elicited low EAG responses (relative to a standard), geranyl acetate elicited a moderate response, and ethyl (*E*)-3-octenoate elicited a high response. Overall, the sexes displayed similar EAG responses to the different pheromonal components. Additional studies (Casaña-Giner and Primo-Millo 1999; Gonçalves et al. 2006) have identified additional components from the volatiles of calling

*C. capitata* males, and Cossé et al. (1995) confirmed strong female EAG responses to some of the previously identified compounds of the male pheromone.

Since Jang et al.'s (1989b) seminal paper, few studies have examined behavioral responses to the sex pheromone of *C. capitata* males. These investigations have employed simplified blends, including only the major components or a subset thereof, owing to (i) the difficulty of creating close mimics to the naturally complex male odor and (ii) the assumption that only a small portion of the pheromonal chemicals identified actually have biological activity (Landolt et al. 1992a). Thus, working in a coffee field in Guatemala, Heath et al. (1991) demonstrated attraction of medfly females to a synthetic blend containing three of the major components (ethyl (*E*)-3-octenoate, geranyl acetate, and (*E*, *E*)- $\alpha$ -farnesene). In two testing periods (lasting 6 and 8 days, respectively), 259 and 368 wild females, respectively, were captured in traps baited with the synthetic blend. However, the effectiveness of the blend as a trap-bait, could not be ascertained, because (i) no estimates of the size of the wild population were made and (ii) no traps baited with live males were operated, thus precluding assessment of the relative competitiveness of the simplified blend. Working with the same 3-component blend, Landolt et al. (1992a) reported an oriented response (i.e., upwind movement coupled with course-correcting, zigzagging flight) of female medflies to the stimulus in a wind tunnel. However, only a small proportion (3 %) of the females actually contacted the odor source, a level not significantly different from the contact rate observed in the absence of an olfactory stimulus. Jang et al. (1994) studied female response to live males, each of the five major components, and a mixture of these five compounds in a wind tunnel. Although females showed greatest attraction to live males, the five component blend was more attractive than the individual compounds and appeared to elicit a much greater female response than the 3-component blend used by Landolt et al. (1992a). While the above studies reveal the attractiveness of simple pheromone blends, Casaña-Giner et al. (2001) reported very low catch of female medflies in traps baited with a 6-component mixture and questioned the long-range effectiveness of male pheromone-baited traps.

Adopting a different approach, Mavraganis et al. (2008) obtained whole body extracts of medfly males and monitored female attraction to complete extracts of laboratory vs. wild males as well as the major components of the extracts either individually or in different combinations. Interestingly, females showed greater attraction in laboratory assays to the extracts from wild males than laboratory males. Samples from wild males contained larger amounts of the compound  $\alpha$ -copaene than those from laboratory males, and this compound was found to have greatest attractancy to females in comparisons of the individual components. Field trials further revealed that total male extracts as well as synthetic blends of major components were highly attractive to wild females, the majority of which were virgin. Thus, in contrast to other studies (Heath et al. 1991; Casaña-Giner et al. 2001), the total extracts and blends tested by Mavraganis et al. (2008) appear to be highly attractive to female medflies and clearly merit additional field testing.

The chemical complexity of the male sex pheromone has, it appears, discouraged efforts to develop or improve the attractiveness of synthetic sexual lures to

medfly females. Not only might some trace components await identification, but knowledge of the relative amounts of the constituent compounds is imprecise. In addition, the blend containing the five major components was far less attractive to females than the odor emitted by live males, suggesting that simplified formulations will not be able to compete against calling males in the wild (Jang et al. 1994). Similarly, whole body extracts were far more attractive to wild females than simplified blends with relatively few components (Mavraganis et al. 2008). In this regard, Howse and Knapp (1996), noting similarity in the volatiles released by host fruit, citrus in particular, and calling male medflies, suggest that competition with host fruit odors may further limit the effectiveness of male pheromonal traps in orchards (but see Mavraganis et al. 2008). In addition to the chemical composition, the importance of release rate in the development of a potent pheromone-based lure is uncertain as relevant data are inconsistent. In particular, results from Ohinata et al. (1977) and Jang et al. (1994) suggest that the amount of male emission does not have a marked effect on its attractiveness, whereas Heath et al. (1991) found that an intermediate release rate resulted in higher female captures than lower or higher rates. Finally, while the identification of a female lure for *Ceratitis* species is recognized as a worthy research objective, the wide usage of a male-lure (trimedlure) may lessen the impetus to achieve this goal.

## 2.4 *Dacus Pheromones*

To date, little effort has been devoted to identifying possible sex or aggregation pheromones of *Dacus* species. This lack of interest is probably due to a combination of several factors, such as insufficient funding, the small number of pest species in the genus, which are generally moderate pests relative to highly invasive *Bactrocera* species, and the availability of male lures for surveillance purposes.

## 2.5 *Rhagoletis Pheromones*

Male sex pheromones have been demonstrated in several *Rhagoletis* species. Using caged host trees, Prokopy (1975) and Katsoyannos (1976) furnished evidence for a male sex pheromone in *R. pomonella* (Walsh), the apple maggot fly, and *R. cerasi* Loew, the cherry fruit fly, respectively, by reporting attraction of mature, virgin females to cages of live males as well as to empty cages that had housed males. No male-to-female or male-to-male attraction was observed in either of these species. Also, males of these two species did not display any behavior typically associated with pheromone release in other tephritids (e.g., wing fanning), and consequently the manner of pheromone release was unclear. Additional tests on *R. cerasi* further showed that immature and mated females do not respond to male pheromone and that mature virgin females responded to an extract obtained from whole body

preparations of mature males (Katsoyannos 1982). In addition to the male pheromone, several studies (Prokopy and Bush 1972; Katsoyannos 1975) have shown that female host marking pheromone acts as a male arrestant, possibly to increase the frequency of intersexual encounters. Research on sexually-oriented, pheromonal communication has not continued beyond these few studies, and the potential use of male pheromones in *Rhagoletis* trapping or detection has not been investigated.

## 2.6 *Toxotrypana curvicauda* Pheromone

Landolt and Hendrichs (1983) reported “puffing” of the pleural areas of abdomen in male *Toxotrypana curvicauda* Gerstaecker, the papaya fruit fly, a behavior associated with pheromone release in other tephritids, and Landolt et al. (1985) later demonstrated female attraction to male pheromone in laboratory assays, including wind tunnel trials. The pheromone has a single chemical component, which was identified as 2-methyl-6-vinylpyrazine (Chuman et al. 1987). Additional observations (Landolt and Heath 1988; Landolt et al. 1991) showed that the pheromone attracts, not only virgin females, but also mated females and males and that female response is increased when green papaya fruit or an extract thereof was presented with the male pheromone (Landolt et al. 1992b).

The male pheromone with sticky-coated green spheres was tested in Florida and resulted in high captures of *T. curvicauda* females (Landolt et al. 1988; Landolt and Heath 1990). To facilitate field use, Heath et al. (1996) developed a membrane-based formulation system and showed that release rates, which were dependent on the amount of pheromone loaded into the system, were relatively constant over trials lasting 23 days. They also showed that green opaque cylindrical traps yielded higher captures than spherical traps. In field tests conducted in a papaya orchard in Guatemala, greater numbers of females were, as expected, captured in pheromone-baited than blank cylinders. Surprisingly, however, similar tests run in a Mexican papaya plantation detected no influence of pheromone presence/absence on female captures in green cylindrical traps. Reasons for this discrepancy are unknown, and additional field trials are required to evaluate the efficacy of pheromone-baited traps in detecting and/or suppressing populations of *T. curvicauda*.

## 3 Male Lures

There are two types of male lures: anthropogenic (e.g., CL, trimedlure [TML], fluorinated methyl eugenol analogs, raspberry ketone-formate (RKF)) and plant-borne (e.g.,  $\alpha$ -copaene, ME, RK, and zingerone). For certain species, male lures are relatively cheap to synthesize due to the simplicity of the chemical structures, which are often not stereoisomeric. In addition, they are very potent attractants in

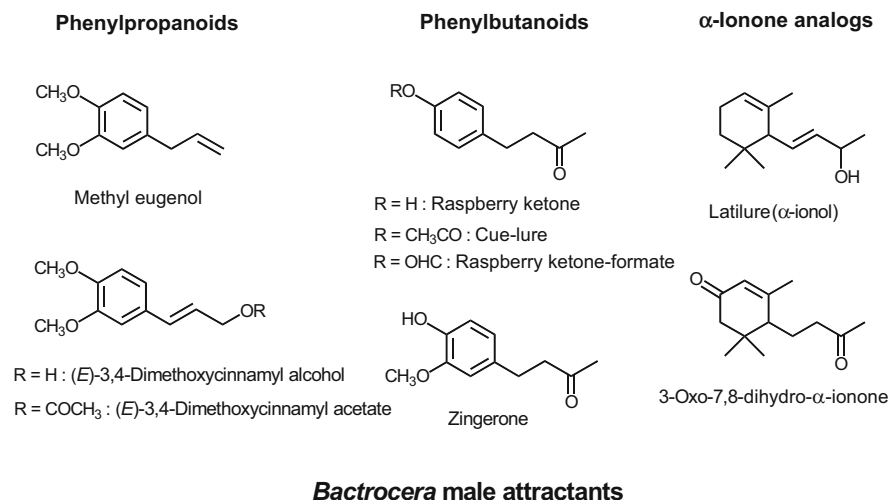
most cases and thus appear a more robust option for trapping programs than the development of the male sex pheromone as baits. As a result, they are frequently used as baits in trapping for surveys and detection of invasive species, delimitation of an infestation, and control or eradication via the male annihilation technique. Because of their importance in trapping, numerous reviews (Chambers 1977; Cunningham 1989; Metcalf 1990; Millar 1995; Jang and Light 1996; Sivinski and Calkins 1986; Oliver et al. 2004; Vargas et al. 2010a) of male lures already exist, and rather than re-hashing information, our present aim was to address a few selected topics.

### 3.1 *Anastrepha*

At present, there are no identified male lures for any *Anastrepha* species. This fact does not reflect a lack of effort. Approximately 8,000 compounds were screened as possible attractants for *A. ludens* (Chambers 1977) and 1,320 compounds were tested for *A. suspensa* (Burditt and McGovern 1979; cited in Cunningham 1989). Despite intense screening, no male attractant was identified in both the investigations.

### 3.2 *Bactrocera*

While most species in the genus remain untested, *Bactrocera* has been broadly categorized into three groups of species based on male response to two very potent attractants (Drew 1974; Hardy 1979; Drew and Hooper 1981; White and Elson-Harris 1992; Fig. 2.5). Nearly 200 species have been identified as CL/RK responders and 81 species as ME-responders (IAEA 2003). A third group includes approximately 15 species (limited to an Australian survey) that do not respond to either CL/RK or ME as evidenced by their absence in traps from areas where species were known to be present (Drew and Hooper 1981). No species has been identified that responds to both CL/RK and ME. Response to these compounds correlates with morphologically-based taxonomic classification (Drew 1974; Drew and Hooper 1981), and several authors (Metcalf et al. 1979, 1981, 1983, 1986; Metcalf 1990; Raghu 2004) suggest that the existence of distinct CL/RK- and ME-responding species groups reflects evolutionary divergence from a common saprophytic relationship with rotting fruits. Broadly, coevolution between plants, specifically the appearance of novel metabolic pathways and the subsequent integration of those products into essential oils, and dacine tephritids, specifically adaptation of olfactory receptors to chemically diversified plant essential oils, is considered to underlie the present-day CL/RK or ME distinction in species responsiveness.



**Fig. 2.5** Chemical structures of lures for *Bactrocera* males

### 3.2.1 Methyl Eugenol

ME is widely recognized as the most powerful male lure currently in use for detection, control, and eradication of any pestiferous tephritid species. The chemical occurs naturally in more than 450 plant species representing 80 families spanning 38 different orders in varying amounts, from a trace quantity to over 90 %, in essential oils extracted from flowers, leaves, roots, stems, or whole plant extracts (see review by Tan and Nishida 2012). It was first discovered as a fruit fly attractant by Howlett (1912, 1915), who observed males of *B. dorsalis* and *B. zonata* responding to ME-containing citronella grass, *Cymbopogon nardus* (L.) Rendle. Steiner (1952) further documented the strong attraction of *B. dorsalis* male to ME and noted their vigorous feeding on the chemical. Metcalf et al. (1975) exposed *B. dorsalis* males to ME as well as 34 analogs and found that ME elicited the greatest feeding response. The powerful attraction of this lure was further demonstrated by (a) a simple test in which approximately 1 nanogram ( $10^{-9}$  g) of ME spotted on a silica gel TLC plate placed in the field attracted *B. papayae* males, which readily consumed the minute amount of attractant (Tan and Nishida 2000); and (b) trap placement for trapping *B. dorsalis* and *B. umbrosa* hung at different heights – ground level (0.3–0.5 m), below (1.5–2 m), middle (5–7 m) and above (10–12 m) tree canopy – using traps baited with 0.5 ml ME/trap and set up using a  $4 \times 4$  Latin square design in a 5 ha Penang village (a 4-day experiment conducted in two fruiting seasons), showed no significant difference in daily fly captured (flies/trap/day) (Tan 1984).

Because of its potency, ME-baited traps have been used in a variety of ways including (i) detection and surveillance of invasive species (Drew et al. 2005; McQuate et al. 2008a; Jessup et al. 2007), (ii) quarantine surveys and delimitation



(Allwood 2000; Sookar et al. 2008; OEPP/EPPO 2010), (iii) suppression and eradication (Steiner et al. 1965; Hancock et al. 2000; Hsu et al. 2010; Vargas et al. 2008), and (iv) ecological studies, including faunal surveys (Tan and Lee 1982), population dynamics and phenology (Tan 1985; Tan and Serit 1988, 1994; Ye and Liu 2005; Han et al. 2011; Kamala Jayanthi and Verghese 2011), adult survivorship (Tan and Jaal 1986), and dispersal (Iwahashi 1972; Tan and Serit 1988; Chen et al. 2006; Froerer et al. 2010). As noted above, existing reviews address many of these topics (see, in particular, Vargas et al. 2010a, b), and here we briefly address three topics, namely (i) the effect of ME feeding on subsequent attraction to ME-baited traps, (ii) age-dependent variation in response to ME, and (iii) interspecific differences in attraction to ME.

There is some evidence that feeding on ME reduces the likelihood of future ME feeding. Males of *B. dorsalis* given access to ME for 0.5–24 h prior to release were captured in ME-baited traps at much lower rates (1–4 %) than control, unfed males (22 %; Shelly 1994). In a second test, *B. dorsalis* males exposed to ME for 2 h and then held for 7–35 days prior to release were also captured at lower rates (11–18 %) than control, unfed males (34 %). Other studies, however, indicate that these results may be an artifact of the experimental design. When treated males were provided ME-bearing flowers instead of commercial ME, there was no difference in capture rate in ME-baited traps between floral-exposed and control males, indicating that the unnaturally high purity and availability of synthetic ME in the previous study may have accounted for the diminished capture rate of treated males (Shelly 2000d). Moreover, dissection of wild males of several *Bactrocera* species attracted to ME-baited traps (designed to prevent feeding) revealed the presence of ME metabolites in the rectal gland of nearly all individuals. Wee and Tan (2001) extracted the rectal gland from 76 wild *B. papayae* males in Penang, Malaysia, and found that all individuals possessed some ME-metabolites, ranging from trace quantities to approximately 103 µg per male. Similarly, Tan et al. (2011) reported that nearly all wild-caught *B. invadens* and *B. zonata* males dissected contained at least trace amounts of ME metabolites (maximum observed: 10 µg per gland for both species). Interestingly, after ad libitum feeding on synthetic ME, laboratory measurements regarding accumulation of ME breakdown products showed that males of *B. papayae*, *B. invadens*, and *B. zonata* sequester, on average, 20, 170, and 25 µg/gland 1–2 days after feeding (Wee and Tan 2001; Tan et al. 2011; see also Tokushima et al. 2010 for comparable data on *B. correcta*). As the quantity of ME derivatives detected in wild males attracted to ME traps was often less than these averages, it appears that, in general, males are unable to “tank up” at any one ME source and therefore must visit multiple ME sources to gather a sufficient amount of the chemical, a result consistent with the aforementioned result regarding the high capture rate at ME traps of *B. dorsalis* males experimentally fed ME-bearing flowers in the laboratory (Shelly 2000d).

Interestingly, when *B. papayae* males were exposed to commercial ME (isolated to prevent feeding) for various time periods within a trap, they became habituated after an hour and would not respond to subsequent ME exposure for a week (unpublished data, discussed in Tan et al. 2002). Because of this, the trapped

males were removed from ME-traps every 0.5 h to avoid possible habituation to ME when using the mark-release-recapture technique to estimate population size (Tan 1985). While access to commercial ME of high purity may induce habituation depending on the length of exposure and underestimate the incidence of repeat ME feeding in nature, it nonetheless suggests a means of improving the effectiveness of control programs against *B. dorsalis* (or related species), namely the simultaneous application of the male annihilation and sterile insect techniques. Providing sterile males access to ME before release may both increase their mating competitiveness (McInnis et al. 2011) and reduce their attraction to insecticidal-laden ME sources deployed for male annihilation. Barclay and Hendrichs (Chap. 11, this volume) examine the improved control afforded by this strategy through a modeling approach.

As another caveat, to the extent that male responsiveness to ME has a heritable component, it seems possible that prolonged application of a male annihilation program might select for males showing low attraction to ME, thus eclipsing the effectiveness of the program. Faced with persistent populations of *B. dorsalis* on several Japanese Islands despite prolonged attempts at male annihilation, Itô and Iwashashi (1974) and Habu et al. (1980, 1984) suggested that selection for ME-insensitive males was responsible, and, as a result, SIT was implemented and finally achieved eradication. In support of their claim, Itô and Iwahasi (1974) exposed *B. dorsalis* males to ME in the laboratory and selected non-responding males as sires. Within only two generations of such selection, they produced a strain with lower ME responsiveness than a control line. Working with *B. dorsalis* in Hawaii, Shelly (1997) likewise reported a consistent reduction in ME responsiveness over 8 generations for several lines sired by non-responding males. These studies indicate that, while the evolution of lure-insensitivity has not been demonstrated conclusively, programs of male annihilation are most effective when applied intensely with the aim of rapid eradication.

Age-dependent response to ME has been examined in some detail for *B. dorsalis*. While all studies confirm that ME response increases with male age, they differ in their estimates of ME responsiveness among immature individuals. On one hand, several studies (Umeya et al. 1973; Itô and Iwashashi 1974; Habu et al. 1980; Tan et al. 1987) report no or very little attraction by very young males (1–5 days-old) and a close association between ME response and male sexual maturation (see also Fitt 1981b for data on *B. opiliae*). Tan et al. (1987), for example, found that less than 2 % of 5 days-old laboratory-reared males responded to ME in a wind tunnel and no wild males, emerged from naturally infested star fruits (*Averrhoa carambola* Linn.), marked, and released, at less than 7 days of age were captured in ME-baited traps. In contrast, several other studies (Steiner 1952; Steiner and Lee 1955; Wong et al. 1989; Shelly et al. 2008) reported young males (<5 days of age) showed relatively high response to ME. Wong et al. (1989), for example, found that nearly 50 % of males responded to ME before their age of first mating (13 days). Collectively, these studies involved different strains, different procedures, and different test conditions, making it impossible to draw a robust conclusion. Resolution is far from an arcane academic exercise, however, as

knowledge of age-dependent response to ME is critical to predicting the success of male annihilation efforts (see Barclay and Hendrichs, Chap. 11, this volume).

In contrast to intraspecific, age-dependent variation, little attention has been given to interspecific differences in attraction to ME. In the most comprehensive study to date, Wee et al. (2002) monitored the response of males of three closely related *Bactrocera* species to serial dilutions of ME in small laboratory cages as well as consumption of ME from microcapillary pipettes. The two assays yielded the same trend, i.e., in decreasing order, the level of ME sensitivity was *B. dorsalis* > *B. papayae* > *B. carambolae*. Most notably, males of *B. carambolae* showed relatively weak attraction to the lure: the ME dose required to elicit response of 50 % of *B. carambolae* males was 9 and 17 times higher than that observed for *B. papayae* and *B. dorsalis*, respectively. Given the importance of ME in trapping programs, additional studies of this type are clearly needed to better characterize the detection sensitivity of area-wide trapping grids.

### 3.2.2 Fluorinated Analogs of Methyl Eugenol

One of the potential problems with the use of ME for fruit fly control is the reported carcinogenicity of this compound in mice and rats (Miller et al. 1983) and microbes (Schiestl et al. 1989; Sekizawa and Shibamoto 1982). ME has also been shown to form DNA adducts in cultured human cells and thus may contribute to human carcinogenesis (Zhou et al. 2007). However, several reviews (Smith et al. 2002; Robinson and Barr 2006) conclude that ME does not pose a significant cancer risk in humans, primarily because ME exposure in humans is as much as 1,000 times below the level utilized to produce hepatic carcinoma in rats. Human subjects fed approximately twice the daily average intake of safrole (a phenylpropene related to methyl eugenol) over a 2 year period showed no carcinogenetic symptoms (Long et al. 1963). In addition to the low exposure, ME in human blood serum is rapidly eliminated and excreted (Schechter et al. 2004). ME may, in fact, have some benefits to human health, e.g., reduction of cerebral ischemic injury (Choi et al. 2010) as well as anti-anaphylactic properties (Kim et al. 1997). ME is a regular component of the human diet (e.g., flavoring in baked goods and candy, Smith et al. 2002) and is found in most spices and some plants, particularly in the family Lamiaceae, e.g., *Ocimum basilicum* (sweet basil) and *O. sanctum* (holy basil), which have high ME contents and are regularly consumed as vegetables or used for culinary and medicinal purposes in Southeast Asian countries (Tan and Nishida 2012).

The fear of ME carcinogenicity and hepatotoxicity to human health, whether legitimate or a case of overreaction, has prompted some fruit fly scientists to search for ‘safer’ alternative attractants for ME-responsive *Bactrocera* species and evaluate various phenylpropanoids with structural similarities to ME (Khrimian et al. 1993, 1994, 2006, 2009; Liquido et al. 1998; Metcalf et al. 1975; Mitchell et al. 1985). Two such analogs of ME are 4-[(2*E*)-3-fluoroprop-2-en-1-yl]-1,2-dimethoxybenzene (FME), an analog fluorinated at the terminal carbon of the ME side chain, and 1-fluoro-4,5-dimethoxy-2-(prop-2-en-1-yl)benzene (RFME), an

analog fluorinated at the 4 position of the ME aromatic ring. In field tests, FME was as attractive to *B. dorsalis* males as ME (Khrimian et al. 1994), while RFME was only about 50 % as attractive as ME (Khrimian et al. 2009). The good performance of FME in field bioassays (Khrimian et al. 1994, 2006, 2009; Liquido et al. 1998) showed that this compound is not only equally attractive to *B. dorsalis* but has an added value as a more persistent lure. The carcinogenicity of the terminal carbon fluorinated compound has not yet been determined, but, if negative, FME could serve as an excellent replacement for ME in trapping programs.

Jang et al. (2011) synthesized two additional fluorinated ME analogs, 1-(3,3-difluoroprop-2-en-1-yl)-2-fluoro-4,5-dimethoxybenzene, a ME analog trifluorinated at the 4 position of the aromatic ring and at the terminal carbon of the side chain, and 1-fluoro-2-(3-fluoroprop-2-en-1-yl)-4,5-dimethoxybenzene, a ring and side-chain difluorinated analog. Although *B. dorsalis* males were attracted strongly to and fed on the trifluoroanalog and difluoroanalog in a cage experiment, field attractiveness of male oriental fruit fly to both was markedly lower than to ME. In field bioassays, traps baited with difluoroanalog captured roughly 50 % as many flies as traps baited with ME, while the trifluoroanalog captured only about 10 % as many males. Thus, di- or tri-fluorinated ME are likely not viable replacements for ME as attractants for *B. dorsalis* and related species.

### 3.2.3 Plant Phenylpropanoids, Dimethoxycinnamyl Analogs as Parapheromones of ME-Responsive Species

*E*-3,4-dimethoxycinnamyl alcohol and *E*-3,4-dimethoxycinnamyl acetate from *Spathiphyllum cannaefolium* Schott (Araceae) (Chuah et al. 1996) and Hawaiian lei flower, *Fagraea berteriana* A. Gray ex Benth. (Loganiaceae) were characterized as attractants for *B. dorsalis* (Nishida et al. 1997). Although these compounds are less volatile than ME, the feeding stimulant activity of the former was as high as that of ME (Nishida et al. 1997). However, they will not replace ME in trapping of *B. dorsalis* because of their low volatility and attractancy.

### 3.2.4 Raspberry Ketone, Raspberry Ketone Formate, and Cue Lure

As noted above, among lure-responsive *Bactrocera* species, the majority is attracted to RK/CL. RK (Fig. 2.5) is found naturally as a fungal metabolite (Ayer and Singer 1980) and in many plants besides raspberries (*Rubus idaeus* L.), including other species in Rosaceae, Asteraceae, and Lamiaceae (formerly Labiatae) (Hirvi et al. 1981; Hirvi and Honkanen 1984; Lin and Chow 1984; Marco et al. 1988) as well as Orchidaceae (Nishida et al. 1993; Tan and Nishida 2005; Tan 2009). Drew (1974) reported that RK was developed as a male attractant for *B. tryoni* in Australia in 1959 but provided no additional information regarding the nature of this discovery. At approximately the same time, the United States Department of Agriculture (USDA) was engaged in a large-scale screening of

thousands of chemicals as potential fruit fly baits (Beroza and Green 1963). Based on this screening process, Barthel et al. (1957) reported attraction of *B. cucurbitae* males to anisylacetone (4-(4-methoxyphenyl)-2-butanone), a synthetic aromatic ketone. In turn, Beroza et al. (1960), through continued testing of compounds related to anisylacetone, synthesized CL (4-(4-acetoxyphenyl)-2-butanone), which was a much more potent attractant for *B. cucurbitae* males and is now used worldwide in detection efforts for this species and other RK/CL-responsive *Bactrocera* species (Jang et al. 2007). CL has not been isolated as a natural product but is hydrolyzed to RK (also known as rheosmin; 4-(4-hydroxyphenyl)-2-butanone), which as noted above is widespread in nature (Metcalf 1990; Metcalf and Metcalf 1992b). In field tests, CL is a more potent attractant than RK (Alexander et al. 1962; Keiser et al. 1973), likely owing to its high volatility relative to that of RK (approximately 20 times greater, Metcalf 1990).

At this juncture, it is pertinent to point out that Nishida, Howcroft and Tan (unpublished data) recently detected anisylacetone and CL (hitherto, not known as natural products as mentioned above) in certain bactroceroiphilous orchid flowers (*Bulbophyllum* spp.) found in Papua New Guinea. They also showed that both the compounds have differential attraction against RK-sensitive *Bactrocera* species in field capture of wild males – with significantly more *B. cucurbitae* and *B. triangularis* (Drew) captured in RK- than anisylacetone-baited traps and vice versa for *B. atramentata* (Hering), *B. bryoniae* (Tryon) and *B. frauenfeldi* (Schiner) (unpublished data). This shows that anisylacetone and CL, along with RK and zingerone (see below), in nature may (a) play an important evolutionary role in the *Bactrocera* fruit fly-orchid interactions, and (b) affect trapping of wild flies in surveillance and quarantine detection for an areawide IPM/SIT program.

Although quantitative data are scant, it is generally accepted that CL is a weaker attractant than ME (Cunningham 1989; Jang and Light 1996). Data from a mark-release-recapture study (Shelly and Nishimoto 2011) conducted in Hawaii and California confirmed this notion. For example, among flies released 100 m from the lure source, 1–19 % of *B. dorsalis* males were captured in an ME-baited trap compared to only 0.4–1.2 % of *B. cucurbitae* males captured in a CL-baited trap. Correspondingly, with 5 ME- and 5 CL-baited traps per 2.59 km<sup>2</sup> (operational density in California, for example), there would be near certainty (>99.9 %) of detecting incipient *B. dorsalis* populations as small as 50–162 males, whereas the same likelihood of detection for *B. cucurbitae* would require 310–350 males in the population.

Although less potent, CL has been used in the same ways as ME, i.e., (i) detection and surveillance of invasive species (Gonzalez and Troncoso 2007; Jessup et al. 2007), quarantine surveys and delimitation (Allwood 2000), suppression and eradication (Matsui et al. 1990; Vargas et al. 2000; Sookar et al. 2008), and ecological studies, including faunal surveys (Osborne et al. 1997; Allwood 2000), population dynamics and phenology (Itô et al. 1974; Harris et al. 1986; Vargas et al. 1990), and dispersal (Fletcher 1989; Vargas et al. 1989; Kohama and Kuba 1996; Peck et al. 2005). As noted above, existing reviews address many of these topics (see, in particular, Vargas et al. 2010a), and here we briefly address two

topics, namely (i) age-dependent variation in response to ME and (ii) comparative performance of CL and raspberry ketone formate.

As with the *B. dorsalis*-ME association, attraction of *B. cucurbitae* males to CL is related to sexual maturation, and findings have been inconsistent regarding the level of response displayed by very young males. In particular, whereas Beroza et al. (1960) observed attraction of newly emerged *B. cucurbitae* males to CL, other studies (Monro and Richardson 1969; Fletcher 1974; Wong et al. 1991) report no attraction until males are at least several days old. In the most comprehensive study, Wong et al. (1991) found that wild *B. cucurbitae* males did not respond to CL until 10 days of age and that the timing of CL response and mating activity were highly correlated. Based on this finding, these authors concluded that male annihilation would be less effective against *B. cucurbitae* than *B. dorsalis*, because the closer coincidence of lure response and sexual maturation in the former than the latter means that fewer *B. cucurbitae* males would be killed in lure-baited traps prior to mating than would be the case for *B. dorsalis*.

In attempting to identify a more potent lure than CL, several studies have investigated the attractancy of the formate ester of RK, formic acid 4-(3-oxobutyl) phenyl ester (RKF). In the early 1990s, Metcalf and Mitchell (1990) and Metcalf and Metcalf (1992a, b) showed that RKF was more attractive to *B. cucurbitae* males than either RK or CL. Despite this finding, no further research on RKF was undertaken for about a decade, apparently because of concern regarding the rapid hydrolytic conversion of RKF to RK (which, as noted above, is less volatile and less attractive than CL, which hydrolyzes to RK at a slower rate, Beroza et al. 1960). However, subsequent work (Casaña-Giner et al. 2003a, b) showed that rate of hydrolysis of RKF to RK was likely overestimated. Furthermore, field testing (Casaña-Giner et al. 2003a, b; Oliver et al. 2004; Jang et al. 2007) showed that RKF-baited traps generally captured more *B. cucurbitae* males than CL-baited traps. Additional field data, however, have not corroborated this result. Working with *B. cucurbitae*, Vargas et al. (2010c) reported no difference in the catch of traps baited with CL or RKF embedded in a biologically inert, waxy matrix (SPLAT), and Shelly et al. (2012a) reported that traps baited with liquid CL had significantly higher captures than traps baited with RKF presented as a liquid or in a polymeric dispenser. Reasons for these inconsistent results are unknown, though it is possible that variation in abiotic factors, which affected the conversion of CL and RKF to RK, is responsible.

RKF has also been found to attract many other RK-responsive *Bactrocera* species. Preliminary tests (Jang et al. unpublished) in Australia showed that RKF plugs recaptured 1.5 times more sterile male Queensland fruit flies compared to a CL plug. In an unpublished survey, Jang and colleagues found 19 *Bactrocera* species in traps baited with CL and RKF in the northern territories of Australia. Most of the species responded equally to either CL or RKF, but a few showed higher trap captures to RKF than CL. The results from trap evaluations in the Northern Cape York Peninsula and the Torres Strait showed that RKF had higher trap captures of *B. frauenfeldi*, *Bactrocera peninsularis* (Drew and Hancock), and *Bactrocera neohumeralis* (Hardy) compared to the CL plug.

### 3.2.5 Presentation of ME and RK/CL

In the early 1980s, a proprietary product of International Pheromones Ltd was marketed as ‘dorsalure’ (a mixture, in unknown proportions, of ME and CL) in order to capture males of both ME- and RK/CL-sensitive species. In a species survey conducted in five different ecosystems in Penang Island, Malaysia, it was shown that CL and ME traps caught five RK-responsive and two ME-responsive species, respectively, while ‘dorsalure’ traps caught only two RK- and one ME-responsive species of the seven total species (Tan and Lee 1982). In addition, Tan (1983) tested combinations of ME and CL (three liquid mixtures (v:v) of 2:1, 1:1 and 1:2) in the same trap, and all blends caught significantly fewer males of two ME-responsive species – *B. dorsalis* and *B. umbrosa* – when compared with ME-only baited traps. Thus, CL appeared to have caused a slight interference in the male olfactory system of the ME-responsive species. More studies (Hooper 1978; Vargas et al. 2000; Shelly et al. 2004) have corroborated a reduction in ME-responsive species with bait mixtures of ME and CL. Data regarding effects on RK/CL responding species are inconsistent, however, as ME/CL blends have been found to increase (Taiwanese data, cited by Hooper 1978), decrease (Hooper 1978), or have no effect (Vargas et al. 2000) on catch numbers of RK/CL sensitive species.

In several large-scale detection programs (e.g., California, USA), *Bactrocera* lures are applied as liquids to cotton wicks, which are then placed in Jackson traps. To minimize worker risk owing to inadvertent spillage and exposure, field tests, conducted primarily in Hawaii, have compared the efficacy of the standard liquid formulation with different solid dispensers containing ME and CL separately or in combination in the same device. In general, studies (Hiramoto et al. 2006; Suckling et al. 2008; Jang 2011; Jang et al. 2013; Vargas et al. 2009, 2010b; Shelly 2010b; Shelly et al. 2011a, b; Leblanc et al. 2011) have shown that the solid dispensers perform as well as or even better than the liquid application (but see Wee and Shelly 2013 for an exception). Interestingly, two studies (Vargas et al. 2012; Shelly et al. 2012b) conducted in Hawaii further reported that traps baited with solid wafers containing ME, RK, and TML captured as many males of *B. dorsalis*, *B. cucurbitae*, and *C. capitata* as traps baited with a single lure in liquid form. The use of such triple-lure dispensers holds promise, not only in reducing worker safety, but also in reducing costs of trapping supplies and trap monitoring and servicing.

### 3.2.6 Zingerone

Zingerone (4-(4-hydroxy-3-methoxy-phenyl)-2-butanone, 4-hydroxy-3-methoxybenzyl- acetone, vanillylacetone) (Fig. 2.5) is a phenylbutanoid responsible for the pungency of ginger, *Zingiber officinale* (L.) H. Karst. Field studies showed that zingerone present in flowers of *Bulbophyllum patens* King and *B. baileyi* F. Muell. attracted males of both ME- and RK-responsive *Bactrocera*



species, particularly, *B. dorsalis* and *B. cucurbitae*/*B. albistrigata* (Tan and Nishida 2000, 2007). Because of the presence of a hydroxyl group and a butanone side chain (both are also found in RK) as well as a methoxy (found in ME) moiety attached to the benzene ring (Fig. 2.5), zingerone attracts males of both ME- and RK-responsive *Bactrocera* species, albeit relatively very weak attraction in comparison to ME and RK (Tan and Nishida 2007). Zingerone, when consumed by *B. dorsalis* males, is converted to zingerol, attractive to conspecific females, as a component of male sex pheromone (Tan and Nishida 2007). However, in *B. cucurbitae* males, zingerone is sequestered largely unchanged into the rectal gland (Nishida et al. 1993). Khoo and Tan (2000) and Kumaran et al. (2013) have further examined the effects of male feeding on zingerone on their success in attracting mates and obtaining matings in *B. cucurbitae* and *B. tryoni*, respectively.

After the discovery of floral zingerone attracting both ME and RK-responsive species (Tan and Nishida 2000, 2007), Fay (2010) explored the structure-activity relationships of 50 different phenylpropanoids and phenylbutanoids that might attract the non-responsive *Bactrocera* and *Dacus* to the two potent attractants. It was shown that certain non-responsive *Bactrocera* species, namely *B. aglaiae* (Hardy), *B. aurea* (May), and *B. speewahensis* Fay and Hancock (a new species), as well as a rarely trapped *Dacus secamoneae* Drew, were captured only in traps baited with zingerone and not in ME and RK/CL traps (Fay 2010). Further, a qualitative field evaluation using traps baited with zingerone, RK/CL, or ME conducted in north-eastern Australia showed that *Bactrocera jarvisi* (Tryon), previously known to be attracted to RK/CL, was strongly attracted to zingerone, with more than 97 % of flies of this species captured in traps baited with the attractant. In contrast, *B. neohumeralis* and *B. tryoni* males were caught more frequently in RK traps (Fay 2012). In north Queensland, *B. jarvisi* invariably constituted 97–99 % of the total catch, and zingerone is “now starting to be used in various places around the country (Australia) for both detection and male annihilation purposes” (Harry Fay 2012 – personal communication). These very interesting results certainly suggest that zingerone should be tested more widely throughout the Asia-Pacific region for possible attraction of other non-responsive *Bactrocera* species (which constitute approximately 50 % of the total *Bactrocera* species) to the commonly used ME and RK/CL attractants.

### 3.2.7 $\alpha$ -Ionone Analogs for *Bactrocera latifrons*

$\alpha$ -Ionol (latilure) and its analogs (Fig. 2.5) were found as attractants for trapping males of the solanaceous fruit fly, *B. latifrons*, which shows no affinity to either ME or CL (Flath et al. 1994a). Although the attractiveness of  $\alpha$ -ionol is much lower than that of ME and CL for *B. dorsalis* and *B. cucurbitae*, respectively, cade oil and its ingredients (e.g., eugenol) synergistically enhanced the attraction (McQuate and Peck 2001; McQuate et al. 2004, 2008a, b). On the contrary, isophorone (3,5,5-trimethyl-2-cyclohexene-1-one) and isophorol mixed with  $\alpha$ -ionol attracted more males than the respective individual compounds (Ishida et al. 2008). Furthermore, a



series of 3-oxygenated  $\alpha$ -ionone analogs have been found as more potent attractants/phagostimulants than  $\alpha$ -ionone/ionol (Ishida et al. 2008; Nishida et al. 2009; Enomoto et al. 2010). These  $C_{13}$ -norterpeneoid analogs, resembling raspberry ketone-type phenylbutanoid structure, are present in various fruit tissues (mostly in glycosidic-forms). Ingested 3-oxygenated  $\alpha$ -ionones by *B. latifrons* males were selectively biotransformed to a variety of derivatives, which were eventually sequestered into the rectal gland – suggesting a possible role as sex pheromone, although the actual biological function is still unknown (Nishida et al. 2009; Enomoto et al. 2010).

### 3.3 *Ceratitis*

The history surrounding the development of male lures for *C. capitata* has been recounted numerous times (Chambers 1977; Cunningham 1989; Millar 1995; Jang and Light 1996), and no purpose is served in repeating it here. Instead, we focus on a few selected topics, namely (i)  $\alpha$ -copaene and natural oils as male attractants and (ii) the chemical characterization and modification of trimedlure (TML).

#### 3.3.1 $\alpha$ -Copaene and Natural Oils as Male Attractants

Ripley and Hepburn (1935) first described the attraction of male *Ceratitis*, in particular males of *C. rosa*, to angelica seed oil (*Angelica archangelica* (Linn.)). Steiner et al. (1957) later reported the attraction of *C. capitata* males to the seed oil, which was used intensively in the 1956 Florida campaign against *C. capitata* to the point of exhausting the world supply. Over a decade later, two researchers (Fornasiero et al. 1969; Guiotto et al. 1972) identified  $\alpha$ -copaene as the main attractant in angelica seed oil and  $\alpha$ -ylangene as a secondary attractant. In a series of field trials in Hawaii,  $\alpha$ -copaene was found to be more attractive to medfly males than TML (Flath et al. 1994b, c). In addition, the stereochemistry of this compound was critical in determining its potency as even slight deviations from the dextrorotary form ((+)- $\alpha$ -copaene) led to decreased attractiveness. Although data are not provided and the enantiomer is not identified,  $\alpha$ -copaene was reported to be 2–5 times more attractive to male medflies than TML in field tests (Cunningham 1989).

While highly attractive, (+)- $\alpha$ -copaene has limited practical use, because its synthesis is extremely difficult and expensive and its concentration in most natural (plant) sources is low. Methods for synthesizing (+)- $\alpha$ -copaene have been developed (Heathcock 1966; Heathcock et al. 1967; Corey and Watt 1973), but these are laborious and yield only small amounts. Millar (1995) noted that new synthetic pathways have been developed for copaene isomers (Kulkarni et al. 1987; Wenkert et al. 1992), thus opening the possibility that simpler, and more easily synthesized, analogs might be identified as practical alternatives. Regarding plant sources, where

$\alpha$ -copaene occurs, the levorotatory isomer usually predominates, and in those instances where (+)- $\alpha$ -copaene dominates, the overall content of copaene is typically low (<1 % of the essential oil prepared from the plant – Takeoka et al. 1990). Angelica seed oil differs from most plant species sampled (Buttery et al. 1985; Elzen et al. 1985) in that (+)- $\alpha$ -copaene appears to be the more common stereoisomer and to be relatively abundant (0.16–0.34 % of commercial angelica seed oil) (Jacobson et al. 1987).

Another commercially available, natural product, ginger root oil, also contains relatively high amounts of (+)- $\alpha$ -copaene and has been investigated as a medfly attractant. A distillation procedure has been developed that increases the concentration of (+)- $\alpha$ -copaene from 0.4 % in commercially available oil to 8 % in the enriched oil (Shelly and Pahio 2002). However, when applied as a paste at varying doses to cotton wicks, traps baited with the enriched ginger root oil captured in significantly fewer *C. capitata* males than traps baited with liquid TML (Shelly and Pahio 2002). Moreover, the enriched oil appeared to lose its potency rather quickly: paste aged 5 days resulted in 10–20 % fewer captures than fresh paste. A second study (Shelly 2013) also conducted in Hawaii confirmed the greater attractancy of TML plugs to enriched ginger root oil applied in liquid form. In contrast, Mwatawala et al. (2013), working in Tanzania, found that trap captures with enriched ginger root oil were equal to or greater than those with TML for four *Ceratitis* species (including the medfly) and that the oil captured males of one species (*C. cosyra* not typically found in TML-baited traps). Based on these results, the authors suggest that enriched ginger root oil is a viable alternative to TML in *Ceratitis* detection programs in Africa.

The discrepancy in the results for the medfly between Hawaii and Africa could reflect differences in the composition of the oils used in the two regions. In a study of avocado varieties, Niogret et al. (2011) found that the behavioral and EAG responses of medflies were not directly related to the amount of  $\alpha$ -copaene in the volatiles of the different varieties. For example,  $\alpha$ -copaene comprised 31 % of the sesquiterpenes for one of the least attractive varieties but only 12 % for the most attractive variety. Thus, the presence and concentration of sesquiterpenes other than  $\alpha$ -copaene may affect medfly response to natural oils, and variation in the chemical composition of ginger oils from different suppliers could generate different results in trapping studies.

### 3.3.2 Trimedlure

Since its discovery approximately 50 years ago (Beroza et al. 1961), TML (*tert*-butyl 4(and 5)-chloro-*trans* -2-methylcyclohexane-1-carboxylate) has become widely, but not universally (as noted below), adopted as the chief male attractant used in detection and surveillance programs for *C. capitata* (Jang et al. 2001). These authors recognized TML to be a mixture of isomers, with four isomers predominating (Beroza and Sarmiento 1964), but complete resolution of the isomeric constitution of trimedlure was not achieved until Leonhardt et al. (1982)

reported that the four *trans* isomers comprise 90–95 % of TML and the four *cis* isomers comprise the remaining portion (see also Sonnet et al. 1984; Warthen and McGovern 1986a, b). Nonetheless, prior to this more thorough chemical description, the structure (McGovern and Beroza 1966) and volatility and attractiveness of the *trans* isomers (McGovern et al. 1966) were described, and based on laboratory olfactometer trials, the relative attractiveness of these four isomers was  $C > A > B1 > B2$ , with the latter being essentially inactive. Concerned over variability in the relative amounts of *trans* and *cis* isomers in commercial batches of TML, and in particular, the possibility that *cis* isomers might diminish the attractiveness of the *trans* counterparts (as noted for siglure, Steiner et al. 1958). McGovern et al. (1986) conducted field tests comparing the attractancy of whole TML with pure *trans* and *cis* formulations, respectively, as well as the attractancy of formulations varying in the *trans-cis* ratios. Results of these tests showed conclusively that traps baited with *trans*-TML captured as many *C. capitata* males as whole TML and that both of these formulations were more effective than *cis*-TML. Additionally, only when mixtures contained  $\geq 75$  % *cis* isomers was attractancy reduced. Further field tests confirmed the above mentioned findings (McGovern et al. 1987, 1990). In addition, Jang et al. (1989a) compared the electroantennogram responses of *C. capitata* males to the four *trans* isomers of TML and found the responses were greatest to the *cis* isomer, consistent with behavioral assays. Warthen et al. (1993) later investigated the relation between the molecular structure of the different isomers and their attractiveness.

In addition, to identifying the components of TML and their relative attractiveness, several studies focused on the overall release rate of TML from trap dispensers. When originally incorporated into monitoring programs, TML was applied as a liquid (2 ml) to cotton wicks (Nakagawa et al. 1979). However, owing to its high volatility from the cotton, TML was found to be effective for only 2–4 weeks (Burditt 1975; King and Landolt 1984). Two solutions were explored to extend the effective life of TML. The first involved testing solid dispensers to control (reduce) evaporation rates. These alternatives included incorporation of TML in the adhesive, insect-catching surface of the trap (Nakagawa et al. 1975), the middle layer of laminated polymeric (plastic) sheets (Nakagawa et al. 1979; Leonhardt et al. 1989), cups covered with a semipermeable membrane (Leonhardt et al. 1984), cylindrical polymeric plugs (Leonhardt et al. 1989), or rubber septa (Leonhardt et al. 1984; Baker et al. 1988). In addition, the effectiveness of compressed discs of TML *cis* isomer has also been investigated (Heath et al. 1990). Owing to their ease of handling and their lowered release rates (thus allowing a longer interval between replacement), polymeric plugs have been adopted as standard male lure in *C. capitata* detection programs (IAEA 2003).

The second solution involves adding extenders to TML to slow volatilization (Leonhardt et al. 1984; King and Landolt 1984) as TML is costly to produce, this procedure may also reduce costs. Capilure®, which replaces a portion of TML with proprietary extenders, was developed in the early 1980s and is currently used in *Ceratitidis* detection program in South Africa (T.G. Grout, Pers. Comm.). Field tests (Nakagawa et al. 1981b; Rice et al. 1984; Hill 1987; Baker et al. 1988) confirm that

capilure is more persistent than TML and attracts male medflies (albeit in reduced numbers) as long as 10–36 weeks after deployment. However, these same studies have reported inconsistent results regarding the relative performance of the two lures in the initial weeks of deployment, with several studies (Hill 1987; Nakagawa et al. 1981b; Rice et al. 1984) finding equivalence between capilure and TML but one (Baker et al. 1988) finding TML outperformed capilure in the 8 weeks immediately following field deployment. Likewise, in trials in a Hawaiian coffee field, Shelly (2013) found that TML captured more *C. capitata* males than capilure during weeks 1–6 immediately following placement in the field.

### 3.3.3 Ceralure

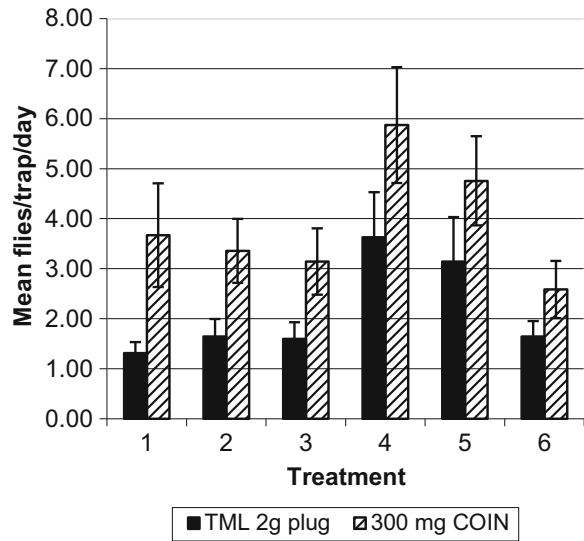
In an investigation into various halogen and ester analogs of TML, ethyl 4- (and 5-) iodo-*trans*-2-methylcyclohexane-1-carboxylate (ceralure), was found to be more potent and persistent than trimedlure (McGovern et al. 1987, DeMilo et al. 1994; Warthen et al. 1998). Ceralure, like trimedlure, is composed of 16 regio and stereoisomers, of which the B1 isomer was reported to be the most attractive (Warthen et al. 1994). This molecule was tested in the field and found to be slightly more attractive and persistent than trimedlure (Leonhardt et al. 1996).

In 2000, a novel method for synthesis of the stereoisomers of the ceralure B1 molecule was developed and tested (Raw and Jang 2000). The (–) enantiomer of ceralure B1 was shown to be more attractive and persistent to laboratory-released sterile flies than the (+) enantiomer, commercial trimedlure or commercial ceralure (Jang et al. 2001). Follow-up studies (Jang et al. 2003, 2005) reported (–)-ceralure B1 to be 4–9 times more attractive than the commercial trimedlure.

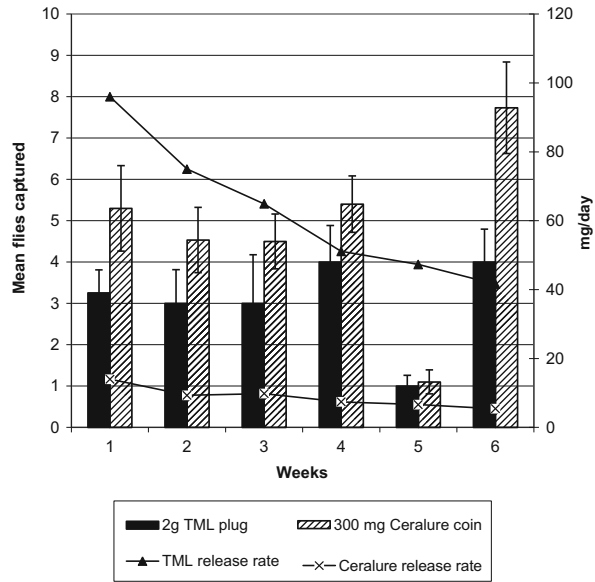
One of the problems that have prevented the adoption of (–)-ceralure B1 has been development of a commercial, cost-effective synthesis of this molecule relative to TML. Khirman et al. (2003, 2004) developed an easier synthesis of the racemic (–/+)-ceralure B1, and subsequent studies showed that > 75 % (–) optically pure ceralure B1 could be as effective as the (98 %) (–)-ceralure B1, and the racemic ceralure B1 could be almost as attractive (Jang et al. 2005). More recent research has focused on the applicability of the racemic ceralure B1 as a replacement for TML.

Recently, Jang et al. (2010) compared the persistence and attractancy of the trimedlure C isomer (racemic) with the ceralure B1 (racemic) isomer to determine which of these two were the most attractive and persistent in a field setting. This was accomplished by comparing equivocal amounts of the two racemic compounds on a standard substrate (cotton wicks) and determining attraction and the residual amounts after 0–7 days. Additionally we initiated studies on polymeric formulations of the racemic ceralure B1 to determine how much of this mixture would be needed to equal or surpass the 2 g TML standard polymer formulation. Results of this test showed that the ceralure coin captured significantly more medflies compared to TML for 6 weeks of testing (Fig. 2.6). The same treatments were tested in sterile medfly release areas in Sarasota, Florida. Although the variation was high in

**Fig. 2.6** Responses of wild Mediterranean fruit flies to ceralure B1 and trimedlure plug formulations



**Fig. 2.7** Responses of sterile released Mediterranean fruit flies to Ceralure B1 and Trimedlure plug formulations (Adapted from Jang et al. 2010)



the weekly evaluations with released flies, results over a 6- week test period showed significantly higher trap captures with the 300 mg ceralure coin compared to the 2 g-trimedlure plug (Fig. 2.7).

On a molecule-to-molecule basis, ceralure B1 was inherently more attractive and more persistent than the C isomer of trimedlure. It also supports an earlier published results showing that when applied to cotton wicks, as little as 40 mg of the (–)

ceralure B1 (50 X less material) was as attractive as 2 g of commercial trimedlure for the first few days in the field (Jang et al. 2003).

As little as 150 mg of ceralure B1, (13 times less compound), formulated in PVC was not significantly different in trap capture compared to a 2 g also PVC-formulated commercial trimedlure plug. Further, increasing ceralure load to 300 mg per coin, which is 6.6 times less than trimedlure, captured significantly more medflies compared to a 2 g trimedlure plug in the entire 6 week test period.

Survey and detection programs are the first line of defense in keeping exotic pests such as medfly from becoming established in key agricultural states such as California, Florida and Texas. While costs of the lures used in detection programs are a consideration in overall program management, it is generally acknowledged that personnel and related costs of conducting surveys represent a much higher proportion of the total costs than the chemical lures. Further tests of ceralure B1 coins versus 2 g trimedlure plugs weathered under environmental conditions found in California, Florida and Texas are needed as to whether the increased cost of ceralure B1 synthesis and formulation are justified. Several additional uses of ceralure B1 might justify the additional costs of the product. As mentioned above labor costs for deployment of detection traps are the most costly part of a survey program. A more potent lure may reduce the number of traps required in a detection array resulting in some cost savings. We have not tested whether ceralure B1 might possibly catch younger aged flies that represent the “founder” population of an incipient introduction. Early detection is arguably more important than merely capturing the most flies, in that early detection allows for a more rapid eradication response thus reducing the overall program costs (bait sprays, fruit stripping, sterile insect releases and associated costs of quarantines). Ceralure B1, although currently expensive might also be considered for mass trapping in small outbreaks, where, when used with other control techniques would increase the likelihood of eradication.

### 3.4 *Dacus*

This genus consists of approximately 300 species with a handful of pest species (<http://www.globalspecies.org/ntaxa/2083501>). Over 40 species are known to respond to CL while only two species respond to ME (IAEA 2003). A major pest species in the Middle East region, *Dacus persicus* Hendel, but considered a beneficial insect that infests weeds in India (Kapoor 2005/2006), is attracted to ME, which has been used as bait in trapping of male flies.

Methyl paraben (methyl-4-hydroxybenzoate – detected in small quantity in the rectal gland of *B. cucurbitae* see Sect. 2.2.2.4.) was discovered to be highly attractive to the males of *Dacus vertebratus* Bezzi (Hancock 1985). It is currently marketed as “vert-lure”, and used as a male attractant/lure for mass trapping of *D. vertebratus* males in control or male annihilation techniques.

For *Dacus ciliatus* Loew, pumpkin fly (a non-responder to either CL or ME), a combination of four or five acetates isolated and identified from host fruits, benzyl, hexyl, (Z)-3-hexenyl, octyl, (Z)-3-octenyl, and (Z)-3-decenyl, was most attractive, but an addition of (*E*)- $\beta$ -farnesene had a deterrent effect, albeit both sexes of this species were responsive to each of the synthetic acetates in the laboratory (Alagarmalai et al. 2009). It needs to be pointed out that the host fruit acetates apparently are acting as a plant allelochemic, if they are released naturally, in the insect-plant interaction. As to whether these fruit volatiles when released act as a plant kairomone or synomone warrants further in depth chemo-ecological investigation.

### 3.5 *Rhagoletis*

No male lure has yet been identified for any *Rhagoletis* species, though male attraction to certain plant volatiles has been reported (Light and Jang 1996). Therefore, this investigation represents a potentially productive avenue for future research.

### 3.6 *Toxotrypana*

Other than the identified pheromone (see Sect. 2.2.6), there are few other attractants used routinely for detection of *T. curvicauda* in the field. Early studies on the behavior of *T. curvicauda* (Sharp and Landolt 1984) suggested that, unlike most tephritids, this species is not readily attracted to proteinaceous food baits. They further reported that both brown and white sugar had some attraction. Landolt and Reed (1990) reported oviposition attraction of females to green papaya host fruit and suggested that host odors may influence oviposition behavior. More recently, Castrejón-Gómez et al. (2004) tested brown sugar and pineapple juice as two low cost attractants for use in field trapping of *T. curvicauda*. The success of the pheromone for use in trapping of this species has limited the search for a true parapheromone or kairomone for use in applied trapping programs.

## 4 Conclusion

For most pestiferous species of tephritid fruit flies, aggregation and sex pheromones have limited usage in trapping and control owing to a multitude of factors, including multi-component composition of pheromone, chemo-structural complexity of each component, high cost of synthesis, low effectiveness when compared to male attractants/lures or food attractants, and other abiotic factors related to blending,

chemical stability, changes in vapor pressure, and release ratio of a multicomponent bait/pheromone in the field. In contrast, male lures, particularly ME, CL, and TML, have been extensively and successfully used as bait in trapping and control of *Bactrocera* and *Ceratitis* species, respectively. Moreover, with the knowledge gained via behavioral and chemo-ecological studies, the exposure of sterile males to certain lures to enhance their mating competitiveness in the field is now gaining ground in area-wide SIT programs. There are some issues, which need to be resolved amicably, related to trapping when comparing (i) formulated and unformulated (e.g., liquid versus solid) male lures conducted in different regions/countries, (ii) effectiveness of different colored traps, especially against clear traps, or (iii) individual against a mixture of attractants used as a trap-bait. Also, the urgency of identifying a replacement for a very potent natural male attractant (ME) deemed to be carcinogenic deserves serious consideration. Further research should also be conducted to seek new male lures from plants, like zingerone, that can attract non-responsive species to the commonly used and known male attractants. We are confident that there are a few more attractants for fruit flies, especially for the genera of *Bactrocera* and *Dacus*, may be isolated and identified through proper and in depth behavioral and chemo-ecological investigations, especially via understanding the probable co-evolution between plants and fruit flies.

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Trapping and the Detection, Control, and Regulation of  
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Lures, Area-Wide Programs, and Trade Implications

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