Chapter 9
Chemical Ecology of African Tephritid Fruit Flies

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Abstract African Tephritid fruit flies are distributed in three main genera, *Bactrocera*, *Ceratitis* and *Dacus* constituting both indigenous and invasive species. They use a diverse and complex range of semiochemicals for host location and reproduction. This chapter reviews the identification of these semiochemicals and includes examples of lures developed from some of these chemicals for the management of economically important fruit fly species.

Keywords Tephritid fruit flies • *Bactrocera* • *Ceratitis* • *Dacus* • Semiochemicals • Male lures

1 Introduction

The fruit flies covered in this chapter are those that are of both economic importance in Africa and also have well established chemical communication modes. Before proceeding to discuss fruit fly chemical communication, it is worthwhile defining the chemical classes involved in this mode of communication, which are broadly referred to as semiochemicals (Torto 2004). Semiochemicals are defined as 'chemical signals that convey a message between organisms of the same or different species' and, for the purposes of this chapter, can be divided into three categories: kairomones, allomones and pheromones. Kairomones and allomones mediate 'interspecific' chemical communication, i.e. chemical communication between individuals from different species. Kairomones benefit the receiver and include signals for attraction to feeding or oviposition sites, while allomones benefit the emitter and include some repellents that deter competing or predatory species. Pheromones mediate 'intraspecific' chemical communication, i.e. between

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S. Ekesi et al. (eds.), *Fruit Fly Research and Development in Africa - Towards a Sustainable Management Strategy to Improve Horticulture*,
DOI 10.1007/978-3-319-43226-7_9

individuals of the same species and include signals that mediate the location of conspecifics (aggregation pheromones), mates (sex pheromones) and oviposition sites (oviposition pheromones). Host-marking pheromones may mediate both intra- and interspecific interactions in some species. These terms for classes of chemical communication are not exhaustive and readers are advised to refer to key reference books on chemical ecology for definitions of additional modes of chemical communication (El-Sayed 2015; Matthews and Matthews 2010).

The biology and chemical ecology of fruit flies have been studied for several decades and have recently been comprehensively reviewed for the six major tephritid fruit fly genera (*Anastrepha*, *Bactrocera*, *Ceratitis*, *Dacus*, *Rhagoletis* and *Toxotrypana*) (Shelly et al. 2014). The present review considers only the role of semiochemicals mediating behaviour of African tephritid fruit flies, concentrating specifically on inter- and intraspecific chemical communication. Additionally, we provide a summary of the different assays used to study fruit fly behaviour in response to chemical signals, the antennally- and behaviourally-active compounds identified to date, and the candidate lures used in fruit fly control.

2 Interspecific Interactions

Most studies on chemical communication between tephritid fruit flies and other species have been on interactions with various plant species; chemical cues from plants can act as oviposition stimulants or oviposition deterrents to females, and as either attractants or repellents to one or both sexes (Jayanthi et al. 2012). Studies on interspecific chemical interaction between tephritid fruit flies and plants have largely been conducted with the goal of identifying potent plant-based attractants for managing both sexes of fruit fly pests. Thus these studies have mostly focused on genera and species of economically important fruit flies.

In Africa, fruit flies in the genera *Bactrocera*, *Ceratitis* and *Dacus* are of greatest economic importance since they attack a wide variety of important agricultural fruits including: mango, *Mangifera indica* L.; *Citrus* species; guava, *Psidium guajava* L.; avocado, *Persea americana* Mill.; almond, *Prunus dulcis* (Mill.) Webb; Cucurbitaceae Juss.; tomato, *Solanum lycopersicum* L.; and banana, *Musa* species (Ekesi and Billah 2008). Odours from different parts of these host plants elicit different behavioural responses in fruit flies, acting as attractants, repellents, oviposition stimulants and oviposition deterrents; these behaviours are either olfactory or contact-based, and are characterised by their mode and range of action (Shelly et al. 2014). However, while plant-based attractants and repellents have been studied for a long time, their successful use in integrated fruit fly management has been limited. For instance, despite early recognition that female-biased attractants existed for the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Jang et al. 1997), research efforts in the subsequent two decades have, thus far, only identified oviposition stimulants (Jayanthi et al. 2012). Furthermore, studies on host plant-fruit fly interactions have been strongly influenced by the economic importance and geographic range of the species in question, favouring research on invasive species over their indigenous counterparts. In this section we summarise research efforts on the identification of plant-based attractants and repellents in species from the genera *Bactrocera*, *Ceratitis* and *Dacus*. Host plants referred to in this chapter are defined as plants on which female fruit flies oviposit, whereas non-host plants are defined as those plants for which there are no records of female oviposition. To the best of our knowledge, and with the exception of the melon fly, *Zeugodacus (=Bactrocera) cucurbitae* (Coquillett), from which potent kairomone-based male and female attractants have been identified (Siderhurst and Jang 2010), similar plant-based attractants for other fruit fly species in these three genera remain to be identified.

2.1 **Bactrocera dorsalis** *Species Complex*

Amongst the three fruit fly genera known to occur in Africa, members of the genus *Bactrocera*, and in particular the *B. dorsalis* complex, are highly polyphagous and infest over 40 host plant species (Ekesi and Billah 2008; Georgen et al. 2011). Over two decades of work has documented attractants and repellents for both sexes of the *B. dorsalis* species complex. Some of the earliest work on plant-based attractants was done in the 1990s on papaya, *Carica papaya* L. In windtunnel assays, odours from ripe papaya attracted and stimulated oviposition in females of *B. dorsalis* more than odours from unripe papaya. This was attributed to higher levels of esters and monoterpenes being released from ripe fruit compared with unripe fruit (Flath et al. 1990; Jang and Light 1991). However, this preference for ovipositing in ripe papaya decreased with increasing age of flies. In addition to papaya, fruits such as mango, guava, orange (*Citrus sinensis* (L.) Osbeck.), banana, almond and marula (*Sclerocarya birrea* [Rich.] Hochst.), also attracted more male and female *B. dorsalis* when ripe, than when unripe (Cornelius et al. 2000a, b; Kimbokota et al. 2013; Jayanthi et al. 2012; Siderhurst and Jang 2006a; Biasazin et al. 2014) (Tables 9.1 and 9.2). Using coupled gas chromatography/electroantennographic detection (GC/EAD) and coupled gas chromatography/ mass spectrometry (GC/MS) analyses on the antennae of female fruit flies the components present in the attractive fruit odour were identified as a complex mixture of alkanes, esters, green leaf volatiles (GLVs), ketones and terpenes (Biasazin et al. 2014; Light and Jang 1987; Kimbokota 2011; Kimbokota et al. 2013; Jayanthi et al. 2012; Siderhurst and Jang 2006b) (Table 9.3) (Fig. 9.1). In addition to olfactory attractants, 1-octen-3-ol, ethyl tiglate and γ-octalactone from mango have been identified as oviposition stimulants (Jayanthi et al. 2014a) with a particularly strong innate response to γ-octalactone (Jayanthi et al. 2014b) (Fig. 9.1). However, female *B. dorsalis* are repelled by the essential oil from cinnamon, *Cinnamomum osmophloeum* Kaneh, as demonstrated in Petri dish assays (Diongue et al. 2010). The specific components in cinnamon oil that elicit this response are unknown. In a related study, mango cultivars with high levels of phenolics were less infested by *B. dorsalis* than cultivars with low levels of

Table 9.1 Examples of studies that identified host and non-host plants that elicit specific behaviours in African fruit fly species

Fruit fly									
Scientific name	Common name	Sex studied	Plant source[a]	Plant part	Behavioural role[b]	Extract collection method	Method of analysis[c]	Compound identification[d]	Reference(s)
Bactrocera oleae	Olive fruit fly	Female	Olive	Olive aqueous vegetation extract, olive fruit juice, phenolic extracts,	Oviposition deterrent	Solvent extraction with methanol	GC-MS, TLC, NMR, bioassay	+	Cirio (1971), Fiume and Vita (1977), Girolami et al. (1981), Vita et al. (1977) and Capasso et al. (1994)
				Olive aqueous vegetation extract, olive fruit juice	Oviposition stimulant	Solvent extraction with methanol	GC-MS, TLC, NMR, bioassay	+	Capasso et al. (1994)
				Leaves and fruit	Attractant Repellent Oviposition stimulant and deterrent	Dynamic headspace air sampling of water-based extract	GC-MS, TLC, NMR, bioassay	+	Scarpati et al. (1993) and Scalzo et al. (1994)
				Leaves and fruit (water-based extracts)	Attractant Oviposition stimulant	Solvent extraction with water, dynamic head space sampling, carbon trap 300	GC, GC-MS, colorimetry, bioassay	+	Scarpati et al. (1996)
					Oviposition stimulant	Headspace	GC-MS	+	Panizzi et al. (1960) and Girolami et al. (1974)

Bactrocera dorsalis	Oriental fruit fly	Female	Panax,	Leaf	Attractant	Solvent extraction with dichloromethane and water		–	Jang et al. (1997)
		Female	Papaya	Fruit	Attractant Arrestant Oviposition stimulant	None	Wind tunnel assays	–	Jang and Light (1991)
		Male and Female	Almond		Attractant	Solvent extraction with methanol	GC-MS, bioassays	+	Siderhurst and Jang (2006a)
		Male and Female	Almond	Fruit	Attractant	SPME, dynamic head space collection	GC-EAD, GC-MS, bioassay	+	Siderhurst and Jang (2006b)
		Female	Common and strawberry guava, starfruit, citrus	Fruit	Attractants		bioassays	–	Cornelius et al. (2000a)
		Female	Mango	Fruit	Attractants	SPME, dynamic head space collection	GC-EAD, GC-MS, bioassay	+	Jayanthi et al. (2012)
		Female	Citrus	Fruit, Nu-Lure	Attractants		bioassays	–	Cornelius et al. (2000b)
		Female	Mango (Kent variety), Banana, Citrus Guava	Fruit	Attractant	Dynamic headspace collection	GC-EAD, GC-MS, bioassay	+	Biasazin et al. (2014)
		Female	Mango (Chausa and Alphonso varieties)	Fruit	Oviposition stimulant	Dynamic headspace collection	GC-EAD, GC-MS, bioassay	+	Jayanthi et al. (2014a)
		Male and Female	Mango (Sensation, Apple and Kent varieties), marula, almond	Fruit	Attractant		bioassays	–	Kimbokota (2011)
		Male and Female	Mango (Banganapali, Alphonso, Totapuri, Langra and EC-95862 varieties)	Fruit (peel and pulp)	Repellent	Solvent extraction with methanol	spectrophotometer, bioassays	–	Verghese et al. (2012)
Z. curcubitae	Melon fruit fly	Male and Female	Cucumber	Fruit	Attractant	Dynamic headspace collection, SPME	GC-EAD, GC-MS, bioassay		Siderhurst and Jang (2010)

(continued)

Table 9.1 (continued)

Fruit fly									
Scientific name	Common name	Sex studied	Plant source[a]	Plant part	Behavioural role[b]	Extract collection method	Method of analysis[c]	Compound identification[d]	Reference(s)
B. latifrons	Solanum fruit fly	Male and Female	Various essential oils, formulated aromas and synthetic compounds	–	Attractants	Liquid chromatography	GC-MS, bioassays	+	Flath et al. (1994b)
Ceratitis capitata	Mediterranean fly	Male and Female	Garden Angelica	Seed	Attractants	Fractional distillation	GC, GC-MS, infrared spectroscopy, bioassays	+	Flath et al. (1994a)
		Male	Peruvian peppertree	Leaf	Attractant	solvent extraction with hexane	GC-MS	+	Gikonyo and Lux (2004)
		Male and Female	Citrus (navel variety)	Fruit	–	Dynamic headspace collection	GC-EAD, GC-MS,	+	Hernandez et al. (1996)
		Female	Coffee	Fruit	Attractant	Solvent extraction with water	bioassays	–	Prokopy et al. (1998)
		Female	Coffee	Fruit	Attractants	Dynamic headspace collection	GC-MS, bioassays	+	Warthen et al. (1997)
		Male and Female	Citrus	Fruit	Insecticidal	Solvent extraction of peel in diethyl ether	GC-MS, UV spectroscopy, bioassays	+	Salvatore et al. (2004)
		Female	Polypod fern (*Elaphoglossum piloselloides*)	–	Oviposition deterrent		Column chromatography, HPLC, infrared spectroscopy, MS, bioassay	+	Socolsky et al. (2008)
		Male	Lychee, fig	Leaves, stem and twigs	Attractant and phagostimulant	Extraction using isooctane, n-hexane, ethylether, ethylacetate dichloromethane		+	Warthen and McInnis (1989)

C. rosa		Male	Peruvian peppertree	Leaf	attractant	Solvent extraction with hexane	GC-MS	+	Gikonyo and Lux (2004)
C. cosyra		Male	Peruvian peppertree	Leaf	Attractant	Solvent extraction with hexane	GC-MS	+	Gikonyo and Lux (2004)
Dacus ciliatus	Ethiopian fruit fly	Male and Female	Galia melon, squash	Fruit	Attractant	Dynamic headspace collection, SPME	GC-EAD, GC-MS, bioassay	+	Alagarmalai et al. (2009)

[a] Common plant names are used except for the polypod fern and represent both host and non-host plant species

[b] Attractants and repellents refer to compounds/extracts whose volatile state elicited these behavioural responses

[c] *GC-MS* coupled gas chromatography mass spectrometry, *GC-EAD* coupled gas chromatography electroantennographic detection, *GC* gas chromatography, *NMR* Nuclear Magnetic Resonance, *TLC* Thin layer chromatography, *GLC* gas liquid chromatography, *HPLC* high pressure liquid chromatography, *UV* ultra violet

[d] Compound identification '+', means the compound has been identified and '–', means that the potential active components have not been identified

Table 9.2 Examples of arena assays used to elucidate specific behaviours in fruit flies

Odour source	Fruit fly species	Bioassay arena	Observed behaviour	References
Squash	*Dacus ciliatus*	Dual choice still air Plexiglass olfactometer (40 × 40 × 30 cm)	Attraction	Alagarmalai et al. (2009)
Olive aqueous vegetation extracts	*Bactrocera oleae*	Plexiglass-tulle cage	Oviposition deterrence	Capasso et al. (1994)
Olive aqueous vegetation extracts	*B. oleae*	Glass test tube (16 cm long × 2.5 cm ID)	Oviposition deterrence	Scalzo et al. (1994)
Olive aqueous vegetation extracts	*B. oleae*	Plexiglass cage (20 × 20 × 60 cm)	Oviposition deterrence	Scarpati et al. (1993)
Olive leaves and fruit, macerated fruit	*B. oleae*	Glass test tube (16 cm long × 2.5 cm ID) with oviposition substrate placed in Plexiglass cage (20 × 20 × 60 cm)	Oviposition cue, Attraction	Scarpati et al. (1993), (1996)
Cucumber, cantaloupe, tomato, kabocha, bittermelon and zuccini squash	*Zeugodacus cucurbitae*	Wood-framed cage covered with 16-mesh black nylon cloth (100 × 100 × 100 cm)	Attraction	Miller et al. (2004)
Cucumber, zucchini, papaya, tomato and ivy gourd	*Z. cucurbitae*	Hemisphere (8 cm diameter) or hemicylinder (4.3 cm in diameter × 15 cm height) placed outdoors		Piñero et al. (2006)
Cucumber	*Z. cucurbitae*	Outdoor multiple-trap rotating olfactometer in a wooden frame cage (3 × 3 × 2.5 m)		Siderhurst and Jang (2010)
Papaya	*Bactrocera dorsalis*	Wind tunnel (261 × 85.5 × 86.5 cm)	Attraction	Jang and Light (1991)
Panax	*B. dorsalis*	Wind tunnel (280 × 90 × 90 cm), Outdoor multiple-trap rotating olfactometer in a wooden frame cage (75 × 75 × 80 cm)	Attraction	Jang et al. (1997)
Common and strawberry guava, starfruit and oranges	*B. dorsalis*	Yellow spheres (7 cm) and McPhail traps placed outdoors	Attraction	Cornelius et al. (2000a, b)
		Multitrap laboratory rotating cage (90 × 90 × 90 cm), Wind tunnel (280 × 90 × 90 cm), Outdoor multiple-trap rotating olfactometer in a wooden frame cage (3 × 3 × 2.5 m), field cage (15 × 6 × 2.5 m)	Attraction	Siderhurst and Jang (2006a, b)

(continued)

Table 9.2 (continued)

Odour source	Fruit fly species	Bioassay arena	Observed behaviour	References
Mountain pepper, cinnamon, eucalyptus and hinoki	*B. dorsalis*	Conical bug cage (85 × 60 × 60 cm)	Attraction, Repellence	Diongue et al. (2010)
Mango	*B. dorsalis*	Pulp disc (prepared in 9 cm diameter Petridish)	Oviposition cue	Jayanthi et al. (2014a, b)
Mango	*B. dorsalis*	Perspex 4-arm olfactometer (12 cm in diameter)	Attraction	Jayanthi et al. (2012)
Mango (Kent variety), guava, banana and orange	*B. dorsalis*	Glass Y-tube (base arm 14 cm long, side arms 16 m long, internal diameter 3.1 cm) placed in a white box	Attraction	Biasazin et al. (2014)
Orange, guava, papaya, coffee, tomato, cucumber, pumpkin juices and water	*B. dorsalis, Z. cucurbitae* and *Ceratitis capitata*	1 Lt polyethylene bottle	Oviposition cue	Vargas and Chang (1991)
Mango (Sensation, Apple and Kent varieties), marula and almond	*B. dorsalis*	Dual choice olfactometer (100 × 30 × 30 cm)	Attraction	Kimbokota et al. (2013)
Turkey berry and devil's apple eggplants	*Bactrocera latifrons*	500 ml plastic container with a screen mesh lid which held test odours and insects	Oviposition cue	Peck and McQuate (2004)
Cucumber volatile extract	*B. latifrons*	Yellow sticky card	Attraction	McQuate et al. (2013)
Artificial orange scent, limonene and *Ceratitis* lure	*Ceratitis rosa*	Rearing cage	Attraction	Lebusa et al. (2014)
Garden angelica	*C. capitata*	Jackson delta trap	Attraction	Flath et al. (1994a)
Coffee	*C. capitata*	Rectangular cage (30 × 30 × 30 cm) with 3 screen sides	Attraction	Prokopy et al. (1998)

Table 9.3 List of some antennally-active fruit odour components in African fruit fly species

Chemical group	Compound	Plant source	Fruit fly species	References
Carboxylic acid	Acetic acid	Cucumber	*Zeugodacus cucurbitae, Bactrocera dorsalis*	Siderhurst and Jang (2010)
Carboxylic acid	Formic acid	Peach	*Ceratitis capitata*	Light et al. (1988)
Carboxylic acid	Acetic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Propanoic acid	Citrus	*C. capitata*	Light et al. (1988)
Carboxylic acid	2-Propenoic acid		*C. capitata*	Light et al. (1988)
Carboxylic acid	Butanoic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Pentanoic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Hexanoic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	(*E*)-2-Hexenoic acid	Passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Heptanoic acid	Citrus, passion fruit	*C. capitata*	Light et al. (1988)
Carboxylic acid	Octanoic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Nonanoic acid	Citrus, passion fruit	*C. capitata*	Light et al. (1988)
Carboxylic acid	Decanoic acid	Citrus, passion fruit, peach	*C. capitata*	Light et al. (1988)
Carboxylic acid	Dodecanoic acid	Citrus, passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	1-Hexanol	Cucumber	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2010)
Alcohol	1-Octen-3-ol	Cucumber	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2010)
Alcohol	Benzyl alcohol	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Alcohol	(*E*)-2-Octen-1-ol	Cucumber	*Z. cucurbitae, B. dorsalis*	Siderhurst and Jang (2010)
Alcohol	2-Phenylethyl alcohol	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Alcohol	(*E,Z*)-2,6-Nonadien-1-ol	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Alcohol	(*Z*)-6-Nonen-1-ol	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Alcohol	1-Nonanol	Cucumber	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2010)
Alcohol	3-Methyl-1-butanol	Mango (Chausa variety), banana	*B. dorsalis*	Biasazin et al. (2014) and Jayanthi et al. (2012)
Alcohol	(*RS*)-1-Octen-3-ol	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)
Alcohol	Phenylethyl alcohol	Mango (Chausa variety),	*B. dorsalis*	Jayanthi et al. (2012)
Alcohol	Ethanol	Almond	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)
Alcohol	3,6-Nonadien-1-ol	Mango	*B. dorsalis*	Biasazin et al. (2014)
Alcohol	(*Z*)-3-Octen-1-ol	Marula	*B. dorsalis*	Kimbokota (2011)
Alcohol	Octan-1-ol	Marula	*B. dorsalis*	Kimbokota (2011)
Alcohol	(*Z*)-3-decen-1-ol	Marula	*B. dorsalis*	Kimbokota (2011)
Alcohol	5-dodecen-1-ol	Marula	*B. dorsalis*	Kimbokota (2011)
Alcohol	4- pentenol	Almond	*B. dorsalis*	Kimbokota (2011)
Alcohol	Ethanol	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Alcohol	Propan-l-ol	Citrus, papaya, passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	2-Propen- 1-ol		*C. capitata*	Light et al. (1988)
Alcohol	Butan-l-ol	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-2-Buten-l-ol		*C. capitata*	Light et al. (1988)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Alcohol	3-Buten-l-ol		*C. capitata*	Light et al. (1988)
Alcohol	Pentan-l-ol	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-3-Penten-l-ol		*C. capitata*	Light et al. (1988)
Alcohol	Hexan-l-ol	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-2-Hexen-l-ol	Citrus, papaya, peach	*C. capitata*	Light et al. (1988)
Alcohol	(*Z*)-2-Hexen-l-ol		*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-3-Hexen-l-ol	Passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	(*Z*)-3-Hexen-1-ol	Citrus, papaya, passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	Heptan-l-ol	Citrus, papaya, passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	(±)-Heptan-2-ol	Passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	Octan-l-ol	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-2-Octen-l-ol		*C. capitata*	Light et al. (1988)
Alcohol	(*E*)-3-Octen-l-ol	Passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	(+)-l-Octen-3-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	Nonan-l-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	Decan-l-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	Undecan-l-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	Dodecan-l-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	(±)-Undecan-2-ol	Citrus	*C. capitata*	Light et al. (1988)
Alcohol	(±)-Nonan-2-ol	Citrus, passion fruit	*C. capitata*	Light et al. (1988)
Alcohol	Carveol	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Aldehyde	Hexanal	Cucumber	*Z. cucurbitae, B. dorsalis, Ceratitis capitata*	Siderhurst and Jang (2010)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Aldehyde	(*E*)-2-Hexenal	Cucumber, almond	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2006a) and Siderhurst and Jang (2010)
Aldehyde	(*E,E*)-2,4-Heptadienal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*E*)-2-Octenal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*E*)-4-Nonenal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*Z*)-6-Nonenal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*E,Z*)-2,6-Nonadienal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*E*)-2-Nonenal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	Tetradecanal	Cucumber, marula	*Z. cucurbitae, B. dorsalis*	Kimbokota (2011) and Siderhurst and Jang (2010)
Aldehyde	Nonanal	Cucumber	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2010)
Aldehyde	Decanal	Cucumber	*Z. cucurbitae, B. dorsalis, C. capitata*	Siderhurst and Jang (2010)
Aldehyde	(*E,E*)-2,4-Nonadienal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	(*E*)-2-Decenal	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Aldehyde	Propanal		*C. capitata*	Light et al. (1988)
Aldehyde	Butanal	Citrus, peach	*C. capitata*	Light et al. (1988)
Aldehyde	(*E*)-2-Butenal		*C. capitata*	Light et al. (1988)
Aldehyde	Pentanal	Citrus	*C. capitata*	Light et al. (1988)
Aldehyde	Hexanal	Citrus, peach	*C. capitata*	Light et al. (1988)
Aldehyde	(*E*)-2-Hexenal	Citrus, peach	*C. capitata*	Light et al. (1988)
Aldehyde	Heptanal	Citrus, peach	*C. capitata*	Light et al. (1988)
Aldehyde	Octanal	Citrus	*C. capitata*	Light et al. (1988)
Aldehyde	Nonanal	Citrus, peach	*C. capitata*	Light et al. (1988)
Aldehyde	Decanal	Citrus	*C. capitata*	Light et al. (1988)
Aldehyde	Undecanal	Citrus	*C. capitata*	Light et al. (1988)
Aldehyde	Dodecanal	Citrus	*C. capitata*	Light et al. (1988)
Alkane	Heptane	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Alkane	Octane	Banana, guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Alkane	Nonane	Guava	*B. dorsalis*	Biasazin et al. (2014)
Alkane	3-Ethyl-2-methylpentane	Guava	*B. dorsalis*	Biasazin et al. (2014)
Alkene	4-Undecene	Marula	*B. dorsalis*	Kimbokota (2011)
Aromatic	1,2-Diethylbenzene	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Aromatic	1,3-Diethylbenzene	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ester	Ethyl butanoate	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)
Ester	Ethyl methacrylate	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012) and Biasazin et al. (2014)
Ester	Ethyl crotonate	Mango (Chausa variety), guava	*B. dorsalis*	Kimbokota (2011), Jayanthi et al. (2012) and Biasazin et al. (2014)
Ester	Ethyl tiglate	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)
Ester	Ethyl hexanoate	Mango (Chausa variety), almond, citrus (Tommy variety)	*B. dorsalis, C. capitata*	Jayanthi et al. (2012) and Siderhurst and Jang (2006a)
Ester	Ethyl sorbate	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012) and Biasazin et al. (2014)
Ester	Ethyl octanoate	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)
Ester	Ethyl acetate	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Ester	Isopentyl acetate	Almond, banana, guava, citrus (Tommy variety)	*B. dorsalis, C. capitata*	Biasazin et al. (2014), Kimbokota (2011) and Siderhurst and Jang (2006a)
Ester	4-Pentenyl acetate	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Ester	Isopentenyl acetate	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)
Ester	Hexyl acetate	Almond, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014) and Siderhurst and Jang (2006a)
Ester	Linalyl acetate	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)
Ester	2-Phenylethyl acetate	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)
Ester	Ethyl nonanoate	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Ester	Nonyl acetate	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)
Ester	Citronellyl acetate	Almond	*B. dorsalis*	Kimbokota (2011) and Siderhurst and Jang (2006a)
Ester	Geranyl acetate	Almond	*B. dorsalis, C. capitata*	Kimbokota (2011) and Siderhurst and Jang (2006a)
Ester	(*E*)-Ethyl cinnamate	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Ester	Isobutyl acetate	Guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl butyrate	Mango, banana, guava	*B. dorsalis*	Biasazin et al. (2014) and Kimbokota (2011)
Ester	Butyl acetate	Banana	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl isovalerate	Mango	*B. dorsalis*	Biasazin et al. (2014)
Ester	2-Pentyl acetate	Mango, banana, guava	*B. dorsalis*	Biasazin et al. (2014)
Ester	Propyl butyrate	Mango, banana	*B. dorsalis*	Biasazin et al. (2014)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Ester	Isobutyl isobutyrate	Banana, guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	Methyl hexanoate	Guava	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl 3-methylcrotonate	Mango	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl tiglate	Mango	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl-(*E*)-2-pentanoate	Mango	*B. dorsalis*	Biasazin et al. (2014)
Ester	Isobutyl butyrate	Banana, guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	Butyl butyrate	Banana, guava	*B. dorsalis*	Biasazin et al. (2014)
Ester	Isobutyl isovalerate	Banana, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	2-Pentyl butyrate	Banana	*B. dorsalis*	Biasazin et al. (2014)
Ester	Ethyl-(*E*)-2-hexenoate	Mango	*B. dorsalis*	Biasazin et al. (2014)
Ester	Butyl valerate	Guava	*B. dorsalis*	Biasazin et al. (2014)
Ester	Isoamyl butyrate	Mango, banana, guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	Isoamyl isovalerate	Banana, guava, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Ester	3-Methyl butyl-2-methylbutanoate	Banana	*B. dorsalis*	Biasazin et al. (2014)
Ester	Heptan-2-yl acetate	Banana	*B. dorsalis*	Biasazin et al. (2014)
Ester	(*Z*)-ethyl 4-octenoate	Mango	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl octanoate	Mango	*B. dorsali, C. capitata*	Kimbokota (2011) and Cossé et al. (1995)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Ester	Isopropyl acetate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl propionate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl isobutyrate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl butyrate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl 2-methylbutyrate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl isovalerate	Marula, almond	*B. dorsalis*	Kimbokota (2011)
Ester	Isopropyl valerate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Propyl isovalerate	Marula	*B. dorsalis*	Kimbokota (2011)
Ester	Isobutyl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	2-Butenyl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	4-Penten-1-yl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	Prenyl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	Benzyl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	Citronellyl acetate	Almond	*B. dorsalis*	Kimbokota (2011)
Ester	Ethyl acetate	Almond, citrus, papaya, passion fruit, peach	*B. dorsalis, C. capitata*	Kimbokota (2011) and Light et al. (1988)
Ester	Propyl acetate	Papaya	*C. capitata*	Light et al. (1988)
Ester	Butyl acetate	Citrus, papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Ester	Pentyl acetate	Citrus, papaya, peach	*C. capitata*	Light et al. (1988)
Ester	Hexyl acetate	Papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Ester	(*E*)-2-Hexenyl acetate	Peach	*C. capitata*	Light et al. (1988)
Ester	Heptyl acetate		*C. capitata*	Light et al. (1988)
Ester	Octyl acetate	Citrus, passion	*C. capitata*	Light et al. (1988)
Ester	Nonyl acetate	Citrus	*C. capitata*	Light et al. (1988)
Ester	Decyl acetate	Citrus	*C. capitata*	Light et al. (1988)
Ester	(*Z*)-3-hexenyl acetate	Squash, guava	*Dacus ciliatus, B. dorsalis*	Alagarmalai et al. (2009) and Biasazin et al. (2014)
Ester	Hexanyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Ester	Benzyl acetate	Squash, almond	*D. ciliatus, B. dorsalis*	Alagarmalai et al. (2009) and Kimbokota (2011)
Ester	(*Z*)-3-octenyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ester	Octanyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ester	Isopentyl hexanoate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ester	(*Z*)-3-decenyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ester	(*E*)-3-decenyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ester	Butyl hexanoate	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ester	Hexyl hexanoate	Citrus (Navel variety))	*C. capitata*	Hernandez et al. (1996)
Esters	(*Z*)-3-Dodecenyl acetate	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Ketone	3,5-Octadien-2-one	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Ketone	3-Hydroxy-2-butanone	Mango (Chausa variety)	*B. dorsalis*	Kimbokota (2011) and Jayanthi et al. (2012)
Ketone	2-Hexanone	Banana	*B. dorsalis*	Biasazin et al. (2014)
Ketone	Dihyrocarvone	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ketone	Carvone	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ketone	4-Ethyl acetophenone	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ketone	Nootkatone	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Ketone	Geranyl acetone	Cucumber	*Z. cucurbitae*	Siderhurst and Jang (2010)
Lactone	(*RS*)-γ-Octalactone	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)
Lactone	γ-Butyrolactone	Passion fruit	*C. capitata*	Light et al. (1988)
Lactone	γ-Pentalactone	Peach	*C. capitata*	Light et al. (1988)
Lactone	γ-Hexalactone	Papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Lactone	*γ*-Heptalactone	Papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Lactone	*γ*-Octalactone	Mango, papaya, passion fruit, peach	*B. dorsalis, C. capitata*	Light et al. (1988) and Jayanthi et al. (2014a)
Lactone	*γ*-Nonatactone	Papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Lactone	*γ*-Decalactone	Papaya, passion fruit, peach	*C. capitata*	Light et al. (1988)
Lactone	*γ*-Undecalactone	Passion fruit, peach	*C. capitata*	Light et al. (1988)
Terpene	Myrcene	Mango (Alphonso variety), almond	*B. dorsalis*	Kimbokota (2011) and Jayanthi et al. (2012)
Terpene	(*Z*)-*β*-Ocimene	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)
Terpene	(*E*)-*β*-Ocimene	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)
Terpene	Allo-ocimene	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)
Terpene	Myroxide	Mango (Alphonso variety)	*B. dorsalis*	Jayanthi et al. (2012)
Terpene	(*S*)-3-Carene	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012) and Biasazin et al. (2014)
Terpene	*p*-Cymene	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012) and Kimbokota (2011)
Terpene	*α*-Terpinolene	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)
Terpene	Menthone	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Terpene	(*E*)-*β*-Farnesene	Almond	*B. dorsalis, C. capitata*	Siderhurst and Jang (2006a)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Terpene	(*E,E*)-α-Farnesene	Almond, marula	*B. dorsalis, C. capitata*	Kimbokota (2011) and Siderhurst and Jang (2006a)
Terpene	(*Z,E*)-α-Farnesene	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Terpene	α-Pinene	Mango	*B. dorsali, C. capitata*	Biasazin et al. (2014), Kimbokota (2011) and Cosse et al. (1995)
Terpene	β-Pinene	Mango, citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014) and Kimbokota (2011)
Terpene	β-Myrcene	Mango, citrus (Tommy variety), almond	*B. dorsalis*	Biasazin et al. (2014) and Kimbokota (2011)
Terpene	(*R*)-(+)-Limonene	Citrus (Tommy variety), almond	*B. dorsalis*	Biasazin et al. (2014) and Kimbokota (2011)
Terpene	(*Z*)-β-Ocimene	Mango, marula	*B. dorsalis*	Biasazin et al. (2014) and Kimbokota (2011)
Terpene	Tricyclene	Mango	*B. dorsalis*	Kimbokota (2011)
Terpene	Camphene	Mango	*B. dorsalis*	Kimbokota (2011)
Terpene	Sabinene	Mango	*B. dorsalis*	Kimbokota (2011)
Terpene	Terpinolene	Mango, almond	*B. dorsalis*	Kimbokota (2011)
Terpene	α-Humulene	Mango	*B. dorsalis*	Kimbokota (2011)
Terpene	δ-3- Carene	Almond	*B. dorsalis*	Kimbokota (2011)
Terpene	Elemicin	Almond	*B. dorsalis*	Kimbokota (2011)
Terpene	β-Caryophyllene	Squash, mango	*C. capitata, D. ciliatus*	Alagarmalai et al. (2009) and Cosse et al. (1995)
Terpene	(*E*)-β-Farnesene	Squash, almond	*D. ciliatus, B. dorsalis, C. capitata*	Alagarmalai et al. (2009) and Siderhurst and Jang (2006a)
Terpene	Germacrene D	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Terpene	Cadinene	Squash	*D. ciliatus*	Alagarmalai et al. (2009)
Terpene	Limonene	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)

(continued)

Table 9.3 (continued)

Chemical group	Compound	Plant source	Fruit fly species	References
Terpene	Limonene oxide	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Terpene alcohol	Linalool	Cucumber, marula	*Z. cucurbitae, B. dorsalis, C. capitata*	Kimbokota (2011) and Siderhurst and Jang (2010)
Terpene alcohol	Eugenol	Almond	*B. dorsalis*	Siderhurst and Jang (2006a)
Terpene alcohol	Methyl eugenol	Almond	*B. dorsalis*	Kimbokota (2011) and Siderhurst and Jang (2006a)
Terpene alcohol	(*S*)-(+)-Linalool	Citrus (Tommy variety)	*B. dorsalis*	Biasazin et al. (2014)
Terpene	Caryophyllene oxide	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Terpene	Allo-aromadendrene	Citrus (Navel variety)	*C. capitata*	Hernandez et al. (1996)
Thiazole	Benzothiazole	Mango (Chausa variety)	*B. dorsalis*	Jayanthi et al. (2012)

phenolics, a trait that is considered useful in the breeding of resistant mango cultivars (Verghese et al. 2012).

Although visual cues can be attractive to *B. dorsalis* in the absence of odours (Cornelius et al. 1999; Vargas et al. 1991), they also complement olfactory attractants (Jang and Light 1991; Aloykhin et al. 2000). Several authors report that both sexes of *B. dorsalis* prefer yellow-coloured objects over green-coloured objects, the yellow colour being associated with ripening fruit (and the odours they produce) compared with unripe fruit (usually green in these studies) (Seo et al. 1982; Liquido et al. 1989; Liquido and Cunnigham 1990). Several studies using yellow McPhail traps have also demonstrated the importance of the yellow colour in fruit fly attraction (Ekesi and Billah 2008; Mazomenos et al. 2002; Dimou et al. 2003).

2.2 Bactrocera oleae

Unlike members of the *B. dorsalis* complex, *Bactrocera oleae* (Rossi), or the olive fruit fly, is monophagous and a specialist on wild and cultivated olives (Ekesi and Billah 2008). Research on identification of plant-based attractants and repellents for *B. oleae* dates back to the 1960s. One of the first findings on the chemo-ecological interactions between female *B. oleae* and its host plant was the identification of oleuropein as an oviposition stimulant (Panizzi et al. 1960; Girolami et al. 1974).

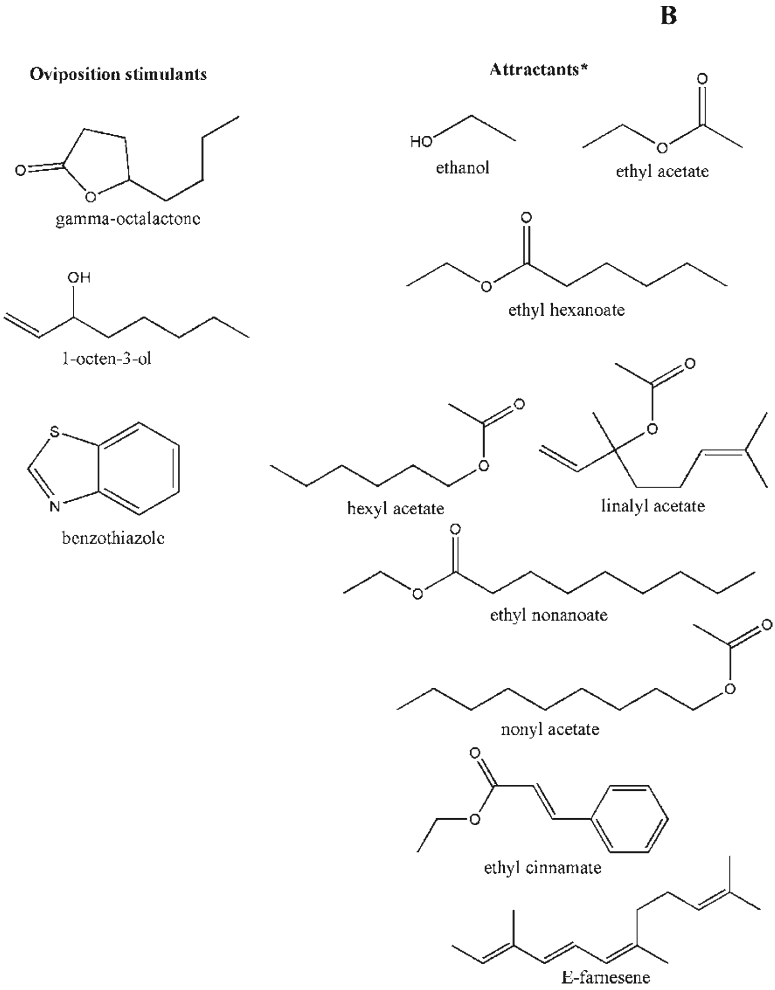

Fig. 9.1 Examples of volatile attractants and oviposition stimulants for the *Bactrocera dorsalis* complex

Catechol, 4-methyl catechol, pyrocatechol and hydroxytyrosol were then identified as oviposition deterrents from methanol extracts of vegetation from olive, *Olea europaea* L. (Capasso et al. 1994; Cirio 1971; Fiume and Vita 1977; Girolami et al. 1981; Vita et al. 1977). Using the same extraction technique, Capasso et al. (1994) identified *o*-quinone as an oviposition stimulant. Scarpati et al. (1993) also identified a number of non-benzenoid and benzenoid compounds as oviposition stimulants. Of these, α-pinene was a more effective oviposition stimulant than *p*-xylene, *o*-xylene, myrcenone and ethylbenzene or n-octane while (*E*)-2-hexenal and hexanal deterred oviposition. In the same study, toluene and ethylbenzene were identified as attractants while (*E*)-2-hexenal and hexanal were identified as repellents to female

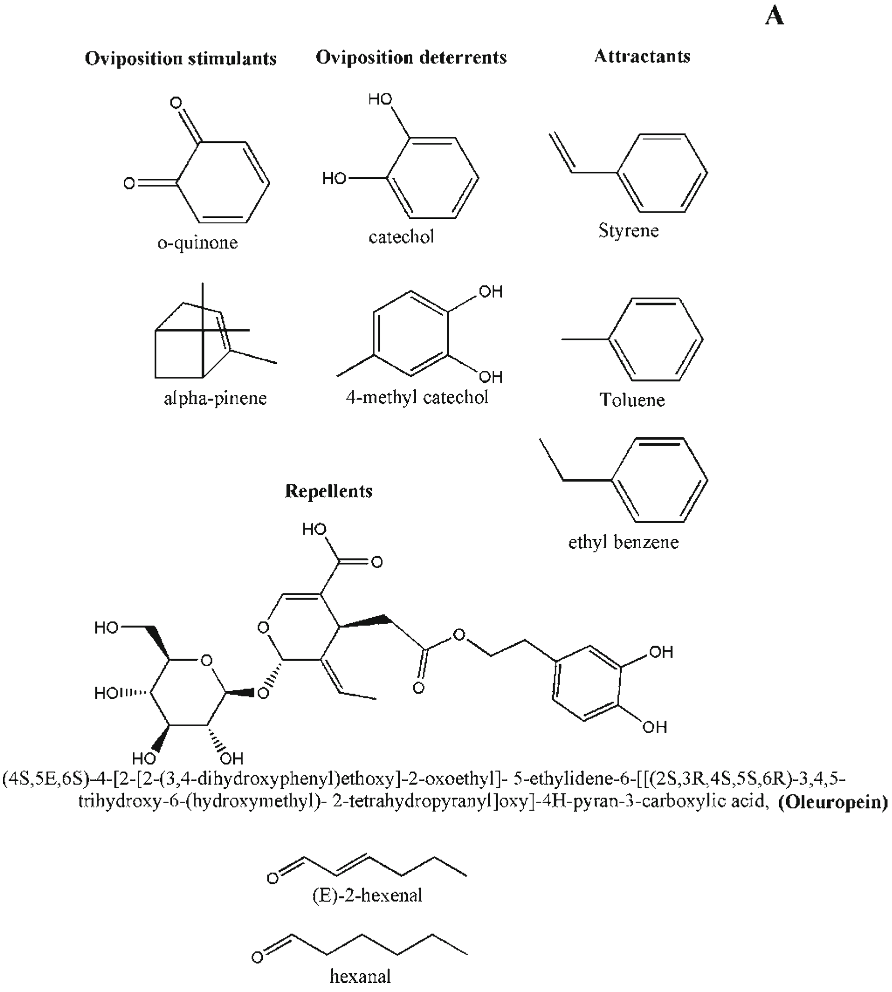

Fig. 9.2 Chemical structures of some attractants, repellents, oviposition stimulants and deterrents in *Bactrocera oleae*

flies (Scarpati et al. 1993) (Fig. 9.2). Styrene from solvent-based extracts of olive fruits and leaves has also been identified as an oviposition stimulant. Ammonia, a by-product of bacterial activity, was also found to be a potent attractant to female *B. oleae* (Scarpati et al. 1996). All these studies were done under controlled laboratory conditions. Their field evaluation will shed more light on their exact role in the chemical communication of this fruit fly species.

In addition to plant odours, there has been increasing interest in elucidating the role of microbial endosymbionts in the chemical ecology of *B. oleae*. Several microbial species have been isolated from *B. oleae* including *Pseudomonas putida* Trevisan and *Candidatus* Erwinia dacicola (Lauzon et al. 2000; Sacchetti et al.

2008). Recently, Liscia et al. (2013) demonstrated that female *B. oleae* were attracted to the volatile thioester, methyl thioacetate, found in odours produced by cultures of *P. putida*; they identified this thioester as a new volatile component within the fruit fly-associated bacterial odour that female *B. oleae* were able to perceive using receptors on their antennae and maxillary palps. The endosymbiont *Ca*. Erwinia dacicolais was more prevalent in wild populations of *B. oleae* than in laboratory-reared populations and it is suspected to affect the reproductive fitness of flies (Estes et al. 2014). These findings suggest that there is potential to develop new attractants based on odours from bacterial endosymbionts that could improve current semiochemical-based management tools for *B. oleae*.

2.3 Zeugodacus cucurbitae

Zeugodacus cucurbitae is considered polyphagous although its preferred host plants are cultivated and wild members of the family Cucurbitaceae. This preference for cucurbits, which has been demonstrated in behavioural assays, explains why *Z. cucurbitae* attacks cucumber, *Cucumis sativis* L., courgette, *Curcurbita pepo* L., bitter gourd, *Momordica charantia* L., kabocha pumpkin, *Curcurbita maxima* Duchesne, cantaloupe, *Cucumis melo* var. *cantalupensis* Naudin, ivy gourd, *Coccinia grandis* (L.) Voigt, although it also attacks tomato (Miller et al. 2004; Piñero et al. 2006). The earliest identification of a kairomone used by *Z. cucurbitae* showed that (*E*)-6-nonenyl acetate was attractive to females (Jacobson et al. 1971) and also stimulated oviposition (Keiser et al. 1973). Three decades later, Siderhurst and Jang (2010) identified several compounds in the headspace odours from ripe fruit of several cucurbit species including the aldehydes (*E,Z*)-2,6-nonadienal, (*E*)-2-nonenal, hexanal and (*E*)-2-hexenal and the alcohols (*Z*)-6-nonen-1-ol, (*E,Z*)-2,6-nonadien-1-ol and 1-hexanol; these compounds were detected by receptors on the antennae of female flies eliciting behavioural responses. Outdoor olfactometer studies demonstrated synergy between some of these headspace compounds when formulated in blends. Both a six-component blend formulated from (*E,Z*)-2,6-nonadienal, (*E*)-2-nonenal, (*Z*)-6-nonenal, nonanal, (*Z*)-6-nonen-1-ol and 1-nonanol, and a nine-component blend comprising of (*E,Z*)-2,6-nonadienal, (*E*)-2-nonenal, (*E*)-2-octenal, (*Z*)-6-nonenal,(*Z*)-6-nonen-1-ol, hexanal, 1-hexanol, acetic acid and 1-octen-3-ol (Fig. 9.3) captured substantial numbers of both male and female flies (Table 9.3) (Siderhurst and Jang 2010). These findings represent the first and most successful attempt to develop a female-biased fruit fly lure that also attracts males (Siderhurst and Jang 2010).

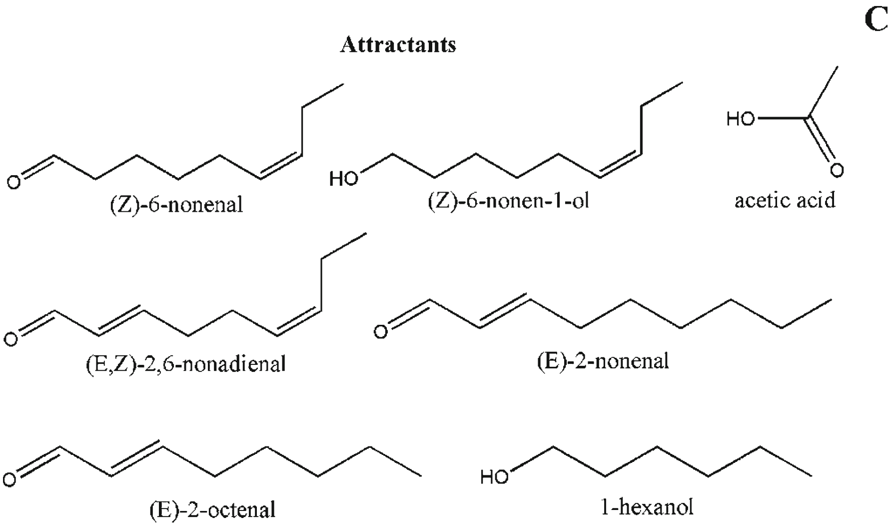

Fig. 9.3 Some examples of components from a cucurbit-based blend attractive to *Zeugodacus cucurbitae*

2.4 Bactrocera latifrons

In Africa, the solanum fruit fly, *Bactrocera latifrons* (Hendel), is an invasive oligophagous species principally infesting solanaceous crops (Ekesi and Billah 2008). Although little is known about the chemical ecology of *B. latifrons* in relation to its host plants, fresh juice from the pepper, *Capsicum annuum* L., does stimulate oviposition (Vargas et al. 1990).

2.5 Ceratitis capitata

The earliest efforts to elucidate the role of host plant odours as attractants for the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), were made by Steiner et al. (1957) who first documented the attractiveness of oil extracts from the seeds of angelica, *Angelica archangelica* L. to male and female *C. capitata*. Following this initial discovery, Beroza and Green (1963) explored the attractiveness to both sexes of extracts from a variety of hosts (i.e. plants that females can oviposit on) and non-host plants (i.e. plants that females do not oviposit on but which may provide exudates on which both sexes can feed) including lesser galangal, *Alpinia officinarum* Hance; *Anaphalis margaritacea* (L.) Benth. & Hook; other *Angelica* species; barberry, *Berberis vulgaris* L.; wintergreen, *Chimaphila umbellata* (L.) Barton; Chinese hemlock-parsley, *Conioselinum chinense* (L.) Britton, Sterne & Poggenb.; cane orchid, *Dendrobium anosmum* var *superbum*; common horsetail, *Equisetum arvense* L.; *Fabiana imbricate* Ruiz & Pav.; *Festuca* species; cow parsnip, *Heracleum lanatum* Michx.; eastern black walnut, *Juglans nigra* L.; tomato; alder buckthorn, *Rhamnus frangula* L.; Provence rose, *Rosa centifolia* L.; and common lime, *Tilia*x *europaea* L.. Oils from other host and non-host plants have also been evaluated by various authors as cited in Warthen and McInnis (1989) and most were attractive to male *C. capitata*: ylang-ylang, *Cananga oderata* (Lam.) Hook.f. & Thomson; lemon, *Citrus limon* (L.) Burm.f.; grapefruit, *Citrus paradisi* Macfad.; sweet orange, *C. sinensis*; copaiba (an extract from tree bark); gingergrass, *Cymbopogon martinii* (Roxb.) Wats.; hop, *Humulus lupulus* L.; dwarf pine, *Pinus pumilio* Haenke; Scots pine, *Pinus sylvestris* L.; and tailed pepper, *Piper cubeba* L.f.. Oil extracts from lychee, *Litchi chinensis* Sonn.; weeping fig, *Ficus benjamina* L.; Cuban laurel, *Ficus retusa* L.; and Indian banyan, *Ficus benghalensis* L. were all short range attractants and feeding stimulants for male *C. capitata* (Warthen and McInnis 1989). Subsequently, α-copaene from *A. archangelica* seed oils was identified as a potent male attractant. Solvent extracts from a wide range of non-host plants were also attractive to *C. capitata* (sexes not indicated) (Keiser et al. 1975). In field experiments Flath et al. (1994a) found that *β*-copaene and *β*-ylangene extracted from *A. archangelica* seeds were less potent male attractants than copaene.

Components of odours from the fruits of host plants can be attractive to both sexes of *C. capitata* under both laboratory and semi-field conditions; although inconsistent, the responses of females towards these odours were stronger than the responses of males. In an electrophysiological study using antennae from both sexes of *C. capitata* and components of the odours from the fruits of several host plant species revealed that the attractive component was heptanal; this was confirmed in field assays (Guerin et al. 1983). Furthermore, when host searching behaviour of females was studied on non-fruiting host plants and non-host plants, it was observed that females spent longer time on the non-fruiting host plants than on non hosts but were able to locate ripe host plant fruits placed on either host or non-host plants (Prokopy et al. 1986). Further studies found that 70 volatile components that are common in the odours of many host plants (mainly aldehydes, alcohols, acids, acetates and lactones), elicited responses in receptors on the antennae of both male and female *C. capitata*; they also responded to components of the odour of nectarines, *Prunus persica* (L.) Batsch (Light et al. 1988, 1992). Receptors on the antennae of female *C. capitata* responded strongly to both odours from 'calling' males (positive control) and from the headspace of mangoes (Cossé et al. 1995). In outdoor field-cage assays Katsoyannos et al. (1997) reported that both male and female *C. capitata* adults responded to odours from sweet oranges and also antennally-active components from another orange variety, the navel orange, that had been identified previously by Hernandez et al. (1996). Surprisingly, at this time there have been no studies on odours from coffee, *Coffea arabica* L., the ancestral host plant of *C. capitata*. However, stimulated by a heavy infestation of coffee berries by *B. dorsalis* in newly planted coffee farms (Vargas et al. 1995; 1997), studies began to identify putative fruit fly attractants associated with coffee; in wind tunnel assays six components of coffee headspace odours were attractive to female *C. capitata* including 3-methyl-1-butanal, decanal, 3-methyl-1-butanol, (*Z*)-2-pentenol, (*E*)-2-hexenol and 2-heptanone (Prokopy et al. 1998). However, in semi-field trials using outdoor

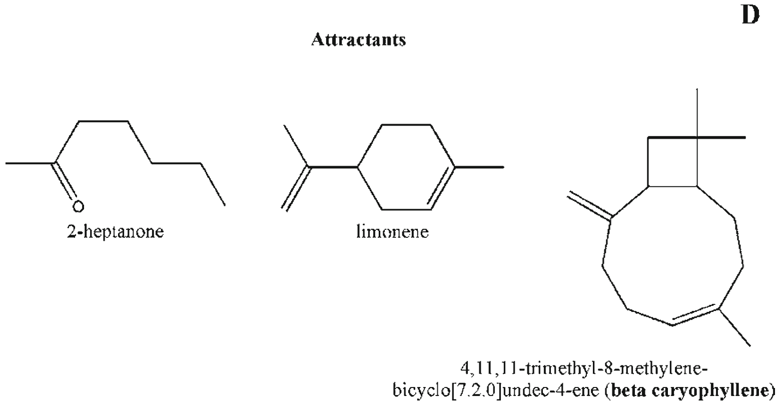

Fig. 9.4 Plant-based compounds reported to attract *Ceratitis capitata* under field conditions either singly or in combination with other attractants

cages, only 2-heptanone showed any potential as either a male or a female attractant (with more consistent results obtained with males) (Prokopy et al. 1998) (Fig. 9.4). Despite these efforts, to date, there have been no field-active plant-based attractants identified for female *C. capitata*.

In mass-rearing experiments Vargas and Chang (1991) demonstrated that, for *C. capitata*, water and the juice extracted from coffee beans were superior oviposition stimulants compared with juice from guava, papaya or orange. Oviposition deterrents have also been reported for *C. capitata* from methanolic extracts of the fern *Elaphoglossum piloselloides* (Presl.) Moore and identified as a mixture of elaphoside-A [p-vinylphenyl (β-D-glucopyranosyl)-(1 → 3)-β-D-allopyranoside] and its racemic derivative p-(1-metoxyethyl) anisole (Socolsky et al. 2003, 2008).

Although *C. capitata* attacks a variety of fruit species, in lemon only overripe or partially decayed fruits are infested suggesting that the peel of the fruit offers some degree of resistance to attack (Quayle 1914, 1929 as cited in Salvatore et al. 2004). Da Silva Branco et al. (2000) have also reported that oxygenated monoterpenes were responsible for the observed resistance to infestation. In a more systematic and organized screening of the effects of extracts from lemon peel on female oviposition, egg hatchability, and larval and adult survival Salvatore et al. (2004) demonstrated that a mixture of citral (itself a mixture of geranial and neral), 5,7-dimethoxycoumarin and linalool was insecticidal to both adults and larvae. This now requires further field evaluation.

2.6 Ceratitis rosa

The Natal fruit fly, *Ceratitis rosa* Karsch, has not been studied extensively, possibly because it is not such a serious pest of fruit compared with other fruit fly species. However, in laboratory assays *C. rosa* (sex not specified) is attracted to limonene and isoamyl acetate, which are volatile compounds from oranges and bananas, respectively (Lebusa et al. 2013) (Fig. 9.4).

2.7 Dacus *Species*

Of the six *Dacus* species found in Africa, host plant attraction has only been studied for the lesser pumpkin fly, *Dacus ciliatus* (Loew), an oligophagous pest of cucurbits (Alagarmalai et al. 2009). Using dual choice air static behavioural assay arenas, electrophysiological recordings of antennae and mass spectrometric analyses, saturated and unsaturated esters and a blend of these were identified as the odour components from Galia melon *Cucumis melo* var. *reticulatus* L. Naud. that were attractive to both male and female *D. ciliatus* (Table 9.3) (Fig. 9.5). When the terpene (*E*)-*β*-farnesene is added to this blend its activity as an attractant is masked and it becomes a deterrent (Alagarmalai et al. 2009). Field studies are now needed to confirm these laboratory findings.

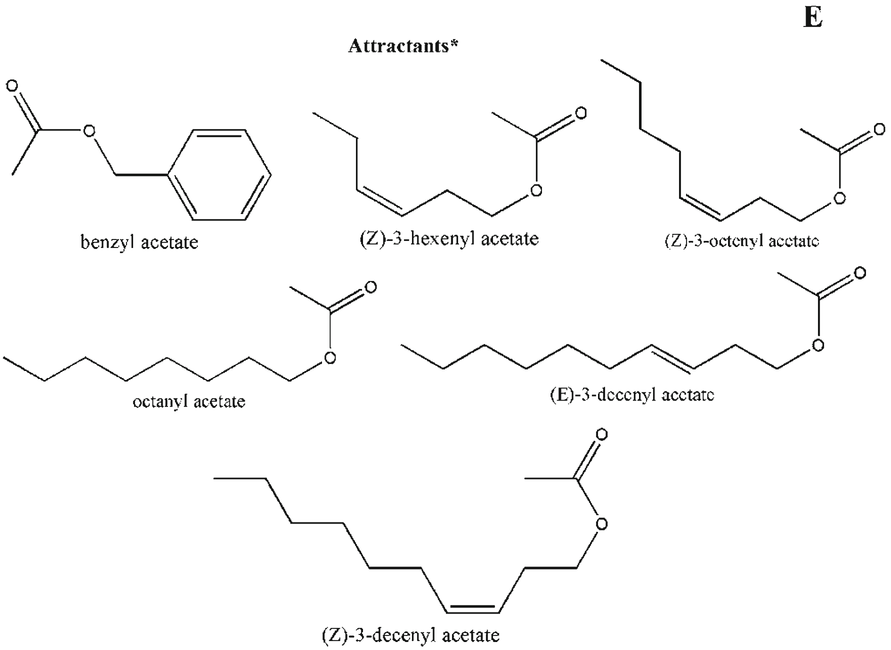

Fig. 9.5 Components of a chemical blend reported attractive to *Dacus ciliatus* in laboratory assays

3 Intraspecific Interactions

Pheromones play a crucial role in both the inter- and intraspecific interactions between fruit flies (Wyatt 2010) and are quite diverse in their behavioural function and chemical structure. There are two types of pheromone that influence the behaviour of conspecifics: sex pheromones and host-marking pheromones, the latter of which are associated with oviposition. In terms of chemical structure, they are mainly alcohols, aldehydes, ketones, esters and aromatics. Sex pheromones are released as volatile airborne chemicals and perceived via olfaction (Regnier and Law 1968), while host-marking pheromones are relatively non-volatile chemicals deposited on the surface of fruit to deter competitors after successful oviposition (Kachigamba et al. 2012). Unlike the highly volatile sex pheromones, host-marking pheromones are more persistent on the surfaces on which they have been deposited (Averill and Prokopy 1987) and, because they are usually polar in nature, they are soluble in water and methanol (Boller 1981; Averill and Prokopy 1982, 1987; Boller and Hurter 1985; Hurter et al. 1987; Aluja et al. 2003).

In African tephritids of economic importance, sex pheromones are predominantly produced by males to attract females (Sivinski and Burk 1989; Tumlinson 1989; Heath et al. 1993; Mavraganis et al. 2010). Females are also known to produce sex pheromones in a few species such as *Z. cucurbitae* (Baker and Bacon 1985), *B. dorsalis* (Baker and Bacon 1985) and *B. oleae* (Gariboldi et al. 1983). Unlike sex pheromones, host-marking pheromones are solely produced by females (Averill and Prokopy 1989). The discovery of the presence of both pheromone types dates back to the late 1950s (Féron 1959). In fruit flies, sex pheromones are secreted and stored in the rectal gland (referred to as the rectal ampulla) (Fletcher 1969; Tan et al. 2002, 2011, 2013), while host-marking pheromones are produced in the posterior half of the midgut and often released along with the faecal matter of females in host-marking species (Averill and Prokopy 1989). Amongst the fruit fly species found in Africa, sex pheromones have been documented for *B. dorsalis*, *B. oleae, Z. cucurbitae* and *C. capitata*, while host-marking behaviour, which points to the existence of a host-marking pheromone, has only been recorded in *C. capitata* and its sibling species the mango fruit fly, *Ceratitis cosyra* (Walker), *Ceratitis fasciventris* (Bezzi) and *C. rosa* (Kachigamba et al. 2012). In addition to these, lek site pheromones have also been reported for *C. capitata* (Feron, 1959, 1962; Jang et al. 1989; Siciliano et al. 2014; Shelly et al. 2014). Sex pheromones are likely to exist in every fruit fly species given their ecology. However, not all fruit fly species produce host-marking pheromones (Silva et al. 2012; Kachigamba et al. 2012). In the sub-sections that follow, a summary of the major pheromone types is provided.

3.1 **Bactrocera dorsalis** *Species Complex*

Males of the *B. dorsalis* complex produce two principal sex pheromone components that have been identified as the phenylpropanoids 2-allyl-4,5-dimethoxyphenol and (*E*)-coniferyl alcohol. These metabolites, present in the rectal gland of males, are synthesized from methyl eugenol ingested by males attracted to specific plants that are rich in this compound. Like most insects producing sex pheromones, the pheromone is released a few hours before the time of mating (Tan and Nishida 1996, 1998; Hee and Tan 1998; Khoo et al. 2000; Nishida et al. 2000; Tan et al. 2013). Females of the *B. dorsalis* complex, including one member of the complex, *Bactrocera invadens* Drew, Tsuruta and White, do not engage in host-marking behaviour after oviposition (Kachigamba 2012).

3.2 Bactrocera oleae

Females of *B. oleae* produce 1,7-dioxaspiro [5.5] undecane, α-pinene, n-nonanal and ethyl-dodecanoate as major components of their sex pheromone, with 1,7-dioxaspiro [5.5] undecane being the most attractive to males (Mazomenos and Haniotakis 1985). The identification of 1,7-dioxaspiro [5.5] undecane (‘olean’) and α-pinene as sex pheromone components was confirmed in recent studies (Levi-Zada et al. 2012; Gerofotis et al. 2013) with the latter compound demonstrated to enhance mating performance and success in both sexes of *B. oleae*. Also, females produce 1,5,7-trioxaspiro [5.5] undecane, as an additional pheromone component. Likewise, males also produce a female attractant contained in their rectal glands with the hydrocarbon (*Z*)-9-tricosene identified as one of its components (Carpita et al. 2012).

3.3 Zeugodacus cucurbitae

Although the rectal glands of male *B. curcubitae* contain a complex mixture of compounds, the most dominant and behaviourally-active of these is the diol, 1,3-nonanediol, which is a component of the sex pheromone. This compound is thought to have a dual function: as a pheromone to attract females and as a chemical defence against predation by the common house gecko, *Hemidactylus frenatus* Schlegel, which is reported to avoid fruit flies as a food source (Tan 2000). The quantity of 1,3-nonanediol in the rectal gland increases with age of the fruit fly (Nishida et al. 1993). A similar defensive phenomenon has been observed in the papaya fruit fly, *Bactrocera papaya* (Drew and Hancock), and the carambola fruit fly, *Bactrocera carambolae* Drew and Hancock, both sibling species of *Z. cucurbitae*. In *B. papaya* and *B. carambolae* the pheromone component, 6-oxo-1-nonanol, also serves as an antifeedant against the predatory spotted house gecko *Gekko monarchus* (Schlegal) (Wee and Tan 2001, 2005). Like females of the *B. dorsalis* species complex, female *Z. cucurbitae* have not been observed depositing a host-marking pheromone after oviposition (Prokopy and Koyama 1982).

3.4 Bactrocera zonata

Nishida et al. (1988) determined that the female-produced sex pheromone of *B. zonata* was composed of the phenylpropanoids 2-allyl-4,5-dimethoxyphenol and (*E*)-coniferyl alcohol. As mentioned previously, these two components are also sex pheromones for *B. dorsalis*.

3.5 Ceratitis capitata

In *C. capitata* sex pheromones are produced by males. The earliest study of this male-produced sex pheromone was done by Jacobson et al. (1973) who isolated, identified and synthesized two components from the headspace odours of males that were attractive to females: methyl (*E*)-6-nonenoate and (*E*)-6-nonen-1-ol. The complexity of the headspace odours of males was revealed in subsequent studies carried out by Baker et al. (1985) who identified nine additional components: (3,4-dihydro-2H-pyrrole, ethyl (*E*)-3-octenoate, (*E*)-3,7-dimethyl-2,6-octadienyl acetate, (*E,E*)-3,7,11-trimethyl-1,3,6,10-dodecatetraene, (*E*)-2-hexenoic acid, dihydro-3-methyl-furan-2(3H)-one, 3,5-dimethyl-2-ethylpyrazine, 2,6-dimethyl-2,7-octadien-6-ol and ethyl acetate. Behavioural assays confirmed the role of the 3,4-dihydro-2H-pyrrole (pyrroline) as a sex pheromone. Further complexity of the headspace odours was reported by Jang et al. (1989, 1994) using electrophysiology and mass spectrometry. In total, 56 components have been identified in the headspace odours of male *C. capitata*. When tested singly the five major compounds (ethyl acetate, 3,4-dihydro-2H-pyrrole, geranyl acetate, ethyl-(E)-3-octenoate and (*E,E*)-α-farnesene) elicited responses in behavioural asaays that were close to the responses to natural male odours. When combined as a blend these five components elicited responses that were indistinguishable from responses to male odours. In a similar study, Heath et al. (1991) identified geranyl acetate, ethyl-(*E*)-3-octenoate and (*E,E*)-α-farnesene as the most abundant components of the *C. capitata* sex pheromone and demonstrated their attractiveness as individual compounds and as a blend in field assays. In addition to the pheromone components, host plant volatiles such as the GLVs (*E*)-2-hexen-1-ol and (*E*)-2-hexenal increase the attractiveness of male odours to females (Dickens et al. 1990). Furthermore, Shelly et al. (2007) observed that female *C. capitata* were more attracted to males exposed to ginger root oil (GRO), with the exposed males having a higher mating frequency than those unexposed to the oil.

Males of *C. capitata* also produce a lekking pheromone which has 2-methyl-6-vinyl pyrazine as one of its components to attract females to lek sites (Chuman et al. 1987; Shelly 2001). Furthermore, female *C. capitata* deposit a host-marking pheromone on fruits after oviposition to deter other gravid females from laying on the same fruit (Prokopy et al. 1978; Arredondo and Diaz-Fletcher 2006).

3.6 Other Ceratitis *Species*

Until recently, little was known about sex communication in sibling species of the *Ceratitis* genus including *C. cosyra*, *C. fasciventris* and *C. rosa*, commonly known as the *Ceratitis* FAR complex. This complex has now been resolved based on larval morphology, developmental biology under different temperature regimes, and airborne volatiles and cuticular hydrocarbons (CHCs) associated with adults of these species (Steck and Ekesi 2015; Tanga et al. 2015; Břízová et al. 2015; Vaníčková et al. 2015). Břízová et al. (2015) demonstrated that adult male flies of the three species formed leks (Aluja and Norrbom 2001) in response to specific male odours detected also by females, suggesting a pheromonal role of male odours. Using GC/MS and GC/EAD analyses, twelve antennally-active components in male odours were detected by female antennae. Five of these components, namely methyl (*E*)-hex-2-enoate, 6-methyl-5-hepten-2-one, linalool, (*E*)-non-2-enal and methyl (2*E*, 6*E*) farnesoate were common to all three species. On the other hand, whereas (*E*,*E*)-α-farnesene was common to the male odours from both *C. anonae* and *C. rosa*, geranyl acetone was only identified from the male odours of *C. rosa*. The remaining five components (methyl (*E*)-hex-3-enoate, methyl (*E*)-hex-2-enoate, ethyl (*E*)-hex-3-enoate, ethyl (*E*)-hex-2-enoate and methyl (*Z*)-oct-3-enoate) were specific to *C. fasciventris*.

A similar study examined the cuticular hydrocarbon profiles of two *C. rosa* morphotypes derived from lowland (coastal) and highland regions of Kenya and reported their discriminatory potential. Using two-dimensional GC/MS, hydrocarbons with carbon backbones that ranged from C_{14} to C_{37} were identified (Vaníčková et al. 2015). These cuticular hydrocarbons, comprising n-alkanes, monomethyl alkanes, dimethylalkanes and unsaturated hydrocarbons varied qualitatively between the sexes in each morphotype and quantitatively between the morphotypes. Amongst these compounds, C_{29}, C_{31}, C_{33} and C_{35} hydrocarbons were thought to contribute to the differential sensitivity and tolerance of the different morphotypes to different temperature regimes. These authors also reported sexual dimorphism in the cuticular hydrocarbons produced, as potential short-range pheromones involved in the mating of *C. rosa*.

Aside from their apparent display of olfactory and tactile-based communication via volatile compounds and cuticular hydrocarbons, these species also display host-marking behaviours, suggestive of an ability to produce host-marking pheromones (Kachigamba et al. 2012).

4 Male Lures

Worldwide, male lures, also known as male attractants, have been used extensively for fruit fly detection, monitoring and mass trapping. They can be natural or synthetic compounds and are known to attract only male fruit flies. In Africa, fruit fly detection, monitoring and mass-trapping using synthetic pheromones, or parapheromones, has been reported in countries such as Mozambique (Correia, et al. 2008), Ghana (Appiah, et al. 2009) and Sudan (Ali et al. 2014). A comprehensive list of key male lures used in detection, monitoring or mass-trapping programmes has been compiled by Ekesi and Billah (2008).

4.1 **Bactrocera dorsalis** ***Species Complex***

Nishida et al. (1997) found that males of *B. dorsalis* were strongly attracted to a number of phenylpropanoid compounds from the perfume flower tree, *Fagraea berteroana* Gray ex Benth: (*E*)-3,4-dimethoxycinnamyl alcohol, its acetate, and (*E*)-3,4-dimethoxycinnamaldehyde. Since then many researchers have reported additional male lures. Males of *B. invadens* are attracted to methyl eugenol in the field (Sidahmed et al. 2014) and laboratory assays have identified additional candidate compounds to attract males, such as 4-methyl-3-penten-2-one and 4-hydroxy-4-methyl-2-pentanone (Kimbokota and Torto 2013). In a recent study the odorant receptor for methyl eugenol was identified (Zheng et al. 2012). The authors discovered a cDNA encoding a *Drosophila melanogaster* Meigen odorant receptor co-receptor (Orco) ortholog in *B. dorsalis*. Using qRT-PCR analysis they established that the Orco was abundantly expressed in the antennae of adult male *B. dorsalis*. Interestingly, a number of volatile compounds derived from the fruit of mango, marula and Indian almond, *Terminalia catappa* L., can also be used to attract both males and females of *B. dorsalis* (Kimbokota et al. 2013). Blends of volatile compounds derived from banana, guava and orange fruits also have potential as attractants (Tables 9.1 and 9.3) (Biasazin et al. 2014). Other examples of compounds attractive to male *B. dorsalis* are synthetic fluorinated analogues of methyl eugenol including 1,2-dimethoxy-4-fluoro-5-(2-propenyl) benzene (Khrimian et al. 2009), 1-fluoro-4,5-dimethoxy-2-(3,3-difluoro-2-propenyl benzene and 1-fluoro-4,5-dimethoxy-2-(3-fluoro-2-propenyl) benzene (Jang et al. 2011).

4.2 **Zeugodacus cucurbitae**

It is known that male *Z. cucurbitae* are attracted to 4-(4-hydroxyphenyl)-2-butanone (cuelure), which is found in flowers of the orchid *D. anosum* var *superbum* (Nishida et al. 1993). However, attraction of this fruit fly species to cuelure is age dependent (Wong et al. 1991).

4.3 **Bactrocera latifrons**

Males of this fruit fly species are strongly attracted to α-ionone and α-ionol (Flath et al. 1994b). In field assays, the attractiveness of α-ionone and α-ionol was enhanced when combined with either cade oil or eugenol; however, the key components of cade oil responsible for this increased attractiveness were not determined (McQuate and Peck 2001; McQuate et al. 2004, 2013). Ishida et al. (2008) and Enomoto et al. (2010) demonstrated the improved attractiveness and phagostimulatory activity of α-ionone, α-ionolin combination with 3-oxygenated α-ionone-based synthetic derivatives, and isophorone in combination with isophorol, with the latter two recovered as secondary metabolites from the rectal gland of males. Further, they observed that mixing isophorone or isophorol with α-ionol enhanced the attractiveness of the lure to males.

4.4 Bactrocera zonata

Of the *Bactrocera* species, semiochemical-based host plant interactions in the polyphagous peach fruit fly *Bacterocera zonata* (Saunders) are the least studied (El-Sayed 2015). Methyl eugenol, putrescine, ammonium acetate and protein baits are the known and most potent commercially available male lures for this species (EPPO 2015).

4.5 Ceratitis capitata

Male *C. capitata* are attracted to tert-butyl 4-(and 5)-chloro-(*E*)-2-methylcyclohexanecarboxylate (Doolittle et al. 1990; Khrimian et al. 2003), which is a component of Trimedlure (a synthetic lure comprising eight esters of methylcyclohexanecarboxylic acid), a commercial lure used in the monitoring and mass trapping of this fruit fly species. Male *C. capitata* are differentially attracted to the different trans isomers found in ceralure (CRL), a commercial attractant composed of a mixture of four isomers of methylcyclohexanecarboxylic acid esters (Warthen et al. 1994). These authors showed that one isomer, ethyl (*Z*)-5-iodo-trans-2-methylcyclobexane- 1-carboxylate, or CRL-BI, was more attractive than the other isomers including (1,l-dimethylethyl 4- (and 5-) chloro- (*E*)- 2-methylcyclohexane-l-carboxylate), and (1,1-dimethylethyl (*Z*)-4-chloro-(*E*)-2-methylcyclohexane-l-carboxylate) when they were compared directly on an equal weight basis. In tests with two stereo-selectively-synthesized enantiomers of CRL-B1, which is a potent lure for male *C. capitata*, the (−) CRL-B1 enantiomer attracted significantly more males than the (+) CRL-B1 antipode (Jang et al. 2001). More recently, it has been shown that male *C. capitata* are attracted to α-copaene (Shelly 2013).

5 Summary and Future Directions

This review demonstrates that there are a diverse range of semiochemicals that mediate host location and reproductive biology in African tephritid fruit flies. This has been possible as a result of advances in the chemical analytical techniques available. Some species of fruit flies have been extensively investigated whereas others have received minimal attention, partly because of their economic importance. Nonetheless, irrespective of the fruit fly species, the identified semiochemicals elicited responses in target sexes when presented either singly or in multi-component blends. This review also revealed that a few of the semiochemicals are of microbial origin and that others play a role in fruit fly defence against natural enemies. Notably, only a few of the semiochemicals identified have been evaluated in the field and there are only a limited number of lures targeted at males that have proved to be effective for monitoring and control of fruit flies. The use of semiochemicals for the control of female fruit flies has only been successful for *Z. cucurbitae*. Therefore, much still remains to be done for control of females of other fruit fly species. The elucidation of the molecular mechanisms underlying the olfactory perception of methyl eugenol in *B. dorsalis* is exciting. A similar approach could be employed for some of the other promising semiochemicals identified for other fruit fly species and this would help us move towards development of more effective environmentally-friendly control tools for these species.

Acknowledgements The research activities were partly funded by grants from GIZ/BMZ and USDA.

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