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REVIEW ARTICLE

Functional significance of phytochemical lures to dacine fruit flies (Diptera: Tephritidae): an ecological and evolutionary synthesis

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Abstract

While lures of plant origin are vital tools in dacine (Diptera: Tephritidae) pest management, the ecological and evolutionary significance of this lure response remains enigmatic. Two hypotheses (the ancestral host hypothesis and sexual selection by female choice) have been invoked to explain the functional significance of these chemicals to dacine fruit flies. These hypotheses are often treated as alternatives to one another and evidence favouring one is used to reject the other. This review highlights that these two hypotheses are not logical alternatives to each other as the ancestral host hypothesis attempts to explain the ultimate function of the response of Dacinae to these plant-derived parapheromones while the sexual selection hypothesis provides a proximate explanation for lure response. Research on lure response, dacine mating behaviour, functional significance of lures, plant phylogeny and biochemistry and dacine pheromone chemistry are used to evaluate the evidence in relation to both these hypotheses. Some of the key findings are that there is evidence both in support of and against these two hypotheses. Response of fruit flies to related phenyl propanoids to those commonly used as lures in pest management and distribution of phenyl propanoids attractive to dacines among plant orders strongly support the ancestral host hypothesis. Evidence from pheromone chemistry, dacine mating behaviour and the functional significance of lures both support and contradict the sexual selection hypothesis. Lures appear to have different proximate functions in different dacine species. Considerably greater research is needed to clarify the functional role of phytochemical lures to dacine fruit flies. The two prevalent hypotheses should be investigated independently. Specific research on dacine phylogeny and distribution of lures in plants in relation to ecological roles played by adult dacines is required to elucidate the ultimate roles of the chemicals. Exploration of female response to lures and the behavioural consequences of dacine response to these chemicals to both the insect and plant may shed light on the proximate functions of these chemicals.

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Introduction

The identification of bombykol in 1959 as a pheromone emitted by female moths is often credited as being a key stimulus to the field of chemical ecology (Karlson & Butenandt, 1959; Mori, 1997). However, nearly a century prior to the chemical characterization of the pheromone, the French naturalist Jean-Henri Fabre had made observations that male moths flew considerable distances, attracted to a female moth caged in his laboratory. In fact Fabre had speculated that the females were emitting something that was attracting the males (Fabre, 1912). Similarly keen, albeit serendipitous observation, was also significant as a forerunner to the discovery of attractants used widely in dacine research today.

Nearly half a century prior to the characterization of bombykol, Howlett (1912) discovered that the citronella oil used by a neighbour to repel mosquitoes was actually attracting a dacine pest species, *Bactrocera zonata* (Saunders) (Diptera: Tephritidae). A subsequent study (Howlett, 1915) demonstrated that methyl eugenol was the active constituent in citronella oil attractive to flies. A similar accident led to the discovery that kerosene was attractive to the Mediterranean fruit fly, *Ceratitis capitata* Weidemann (Diptera: Tephritidae) (Severin & Severin, 1913), and the subsequent systematic search and determination of attractants for this tephritid species (Cunningham, 1989a). While these discoveries and the resultant synthetic production of 'lures' are of tremendous applied entomological value (Metcalf & Metcalf, 1992), the proximate (ecological) and ultimate (evolutionary) functional significance of these chemicals remain largely unresolved.

This review explores the significance of the group of plant-derived secondary chemicals collectively known to tephritid biologists as parapheromones or 'lures' (Cunningham, 1989b). First, the biosynthetic pathways that lead to the formation of these chemicals are presented. Then the two principal hypotheses, viz. the ancestral host hypothesis and the sexual selection hypothesis, invoked in explaining dacine response to lures are elaborated upon. The ancestral host hypothesis provides an evolutionary or ultimate explanation for dacine response to lures, while the sexual selection provides an ecological/ behavioural or proximate explanation to dacine response to lures. They are therefore not alternatives to each other. Rather, they may collectively help explain the ecological and evolutionary significance of dacine lures. A synthesis of the known information is used to evaluate the evidence in support of the two hypotheses, both in the context of organic biochemical pathways, the ecology of the Dacinae and recent developments in plant physiology and phylogenetics.

Biosynthesis of lures

Plant metabolism is broadly classified into primary metabolism, involving those biochemical processes directly supporting growth, development and reproduction, and secondary metabolism, encompassing those processes not directly involved in the aforementioned processes. The products of secondary metabolism are usually more restricted in occurrence or distribution (fig. 1, Edwards & Gatehouse, 1999). The use of the term 'secondary' does not imply a hierarchy of importance to plant function, as illustrated by the variety of roles played by secondary compounds in plant defence and the facilitation of pollination (Swain, 1977; McKey, 1979; Berenbaum, 1995; Haslam, 1995). Likewise, the term 'primary' is unnecessarily restrictive as primary metabolites may play roles normally considered the domain of secondary compounds (Berenbaum, 1995). The application of these labels is often the result of historical precedent, rather than as a result of physiological reasoning (Berenbaum, 1995; Haslam, 1995; Edwards & Gatehouse, 1999).

Secondary chemicals permeate the external surface of plants in various conspicuous (e.g. waxes, odours, resins)

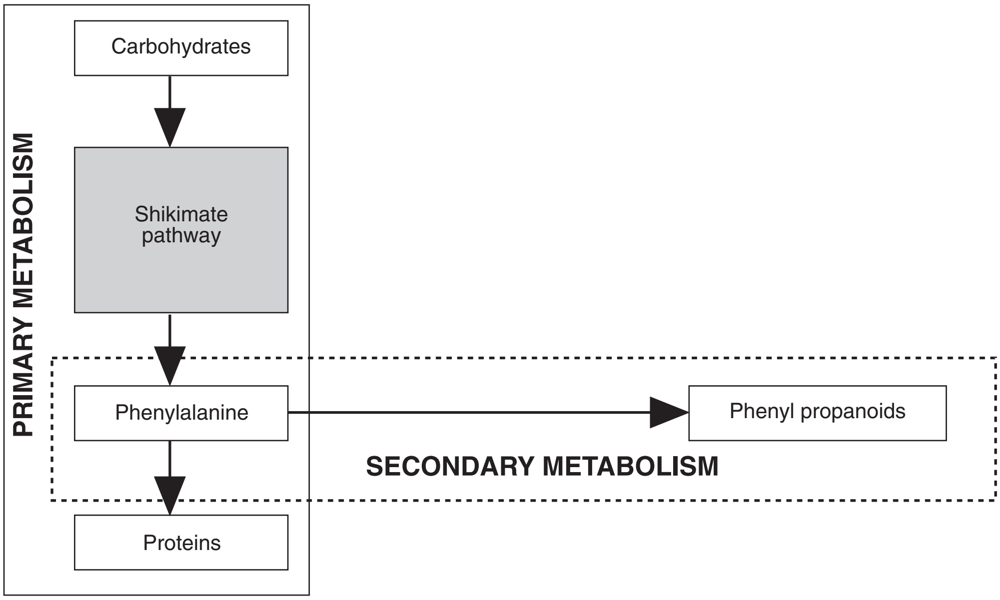

Fig. 1. Schematic illustration of origin of secondary metabolic pathway that leads to biosynthesis of dacine attractants (adapted from Haukioja *et al.*, 1998).

and not so conspicuous forms and mediate the interaction of plants with other components of their environment (Haslam, 1995). The secondary chemicals that dacine biologists are most familiar with are those that are used as attractants/lures in the monitoring and management of pest, and survey of non-pest fruit flies.

The two principal dacine lures are 4-(*p*-acetoxyphenyl-2-butanone) and 4-allyl-1,2-dimethoxy-benzene, commonly known as cuelure and methyl eugenol respectively (Cunningham, 1989a,b). These chemicals belong to the class of organic compounds based on a C_6–C_3 skeleton referred to as phenyl propanoids (Friedrich, 1976). The shikimic acid/shikimate pathway is the main biosynthetic route by which these aromatic compounds are produced from carbohydrates (fig. 1) (Herrmann, 1995a,b; Matsuki, 1996; Herrmann & Weaver, 1999). An end product of the shikimate pathway is the aromatic amino acid phenylalanine that serves as the precursor to phenyl propanoids in biological systems (Herrmann, 1995a,b; Haukioja *et al.*, 1998; Herrmann & Weaver, 1999; Schmid & Amrhein, 1999).

The biosynthesis of dacine lures from *p*-hydroxycinnamic acid (*p*-coumaric acid), derived from phenylalanine, is fairly well understood. The SCoA derivative of *p*-hydroxycinnamic acid serves as the starting point for cuelure synthesis. Conjugation with malonyl CoA, decarboxylation, oxidation and dehydrogenation results in the formation of 4-(*p*-hydroxyphenyl-2-butanone), commonly known as raspberry ketone. Acetylation of raspberry ketone results in the

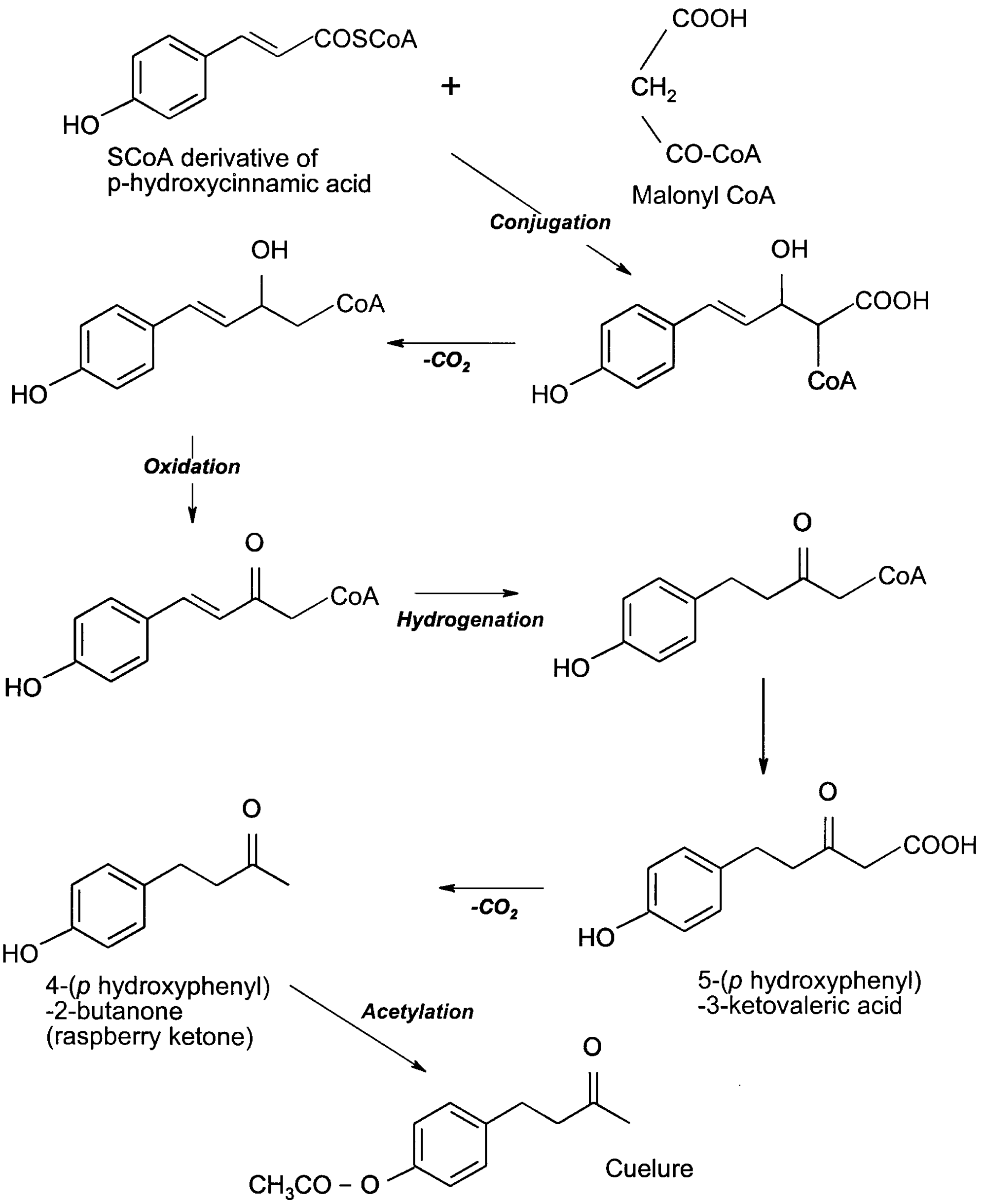

Fig. 2. Hypothesized biosynthetic pathway for raspberry ketone and cuelure (adapted from Geismann & Crout, 1969; Friedrich, 1976; Metcalf, 1979).

formation of 4-(*p*-acetoxyphenyl-2-butanone), cuelure (fig. 2) (Geissman & Crout, 1969; Friedrich, 1976; Metcalf, 1979; Metcalf & Metcalf, 1992). Cuelure is not known to occur in nature and is only found in its analogous form as raspberry ketone.

The biosynthesis of methyl eugenol from *p*-hydroxycinnamic acid is achieved through a process of reduction of the –COOH group, hydroxylation and subsequent O-methylation (fig. 3).

Dacine attractive phenyl propanoids are known to occur in several plant groups among the monocots (fig. 4) and the eudicots (fig. 5).

Ecological and evolutionary basis for dacine attractance to 'lures'

The biological basis for the attractance of chemicals used as lures has intrigued several researchers since their discovery by Howlett (1912). The different explanations put forward fall within two broad categories. One school of thought (Metcalf, 1979, 1987; Metcalf *et al.*, 1979, 1981, 1983) was interested in explaining the evolutionary origin of dacine response to these plant-derived chemicals (i.e. ultimate function) and hypothesized that lures functioned as kairomones. The contemporary approach to dacine attraction to lures is that these chemicals are pheromone precursors that play a proximate role in the sexual behaviour of dacine fruit flies (Shelly & Dewire, 1994; Shelly *et al.*, 1996; Nishida *et al.*, 1997; Tan & Nishida, 1998; Shelly, 2000). In this section these two hypotheses are elucidated.

Ultimate explanations – 'ancestral host hypothesis'

Metcalf (1979, 1987, 1990; Metcalf & Metcalf, 1992) erected this hypothesis to explain the strong response of several dacine species to one of two naturally occurring phenyl propanoids, i.e. raspberry ketone or methyl eugenol. The ancestral habit of Dacinae is believed to be saprophagy and they are hypothesized to have developed an association with rotting fruits (Rohdendorf, 1974; Labandeira, 1997; Korneyev, 2000). Therefore, coumaric acid and its derivatives in rotting fruit probably served as a kairomone regulating the behaviour of ancestral dacines. The positive response of *Bactrocera cucurbitae* Coquillett to *p*-hydroxycinnamic acid and the absence of a similar response by *Bactrocera dorsalis* Hendel (a methyl eugenol responding fly) to the same, suggested that the chemoreceptors in *B. cucurbitae* are more ancient (Metcalf *et al.*, 1983). Based on this evidence, Metcalf (also see White, 2000) suggested that species responding to raspberry ketone were more closely related to the ancestral dacines that evolved in association with plants containing cinnamic acid derivatives. Subsequent evolution of oxygenase enzymes in plants resulted in the transformation of *p*-hydroxycinnamic acid into raspberry ketone and methyl eugenol (figs 2, 3). The processes of acetylation and methylation rendered these derived aromatics lipophilic, and they were subsequently integrated into essential oils. Adaptation of the antennal chemoreceptors of dacines through small mutational changes to these new substances is hypothesized to have followed (Metcalf *et al.*, 1979, 1981, 1983). This

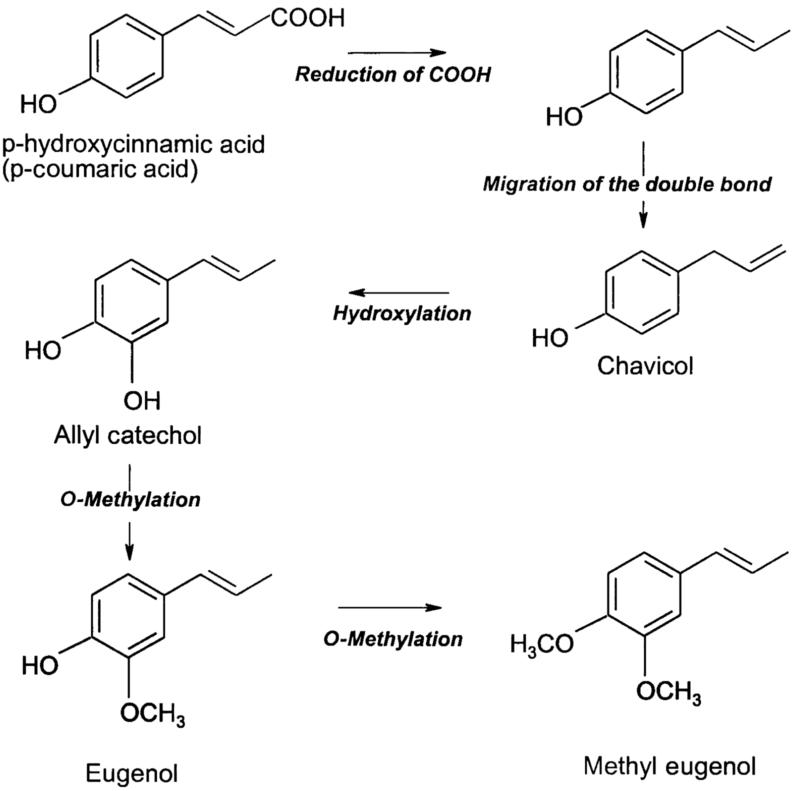

Fig. 3. Hypothesized biosynthetic pathway for methyl eugenol (adapted from Geismann & Crout, 1969; Friedrich, 1976; Metcalf, 1979).

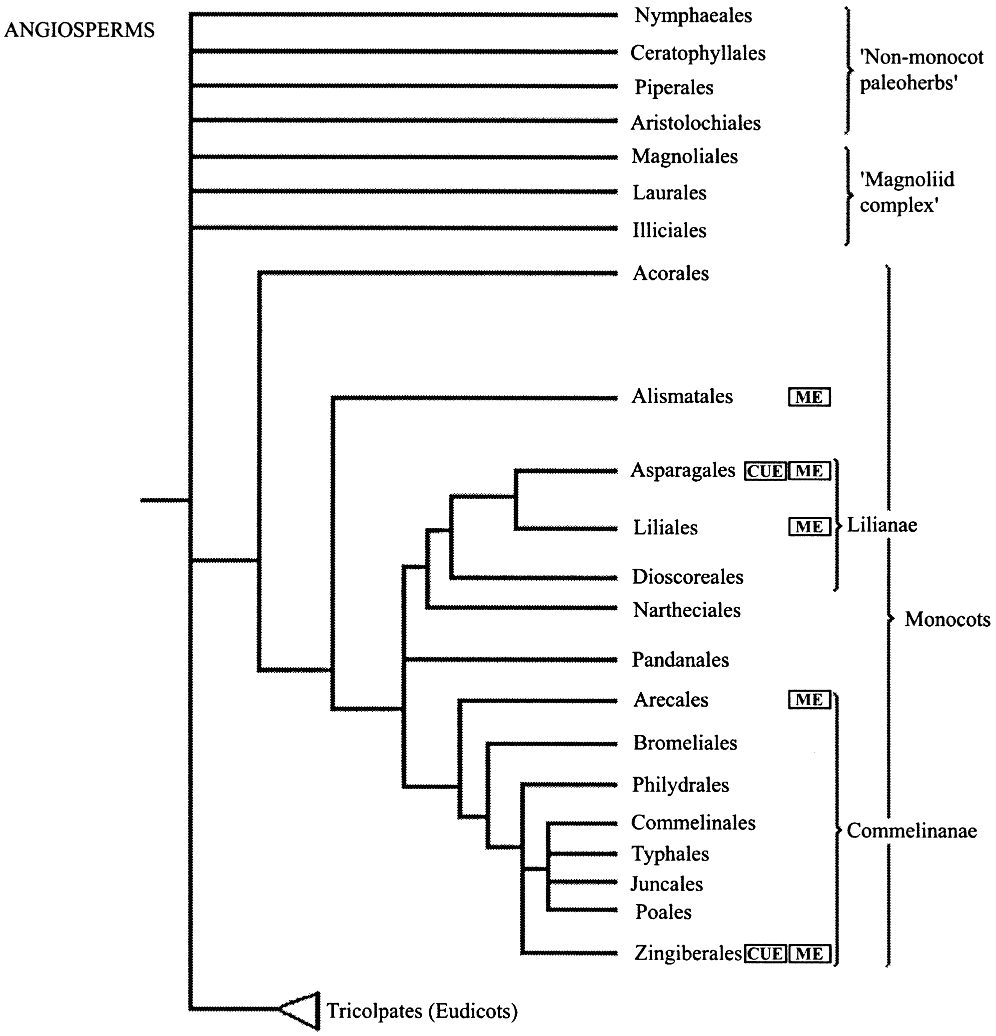

Fig. 4. Cladogram of 'primitive'/basal angiosperms highlighting Orders in which phenyl propanoids attractive to dacine fruit flies are present. ME represents methyl eugenol and its derivatives and CUE represents raspberry ketone and its derivatives. (Angiosperm phylogeny from Judd *et al.*, 1999, data for distribution of dacine attractants from Nursten, 1970; van Buren, 1970; Fletcher, *et al.*, 1975; Thien *et al.*, 1975; Hokkanen *et al.*, 1980; Hirvi, *et al.*, 1981; Gallois, 1982; Hirvi & Hokkanen, 1984; Lewis *et al.*, 1988; Marco *et al.*, 1988; Metcalf, 1990; Metcalf & Metcalf, 1992; Knudsen *et al.*, 1993; Fletcher & Kitching, 1995; Dudareva *et al.*, 1999; Shelly, 2000.)

coevolutionary process is believed to have led to the diversification of dacines in association with the diversification of essential oils in angiosperms (Metcalf, 1979, 1990) (figs 4, 5). The term 'ancestral host hypothesis' for Metcalf's hypothesis was suggested by Tallamy *et al.* (1999).

Metcalf (1987, 1990; Metcalf & Metcalf, 1992) briefly discussed the proximate significance of these chemicals in the behavioural ecology of dacines, arguing that they were principally kairomones, possibly serving as an aggregation chemical for the location of mates or as oviposition stimulants in females (Metcalf *et al.*, 1983). Howlett (1915) had made a similar speculation about the functional significance of these chemicals.

Proximate explanations – sexual selection by female choice

A hypothesis that has been erected in place of the ancestral host hypothesis contends that these phenyl propanoids are precursors to the male sex pheromone and have a role to play in the sexual behaviour of dacines (Fitt, 1981a,b). Female dacines have been demonstrated to have the ability to discriminate between potential mates indicating that sexual selection could be operating in this group (Poramarcom & Boake, 1991). Sexual selection by female choice has subsequently been invoked as the explanation for the attraction of dacine fruit flies to lures (Shelly & Dewire, 1994; Shelly & Villalobos, 1995; Shelly *et al.*, 1996a,b; Nishida *et al.*, 1997; Tan & Nishida, 1998; Shelly, 2000).

Dacine parapheromones elicit strong anemotaxis in male flies and, at least in some species, an equally strong chemotactic feeding response (Meats & Hartland, 1999; Meats & Osborne, 2000; Raghu & Lawson, 2003). Metabolites of these chemicals are then integrated into the rectal gland of adults (Fletcher, 1968; Nishida *et al.*, 1988, 1993, 1997), an organ considered to play a role in the synthesis of the male sex pheromone (Fletcher, 1968; Nation, 1981; Koyama, 1989).

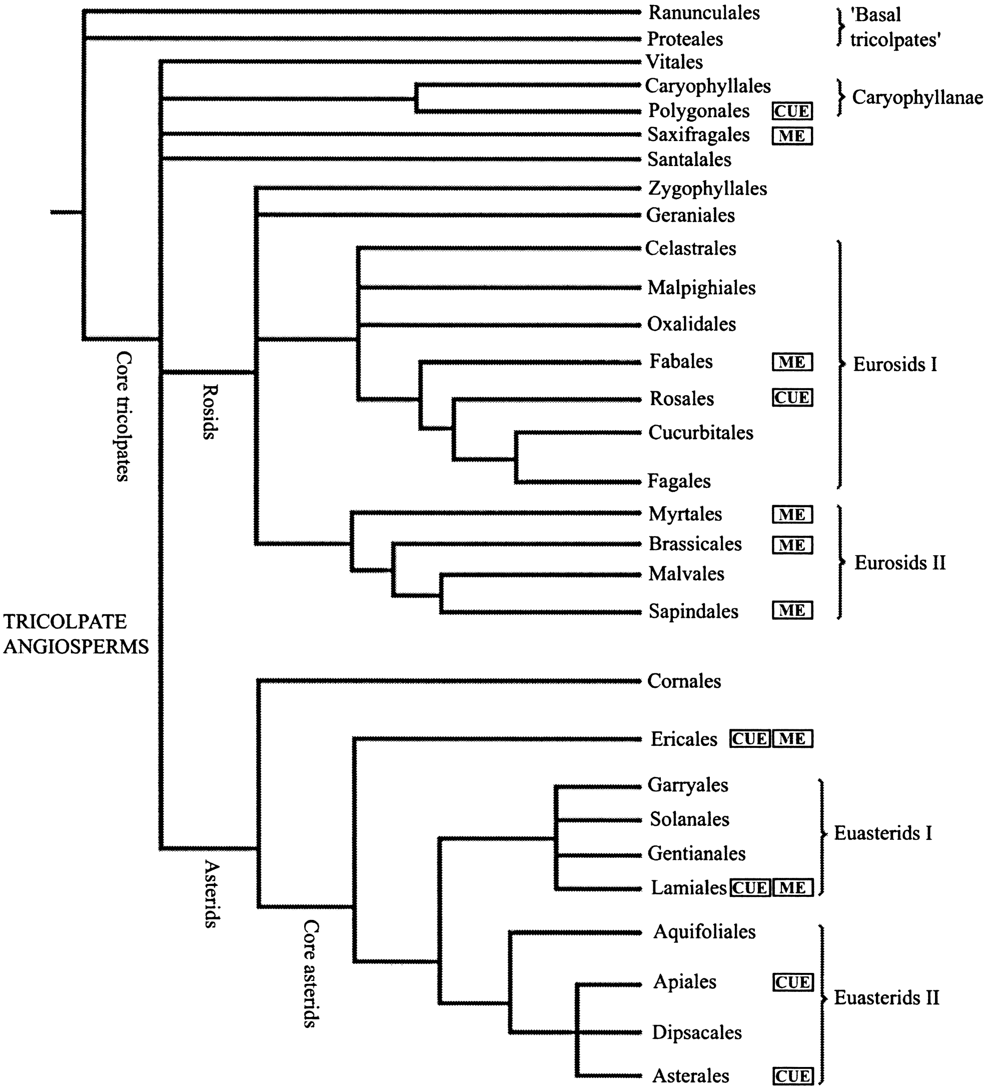

Fig. 5. Cladogram of tricolpate (eudicot) angiosperms highlighting Orders in which phenyl propanoids attractive to dacine fruit flies are present. ME represents methyl eugenol and its derivatives and CUE represents raspberry ketone and its derivatives. (Angiosperm phylogeny from Judd *et al.*, 1999, data for distribution of dacine attractants from Nursten, 1970; van Buren, 1970; Fletcher *et al.*, 1975; Thien *et al.*, 1975; Hokkanen *et al.*, 1980; Hirvi, *et al.*, 1981; Gallois, 1982; Hirvi, & Hokkanen, 1984; Lewis *et al.*, 1988; Marco *et al.*, 1988; Metcalf, 1990; Metcalf & Metcalf, 1992; Knudsen *et al.*, 1993; Fletcher & Kitching, 1995; Dudareva *et al.*, 1999.)

Feeding on lures enhances mating success, with females preferentially mating with lure-fed males over unfed males (Shelly & Dewire, 1994; Shelly *et al.*, 1996a,b; Nishida *et al.*, 1997; Tan & Nishida, 1998; Shelly, 2000). Trends in mating success are not as strong in cuelure responding flies in comparison to methyl eugenol responding flies (Shelly & Villalobos, 1995) and were not apparent in the methyl eugenol responding *Bactrocera cacuminata* (Hering) (Raghu & Clarke, 2003b). However, there are no observable benefits to females mating with lure-fed males in terms of fecundity or subsequent egg hatch (Shelly, 2000). Shelly & Dewire (1994) and Shelly (2000) have suggested that by preferentially mating with lure-fed males, a female may be serving to increase the odds that her sons have a higher ability to forage for these chemicals and subsequently have an enhanced mating success. In sexual selection terms, response to lures could therefore be a trait under runaway selection, where female choice confers her sons an advantage in sexual competition whilst the benefits of choice in the context of offspring viability are arbitrary (Andersson, 1994). Additional benefits to flies that have fed on these lures such as defence against predators (i.e. allomonal function) have been suggested (Nishida & Fukami, 1990; Tan & Nishida, 1998; Tan, 2000). These proximate pharmacophagous functions are therefore believed to be maintaining the strong response of male dacines to cuelure and methyl eugenol.

Synthesis – evaluating the evidence

The evidence against which the two above-mentioned hypotheses can be evaluated, falls into seven main categories.

Male-biased response to synthetic lures

Traps baited with phenyl propanoids lures are the principal method of assessing population dynamics of dacine fruit flies, are vital tools in taxonomic surveys and are used extensively in quarantine surveillance. While the response of virgin females to these chemicals is documented in a few species (see later section), the evidence from such surveys is that the synthetic dacine lures are principally male attractants, with females rarely trapped (Metcalf *et al.*, 1979; Metcalf & Metcalf, 1992).

While Metcalf's coevolutionary explanation may account for the origin of dacine response, it fails to account for the current sex-biased response to lures. If these chemicals serve as mating aggregation stimuli, then one would anticipate a more regular encounter of female flies in trapping surveys. Possible explanations for why we do not observe female response to lures in traps are explored below.

Lures are not mating aggregation stimuli

Metcalf's proximate explanation may be wrong and that these lures do not serve a role as a mate rendezvous stimulus or female attractant in most species. Very few studies have documented such a role for dacine attractants (Fitt, 1981a; Raghu & Clarke, 2003b).

Sensory thresholds

Concentrations of these volatiles from natural sources are not known. It is almost certain that the dose of the pure form of lure used in traps, usually 5 ml, well exceeds the natural volumes of these substances and the sensory thresholds of dacines (Metcalf, 1987). If females have a lower threshold of response than males, they may be distributed at the periphery of the odour plume gradient from the traps and as a result may never enter the trap. But such a difference in sensory thresholds is unlikely if these chemicals play a role in bringing the sexes together for mating.

Disruption of the mate recognition system

The entire mating systems of most dacines are unknown. Lure-baited traps incorporate a contact insecticide (usually 1 ml of the organophosphate malathion). If males are the first to arrive at the mating rendezvous site based on olfaction, then any subsequent male signals (visual, olfactory or auditory) that may form part of the signal-response chain in the fly's mate recognition system (*sensu* Paterson, 1993) will be absent following the males' poisoning. Alyokhin *et al.* (2001) reported that in malathion-baited traps, males were killed on contact prior to exhibition of any calling behaviour.

Females may orientate to a mate rendezvous site by a combination of olfactory and visual stimuli, while males may only use the former. The absence of a visual stimulus at a standard methyl eugenol trap (as was used by Brieze-Stegeman *et al.* (1978)) may therefore impede orientation of females towards lures. Meats & Osborne (2000) found that orientation to lures in male *B. cacuminata* was enhanced by combining olfactory and visual cues.

Female response to lures in specific circumstances

While the strong male-biased response in trapping surveys strongly counters Metcalf's hypothesized proximate function of lures as mating rendezvous stimuli, female flies do respond to lures in specific circumstances. Steiner *et al.* (1965) reported the appearance of female *B. dorsalis* flies in traps at the end of male annihilation programmes when males from the population were depleted and other researchers have reported similar results recently (Abraham & Verghese, 1998). Allan Allwood (personal communication) recorded a similar phenomenon in the fruit fly eradication programme on Nauru when females of the mango fruit fly, *Bactrocera frauenfeldi* (Schiner) outnumbered the males in cuelure-baited traps when populations were low. Such female response has also been documented in the related tephritid species, *C. capitata* (Nakagawa *et al.*, 1970). More recently, both sexes of the univoltine Chinese citrus fruit fly, *Bactrocera* (*Tetradacus*) *minax* (Enderlein), have been documented as responding to methyl eugenol at the time of their life cycle when they are just reaching sexual maturity (R.A.I. Drew and C. Dorji, personal communication). Such behaviour suggests a functional role for these lures to female Dacinae.

Evidence from *B. cacuminata* (Raghu & Clarke, 2003b) clearly suggests that methyl eugenol functions as a mate rendezvous stimulus. Such response is not unique. Virgin females of *Bactrocera opiliae* Drew & Hardy, *Bactrocera aquilonis* May and *Bactrocera tenuifascia* May all respond to their respective phenyl propanoid lures at times of day corresponding to peak periods of sexual activity (Fitt, 1981b).

Response to other related phenyl propanoids

The two major dacine lures (i.e. cuelure and methyl eugenol) attract over a 100 species of dacine flies each (table 1, R.A.I. Drew, personal communication). However, roughly a third of all dacine species have no known lure record (table 1) (Metcalf & Metcalf, 1992), suggesting that there are perhaps other phenyl propanoids that would be more attractive to these dacines than the two widely used lures. This is substantiated by the fact that certain dacine species respond to related phenyl propanoids, but neither to cuelure nor methyl eugenol. Examples of these include the response of *Dacus vertebratus* Bezzi to methyl *p*-hydroxybenzoate (Hancock, 1985) and *Bactrocera latifrons* Hendel to α-ionol (4-(2,6,6,-trimethyl-2-cyclohexenyl)-3-buten-2-ol) (Metcalf & Metcalf, 1992).

Perhaps the most telling supporting evidence for a kairomonal basis to dacine response to phenyl propanoids comes from the fact that benzyl acetate (a benzenoid derived from phenyl propanoids by the loss of C_8–C_9 carbons (Dudareva *et al.*, 1999)) is attractive to *B. dorsalis* (a methyl eugenol responding fly), *B. cucurbitae* (a cuelure responding fly) and *C. capitata* (a tephritid responding to α-copaene from *Angelica archangelica* L. (Apiaceae)) (Lewis *et al.*, 1988). Benzyl acetate occurs in many plants including *Spathiphyllum cannaefolium* Schott. (Araceae) and several orchid species (Dodson & Hills, 1966; Dodson *et al.*, 1969; Lewis *et al.*, 1988). Zingerone (4-(4-hydroxy-3-methoxyphenyl)-2-butanone), synthesized by the methoxylation of raspberry ketone, occuring naturally in ginger and in the orchid species *Bulbophyllum patens* King

Table 1. Summary of lure response in Australasian and Oceanian Dacinae.

Genus	Subgenus	Methyl eugenol	Cuelure	Not known
Bactrocera	*Afrodacus*	0	4	3
	Bactrocera	40	90	51
	Gymnodacus	0	1	2
	Notodacus	1	0	0
	Polistomimetes	3	0	5
	Trypetidacus	1	0	0
	Hemisurstylus	0	0	1
	Hemizeugodacus	0	0	3
	Melanodacus	0	0	2
	Queenslandacus	0	0	1
	Austrodacus	0	0	1
	Diplodacus	0	0	1
	Heminotodacus	0	0	1
	Hemiparatridacus	0	0	1
	Javadacus	2	0	1
	Niuginidacus	0	1	0
	Papuadacus	0	1	0
	Paradacus	0	2	2
	Paratridacus	2	0	4
	Sinodacus	0	10	3
	Zeugodacus	0	13	7
Dacus	*Callantra*	2	4	4
	Dacus	0	8	1
	Didacus	0	4	1
	Semicallantra	1	1	1
Paracallantra		0	0	1
Total		52	139	97

(Data from Drew, 1989.)

and *Bulbophyllum cheiri* Lindl., is another phenyl propanoid that attracts both cuelure and methyl eugenol responding dacines (Tan & Nishida, 2000; Tan *et al.*, 2002). The generic response by dacine flies to these chemicals indicates that their receptors are attuned to the basic phenyl propanoid structure, in accordance with Metcalf's hypothesis.

Anomalous lure records

Though there is a firm belief that dacines respond to either methyl eugenol or cuelure (Metcalf & Metcalf, 1992), there are several records in the literature of flies responding to both chemicals (see e.g. *Bactrocera latilineata* Drew, *Bactrocera furfurosa* Drew and *Bactrocera melanotus* (Coquillett) in Drew (1989)). In each of these cases the response to both lures is dismissed as contamination or incorrect record of the lure. However, the presence of these and other similar anomalous records in the taxonomic literature warrants specific research to clarify if certain species indeed do respond to both lures. Only then can one fully evaluate the validity of Metcalf's hypothesis that dacine chemosensory receptors evolved in association with these phenyl propanoids.

Dacine mating behaviour

The absence of phenyl propanoids attractive to dacines in their current host plants, in conjunction with the view that the host plant serves as a mating site for dacines, has led to the rejection of ancestral host hypothesis by dacine biologists (Fletcher *et al.*, 1975; Fitt, 1981a). The alternative explanation that feeding on these phytochemicals serves to enhance mating success has hence gained prominence in the recent dacine literature. The strongest support for the sexual selection hypothesis comes from work done on some of the major pest species amongst the Dacinae.

Male dacines have a rectal gland that is hypothesized to be significant in the synthesis of the male sex pheromone (Nation, 1981). Upon ingestion of lures, male Dacinae accumulate metabolites derived from these chemicals in the rectal gland that are subsequently released as a volatile emission at a period (Nishida *et al.*, 1988, 1993, 1997), coinciding with the period of peak sexual activity.

Shelly & Dewire (1994) demonstrated that feeding on synthetic methyl eugenol enhanced mating competitiveness in *B. dorsalis* up to 30 days after a single exposure. Such mating benefits have also been demonstrated in *Bactrocera philippinensis* Drew and Hancock (Shelly *et al.*, 1996). For the cuelure feeding melon fly, *B. cucurbitae*, a similar augmentation of mating success has been recorded, albeit not as strong as in the case of the methyl eugenol responding species (Shelly & Villalobos, 1995). Tan & Nishida (1998, 2000) and Shelly (2000) have recently demonstrated similar advantages in mating behaviour for *B. dorsalis* after feeding on natural sources of methyl eugenol.

Evidence to the contrary comes from *B. cacuminata*, where feeding on methyl eugenol does not appear to confer any mating advantage (Raghu & Clarke, 2003b).

Defensive role

In addition to mating benefits, the potential role of methyl eugenol as an allomone has been recently explored. Nishida & Fukami (1990), Tan & Nishida (1998) and Tan

(2000) have reported that feeding on methyl eugenol renders flies 'distasteful' to the house gecko and sparrow. Pairs in copula are usually stationary and hence vulnerable to predation and female flies may preferentially mate with male flies that have fed on methyl eugenol to minimize predation risk. Although predation was not explicitly measured, studies in *B. cacuminata* showed that survival of methyl eugenol-fed flies was not enhanced in the presence of predators (Raghu *et al.*, 2002b). However, studies on allomonal benefits have to date not been undertaken in the natural environment of the fly species in the presence of natural predators.

Botany and plant biochemistry

The origin of angiosperms in the Cretaceous is the outcome of perhaps the greatest botanical evolutionary innovation, the origin of the carpel to protect the genetic material of the plant (Stewart, 1983). Though the origin of insects preceded the origin of flowering plants by over 200 million years, their coevolutionary associations/ interactions with insects (herbivores and pollinators) were significant in enabling them to occupy their current dominant position in the terrestrial world (Crepet & Friis, 1987; Friis *et al.*, 1987; Friis & Crepet, 1987; Judd *et al.*, 1999). The evolving angiosperms, however, would also have contended with pathogenic microorganisms, the truly ancient and dominant life forms on earth (Niklas, 1982).

Microorganisms may have been the *agents provacateurs* for the original diversification of phenyl propanoids by facilitating the production of allelochemicals in plants that subsequently influenced insect–plant interactions (Berenbaum, 1988). Therefore, 'ancestral' phenyl propanoids or precursors to dacine attractants may have evolved as defence chemicals to protect early flowers from bacteria and fungi and their contemporary counterparts may continue to play such an antibiotic role (Walker, 1975; Harrewijn *et al.*, 1995; Janssen *et al.*, 1997). The presence of these chemicals in floral volatiles has been noted from ancient groups such as the Asparagales (Orchidaceae, albeit a rapidly evolving group) and Alismatales, and from more recent groups such as the Myrtales (Onagraceae) and Asterales (figs 4, 5), indicating such an ancient origin of these chemicals.

Flower feeding by adults was a habit in ancient Diptera (Syrphidae, Culicidae, Tipulidae, Mycetophylidae, Empididae, Bombylidae, Anthomyiidae and some Muscidae) (Van der Pijl, 1960, 1961; Rohdendorf, 1974; Crepet & Friis, 1987; Labandeira, 1997) and they were associated with the pseudoflowers of the Gnetophytes, principally for the consumption of the amino acids and polypeptides in the nectar and served as incidental pollinators (Crepet & Friis, 1987; Harrewijn *et al.*, 1995; Gardner & Gillman, 2002). This incidental pollination is an indication of the progression from an anemophilous to a zoophilous pollination syndrome (Van der Pijl, 1961; Crepet & Friis, 1987; Labandeira, 1997). The origin of the angiosperm nectaries in the late Cretaceous (Friis & Crepet, 1987), highlighting the success of this pollination syndrome, coincides with the origin of the tephritids and dacines in the early Tertiary (Rohdendorf, 1974; Metcalf & Metcalf, 1992; Labandeira, 1997).

The benefits of an antibiotic effect and the incidental pollination by primitive Diptera could have thus favoured the sustained production of phenyl propanoids. Dudareva *et al.* (1999) have recently demonstrated that the process of synthesis of methyl eugenol is restricted to the epidermal cells of the petal tissue, with the mRNAs coding for the biosynthetic enzymes detected in petal cells just prior to the opening of the flower. The emission of methyl eugenol peaks at anthesis and gradually declines subsequently. Such a *de novo* synthesis supports the notion that these chemicals could have evolved for antibiotic protection of genetic material and subsequently facilitated pollination, i.e. pollination was an exaptation. Such biochemical exaptations are not uncommon in chemicals evolved for plant defence (Armbuster *et al.*, 1997). Since flowers of several 'ancient' plants also function as mating rendezvous sites and adult feeding sites for insects (Pellmyr & Thien, 1986), response to flowers by olfaction would thus have been maintained in flower visitors, including dacines (Tan & Nishida, 2000; Clarke *et al.*, 2002; Tan *et al.*, 2002).

The stage would have thus been set for the types of coevolutionary processes envisaged by Metcalf. Diversification in phenyl propanoids would have resulted in associated changes in dacine chemoreceptors. The presence of these chemicals in fruits (Nursten, 1970; van Buren, 1970) may have subsequently facilitated the exploitation of the fruit resources by female flies for larval development. The olfactory receptors thus 'tuned' to these phenyl propanoids would explain the attractance of dacines to these chemicals.

A key difficulty, however, with accepting coevolution as an explanation for dacine lure response is that there are no obvious phylogenetic patterns in the distribution of these phenyl propanoids in plants (figs 4, 5). This may be an artefact of the paucity of sampling for these volatiles, rather than a true absence of pattern. Furthermore, while it is conceivable that dacines evolved in response to plant chemistry (based on the receptor sensitivity) and that such response was maintained by a role played by these chemicals as sex pheromones and/ or allomones, the benefits to the plant of interacting with fruit flies in unclear. Only if the fitness benefits to plants emitting these volatiles can be demonstrated (as has been suggested by Tan & Nishida (2000) and Tan *et al.* (2002)), can we invoke coevolution as an explanation.

Dacine pheromone chemistry

A difficulty with the hypothesis that these phenyl propanoids function as precursors to dacine sex pheromones is that if this were the case, by definition of the unique nature of pheromones, one would anticipate there should be over a 100 unique derivations, or at least in blends, for each of these chemicals. Rectal gland composition, at the time of peak sexual behaviour, needs to be examined to evaluate if such species-specific variations in lure metabolites exist.

The role of a long range dacine sex pheromone has been attributed to a class of compounds significantly different from phenyl propanoids, i.e. spiroacetals (Haniotakis *et al.*, 1977, 1986; Bellas & Fletcher, 1979; Francke *et al.*, 1979; Baker *et al.*, 1980; Baker & Bacon, 1985; Baker & Herbert, 1987; Kitching *et al.*, 1989; Mazomenos, 1989; Perkins *et al.*, 1990; Krohn *et al.*, 1991; Fletcher *et al.*, 1992, 2002; Stok *et al.*, 2001). They appear to be more likely candidates as components of the sex pheromone, as has been demonstrated in the case of *Bactrocera oleae* (Rossi) (Haniotakis *et al.*, 1977; Baker *et al.*, 1980; Mazomenos, 1989). *Bactrocera cacuminata* produces spiroacetals independent of exposure to methyl eugenol

(Krohn *et al.*, 1991; Fletcher *et al.*, 2002; S. Raghu and C.J. Moore, unpublished data). These chemicals, in association with N-alkylacylamides that function as short-range aphrodisiacs (Bellas & Fletcher, 1979; Metcalf, 1990), warrant further investigation. Spiroacetals and amides are distinctly different from the plant-based phenyl propanoids and bioassays in the laboratory and field will clarify their role in the mating system of dacines.

Although chemical evidence suggests that spiroacetals are more likely candidates for pheromones, one needs to reconcile the fact that lure metabolites are recovered from the rectal gland. Bellas & Fletcher (1979) have shown that amides from dietary leucine accumulate in the rectal glands of *Bactrocera tryoni* Frogatt and these amides are released at dusk. A similar dietary influence on the terpene composition of the rectal gland has been documented in *Bactrocera passiflorae*, by changing the food source from papaya *Carica papaya* L. (Caricaceae) to rose-apple *Syzigium* sp. (Myrtaceae) (Fletcher *et al.*, 1992). Recent observations in *B. cacuminata* show that metabolites of methyl eugenol are given off by males in the middle of the day and hence not restricted to dusk, when mating occurs in this species (S. Raghu and C.J. Moore, unpublished data). Since dacines ingest phenyl propanoid lures, the presence of their metabolites in the rectal gland may be a simple dietary consequence.

Alternatively, these metabolites and spiroacetals may both be components of the pheromone blend of fruit flies. The relative concentrations of these two chemicals may be a component of the mate recognition system of a particular species. If the pheromone blend of a species had a higher concentration of methyl eugenol metabolites than spiroacetals, then feeding on the synthetic methyl eugenol lure may result in the enhanced mating success documented in certain Dacinae (e.g. Shelly & Dewire, 1994; Shelly, 2000). Alternatively, if the metabolites were not critical in the pheromone or mate recognition system, we may anticipate that they not be any significant effect of feeding on the lure on mating success, as is the case in *B. cacuminata* (Raghu & Clarke, 2003b).

Conclusions – gaps in the knowledge

> *Imagine a Martian peering through a window at a writer whose papers are disturbed by a wilful breeze. The Martian sees him solve the problem by taking out his pocket-watch and using it to restrain the sheets. Think of the problem facing the Martian when, having managed to get hold of the watch, he tries to work out the rationale of its design while believing its function is that of paperweight!*
>
> H.E.H. Paterson (1993)

Dacine biologists are in the position of the proverbial Martian. Having chanced upon this incredibly useful toolkit of chemicals in attracting dacine flies, one is faced with the puzzle of explaining their 'function' in the context of dacine ecology and evolution (table 2). Researchers need to exercise caution about confusing proximate (ecological/ behavioural) and ultimate (evolutionary) functions of dacine lures. The ancestral host hypothesis is an ultimate explanation of the origin of the lure response, while its proximate function may be in the mating behaviour of fruit flies (table 2). So, as mentioned earlier, the two hypotheses outlined above are not logical alternatives to one another and need to be explored independently. It is entirely possible for these chemicals to have the same ultimate function for Dacinae, while having different proximate functions in different dacine species. While there is evidence in support of both hypotheses, considerably greater research is required to explain the phenomenon of lure response in Dacinae.

Testing ultimate hypotheses

Dacine phylogeny

Despite the extensive taxonomic treatment that the Dacinae have received, dacine systematics is still rudimentary (Drew & Hancock, 1994; White, 2000) and the morphogenetic cladistic treatment of this group of insects is still preliminary (Graham *et al.*, 1998; Muraji & Nakahara, 2001). This is one of the key gaps in our knowledge that is impeding our understanding of the evolutionary significance of lures. Such a genealogical treatment will enable us to determine if response to phenyl propanoids/cinnamic acid derivatives is plesiomorphic (an ancestral trait) or synapomorphic (shared derived character). If lure response is plesiomorphic then inferences cannot be made about evolutionary relationships among dacine taxa based on lure response, in the manner they currently are in dacine taxonomy (Drew & Hancock, 1994; White, 2000). Alternatively, if it is synapomorphic then this will enable us to test Metcalf's hypothesis based on receptor evolution in the different monophyletic groups. Recent research in this regard on a small sample of *Bactrocera* species indicates that lure response is labile with response to cuelure as the ancestral trait (Smith *et al.*, 2002, 2003). Lure

Table 2. Summary of evaluation of evidence in relation to proximate and ultimate hypotheses for dacine attractance to phytochemical lures.

Evidence	Ancestral host hypothesis (ultimate)	Sexual selection hypothesis (proximate)
Response to synthetic lures	– –	++ & – –
Response to related phenyl propanoids	++	– +
Anomalous lure records	– +	– +
Dacine mating behaviour	– +	++ & – –
Defensive role	– +	++ & – –
Botany and plant biochemistry	++	– +
Dacine pheromone chemistry	– +	++ & – –

++, Evidence for; – – evidence against; – + evidence neutral.

response has been lost on multiple occasions and response to methyl eugenol has evolved independently several times (Smith *et al.*, 2002, 2003). Whether this is the case for cuelure is unknown.

Distribution of lures in relation to plant phylogeny

There are no clear phylogenetic patterns evident from the distribution of dacine attractants amongst the plant orders (figs 4, 5). But this may be a result of paucity of information, rather than any true evolutionary pattern. Based on the available information, these chemicals are haphazardly distributed among many clades (figs 4, 5), with some plant orders having both dacine lures (e.g. Asparagales, Zingiberales and Ericales), suggesting multiple evolutionary origins of these phenyl propanoids. Further plant chemosystematic information (Harbourne & Turner, 1984) and subsequent investigation of congruence between dacine phylogeny in relation lure response and the distribution of these chemicals in relation to host plants will enable us to test for any coevolutionary association.

A key difficulty in this regard is that designation of plants as hosts for dacines (and phytophagous insects in general) is determined by their ability to support larval development (e.g. Drew, 1989). But adult dacines respond to plants that emit these phenyl propanoid volatiles, independent of their ability to sustain larvae (Fletcher *et al.*, 1975; Shelly, 2000; Tan & Nishida, 2000; Clarke *et al.*, 2002; Tan *et al.*, 2002). Therefore, adult flies need not be restricted to larval host plants (Raghu *et al.*, 2002a; Raghu & Clarke, 2003a) and may indeed have other ecological roles. Preliminary investigations in this regard suggest that this may indeed be the case with adult dacines playing a role in pollination (Tan & Nishida, 2000; Tan *et al.*, 2002). Further research in natural systems may shed light on functional roles played by adult dacines. Any investigation of coevolution must therefore explore the congruence between the phylogeny of plants emitting volatile lures to which adult dacines respond, and dacine phylogeny.

Testing proximate hypotheses

Female response to lures

Female response to lures has been poorly studied. Very few studies have explicitly examined female response to these phenyl propanoids (Fitt, 1981a; Raghu, 2003; Raghu & Clarke, 2003a,b). Assaying the receptor sensitivity of female flies to these chemicals will enable the test of the hypothesis that female flies have a different sensory threshold of response to lures than males. In males, quantifying behavioural and electroantennographic responses to a series of closely related chemicals, incorporating systematic changes in molecular shape and size and associated changes in polarity and lipophilicity of interactive groups, has made the 'mapping' of receptor sites possible (e.g. Metcalf *et al.*, 1979, 1981, 1983, 1987). In dacines that use these chemicals as mate rendezvous stimuli (e.g. *B. cacuminata*), females may have similar receptor site geometry to conspecific males in relation to the respective lure.

Female response to these chemicals may also be driven by a combination of olfactory and visual cues. Meats & Osborne (2000) indicated thus, but their study used artificial visual cues. A similar experiment comparing natural concentrations of lures with and without natural visual stimuli (e.g. natural concentration of lure only vs. flower emitting the compound) may help elucidate this aspect.

Behavioural consequences in relation to natural sources of lures

The concentration of chemicals used to assay response to lures or in field research is likely to be much higher than concentrations in natural sources. Investigation into the natural concentrations of these volatiles is preliminary (e.g. Dudareva *et al.*, 1999; Pichersky & Gershenzon, 2002). Future ecological and behavioural investigations need to take into account the natural concentrations and mechanisms of release of these volatiles. Further investigations of the behavioural consequences of feeding on natural sources of these chemicals, such as those of *Bactrocera dorsalis* feeding on exudates from flowers of *Fagraea berteriana* Benth. (Loganiaceae) (Nishida *et al.*, 1997) and *Cassia fistula* L. (Fabaceae) (Shelly, 2000), and the response to several *Bactrocera* species to orchids of the genera *Bulbophyllum* (Tan & Nishida, 2000; Tan *et al.*, 2002), need to be undertaken to unravel the functional significance of these chemicals (Landolt & Phillips, 1997).

While allomonal benefits of feeding on lures are interesting concepts (Nishida & Fukami, 1990; Tan & Nishida, 1998; Tan, 2000), such benefits need to be determined for predators in natural systems. Only through the assessment of the physiological and behavioural consequences of dacine ingestion of natural doses of these chemicals can any biological significance they may have be understood.

Dacine pheromones

Our understanding of the functional significance of dacine pheromones and their components is still too preliminary to conclusively evaluate the role of lures of botanical origin in dacine mating systems. Analysis of rectal gland composition of males sampled in the wild, in conjunction with bioassays of different constituents, will be crucial in evaluating the relative significance of phenyl propanoids, spiroacetals and amides in the mating systems of dacine fruit flies. More significantly, what role pheromones play in courtship of dacine species needs to be thoroughly investigated, given the poor understanding of the specifics of dacine mating behaviour.

Role of phenyl propanoids in plant biology

The distribution and physiological basis of the synthesis of these chemicals within plants is only now being explored (e.g. Dudareva *et al.*, 1999; Pichersky & Gershenzon, 2002). Further assessment of the role they play in the plant's biology (e.g. antibiotic defence of structures they are released from, attractant for pollinators) may aid clarification of the functional significance of these chemicals.

The spectacular success of dacine attractants in pest management has in some ways impeded our understanding of any biological role they may have. Only an integrated biochemical, botanical and entomological approach, while acknowledging the idiosyncrasies of species, will help unravel the functional significance of phytochemical lures to dacine fruit flies.

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References

Abraham, V. & Verghese, A. (1998) Methyl eugenol attracts female mango fruit fly, *Bactrocera dorsalis* Hendel. *Insect Environment* **4**, 101.

Alyokhin, A.V., Messing, R.H. & Duan, J.J. (2001) Abundance and mating behaviour of Oriental fruit flies (Diptera: Tephritidae) near methyl eugenol-baited traps. *Pan-Pacific Entomologist* **77**, 161–167.

Andersson, M. (1994) *Sexual selection*. Princeton, New Jersey, Princeton University Press.

Armbuster, W.S., Howard, J.J., Clausen, T.P., Debevec, E.M., Loquvam, J.C., Matsuki, M., Cerendelo, B. & Andel, F. (1997) Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. *American Naturalist* **149**, 461–484.

Baker, R. & Bacon, A.J. (1985) The identification of spiroacetals in the volatile secretions of two species of fruit flies (*Dacus dorsalis, Dacus cucurbitae*). *Experientia* **44**, 1484–1485.

Baker, R. & Herbert, R.H. (1987) Isolation and synthesis of 1,7-dioxaspiro[5.5]undecane and 1,7-dioxaspiro[5.5]undecan-3- and 4-ols from the olive fly (*Dacus oleae*). *Journal of the Chemical Society, Perkins Transactions* **1**, 1123–1127.

Baker, R., Herbert, R.H., House, P.E., Jones, O.T., Francke, W. & Ruth, W. (1980) Identification and synthesis of the major sex pheromone of the olive fly (*Dacus oleae*). *Journal of the Chemical Society, Chemical Communications* **1**, 52–54.

Bellas, T.E. & Fletcher, B.S. (1979) Identification of the major components in the secretion from the rectal pheromone glands of the Queensland fruit flies, *Dacus tryoni* and *Dacus neohumeralis*. *Journal of Chemical Ecology* **5**, 795–803.

Berenbaum, M.R. (1988) Allelochemicals in insect–microbe–plant interactions; agent provocateurs in the coevolutionary arms race. pp. 97–163 *in* Barbosa, P. & Letourneau, D.K. (*Eds*) *Novel aspects of insect–plant interactions*. New York, John Wiley & Sons.

Berenbaum, M.R. (1995) Turnabout is fair play: secondary roles for primary compounds. *Journal of Chemical Ecology* **21**, 925–940.

Brieze-Stegeman, R., Rice, M.A. & Hooper, G.H.S. (1978) Daily periodicity in attraction of male tephritid fruit flies to synthetic chemical lures. *Journal of the Australian Entomological Society* **17**, 341–346.

Clarke, A.R., Balagawi, S., Clifford, B., Drew, R.A.I., Leblanc, L., Mararuai, A., McGuire, D., Putulan, D., Sar, S.A. & Tenakanai, D. (2002) Evidence for orchid visitation by *Bactrocera* species (Diptera: Tephritidae) in Papau New Guinea. *Journal of Tropical Ecology* **18**, 441–448.

Crepet, W.L. & Friis, E.M. (1987) The evolution of insect pollination in angiosperms. pp. 181–201 *in* Friis, E.M., Chaloner, W.G. & Crane, P.R. (*Eds*) *The origin of angiosperms and the their biological consequences*. Cambridge, Cambridge University Press.

Cunningham, R.T. (1989a) Population detection. pp. 169–173 *in* Robinson, A.S. & Hooper, G. (*Eds*) *Fruit flies: their biology, natural enemies and control*. Amsterdam, Elsevier.

Cunningham, R.T. (1989b) Parapheromones. pp. 221–230 *in* Robinson, A.S. & Hooper, G. (*Eds*) *Fruit flies: their biology, natural enemies and control*. Amsterdam, Elsevier.

Dodson, C.H. & Hills, H.G. (1966) Gas chromatography of orchid fragrances. *American Orchid Society Bulletin* **35**, 720–725.

Dodson, C.H., Dressler, R.L., Hills, H.G., Adams, R.M. & Williams, N.H. (1969) Biologically active compounds in orchid fragrances. *Science* **164**, 1243–1249.

Drew, R.A.I. (1989) The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian regions. *Memoirs of the Queensland Museum* **26**, 1–521.

Drew, R.A.I. & Hancock, D.L. (1994) The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bulletin of Entomological Research* **Supplement 2**, 1–68.

Dudareva, N., Piechulla, B. & Pichersky, E. (1999) Biogenesis of floral scents. *Horticultural Reviews* **24**, 31–54.

Edwards, R. & Gatehouse, J.A. (1999) Secondary metabolism. pp. 193–218 *in* Lean, P.J. & Leegood, R.C. (*Eds*) *Plant biochemistry and molecular biology*, Chichester, England, John Wiley & Sons.

Fabre, J.H. (1912) *Social life in the insect world*. London, T. Fisher Unwin.

Fitt, G.P. (1981a) Responses by female Dacinae to 'male' lures and their relationship to patterns of mating behavior and pheromone response. *Entomologia Experimentalis et Applicata* **29**, 87–97.

Fitt, G.P. (1981b) The influence of age, nutrition and time of day on the responsiveness of male *Dacus opiliae* to the synthetic lure, methyl eugenol. *Entomologia Experimentalis et Applicata* **30**, 83–90.

Fletcher, B.S. (1968) Storage and release of a sex pehromone by the the Queensland fruit fly, *Dacus tryoni* (Diptera: Tephritidae). *Nature* **219**, 631–632.

Fletcher, M.T. & Kitching, W. (1995) Chemistry of fruit flies. *Chemical Reviews* **95**, 789–828.

Fletcher, B.S., Bateman, M.A., Hart, N.K. & Lamberton, J.A. (1975) Identification of fruit fly attractant in an Australian plant, *Zieria smithii*, as o-methyl eugenol. *Journal of Economic Entomology* **68**, 815–816.

Fletcher, M.T., Wells, J.A., Jacobs, M.F., Krohn, S., Kitching, W., Drew, R.A.I., Moore, C.J. & Francke, W. (1992) Chemistry of fruit flies. Spiroacetal-rich secretions in several *Bactrocera* species from the south-west Pacific region. *Journal of the Chemical Society, Perkins Transactions* **1**, 2827–2831.

Fletcher, M.T., Wood, B.J., I.M., B., Stok, J.E., De Voss, J.J. & Kitching, W. (2002) [18O]-Oxygen incorporation reveals novel pathways in spiroacetal biosynthesis by *Bactrocera cacuminata* and *B. cucumis*. *Journal of the American Chemical Society* **124**, 7666–7667.

Francke, W., Hindorf, G. & Reith, W. (1979) Alkyl-1,6-dioxaspiro[4.4]nonane: a new class of pheromones. *Naturwissenschaften* **66**, 618–619.

Friedrich, H. (1976) Phenylpropanoid constituents of essential oils. *Lloydia* **39**, 1–7.

Friis, E.M. & Crepet, W.L. (1987) Time of appearance of floral features. pp. 145–179 *in* Friis, E.M., Chaloner, W.G. & Crane, P.R. (*Eds*) *The origin of angiosperms and the their biological consequences*. Cambridge, Cambridge University Press.

Friis, E.M., Chaloner, W.G. & Crane, P.R. (Eds) (1987) *The origin of angiosperms and the their biological consequences*. Cambridge, Cambridge University Press.

Gallois, A. (1982) Dosage rapide de la parahydroxyphenyl-1-butanone dans la framboise par chromatographie sur couche mince. *Sciences des Aliments* **2**, 99–106.

Gardner, M.C. & Gillman, M.P. (2002) The taste of nectar – a neglected area of pollination ecology. *Oikos* **98**, 551–556.

Geissman, T.A. & Crout, D.H.G. (1969) *Organic chemistry of secondary plant metabolism*. San Francisco, Freeman, Cooper & Co.

Graham, G.C., Yeates, D.K. & Drew, R.A.I. (1998) *Dacine tephritids: evolutionary studies for identification, ethology and ecology*. Sixth Australasian Applied Entomological Research Conference, University of Queensland, Brisbane, pp. 456–462.

Hancock, D.L. (1985) A specific male attractant for the melon fly, *Dacus vertebratus*. *Zimbabwe Science News* **19**, 118–119.

Haniotakis, G., Mazomenos, B.E. & Tumlinson, J.H. (1977) A sex attractant of the olive fruit fly, *Dacus oleae*, and its biological activity under laboratory and field conditions. *Entomologia Experimentalis et Applicata* **21**, 81–87.

Haniotakis, G., Francke, W., Mori, K., Redlich, H. & Schurig, V. (1986) Sex-specific activity of (R)-(-)-and (S)-(+)-1,7, dioxaspiro[5.5]undecane, the major pheromone of *Dacus oleae*. *Journal of Chemical Ecology* **12**, 1559–1568.

Harbourne, J.B. & Turner, B.L. (1984) *Plant chemosystematics*. London, Academic Press.

Harrewijn, P., Minks, A.K. & Mollema, C. (1995) Evolution of plant volatile production in insect–plant relationships. *Chemoecology* **5/6**, 55–73.

Haslam, E. (1995) Secondary metabolism – evolution and function: products or processes? *Chemoeoclogy* **5/6**, 89–95.

Haukioja, E., Ossipov, V., Koricheva, J., Honkanen, T., Larsson, S. & Lempa, K. (1998) Biosynthetic origin of carbon-based secondary compounds: cause of variable responses of woody plants to fertilization? *Chemoecology* **8**, 133–139.

Herrmann, K.M. (1995a) The Shikimate pathway: early steps in the biosynthesis of aromatic compounds. *Plant Cell* **7**, 907–919.

Herrmann, K.M. (1995b) The Shimikate pathway as an entry to aromatic secondary metabolism. *Plant Physiology* **107**, 7–12.

Herrmann, K.M. & Weaver, L.M. (1999) The shikimate pathway. *Annual Review of Plant Physiology and Plant Molecular Biology* **50**, 473–503.

Hirvi, T. & Hokkanen, E. (1984) The aroma of fruit of the sea buckthorn *Hippophae rhamnoides* L. *Zeitschrift für Lebensmittel-Untersuchung und-Forschung* **179**, 387–388.

Hirvi, T., Hokkanen, E. & Pyysalo, T. (1981) The aroma of cranberries. *Zeitschrift für Lebensmittel-Untersuchung und-Forschung* **172**, 365–367.

Hokkanen, E., Pyysalo, T. & Hirvi, T. (1980) The aroma of Finnish wild raspberries. *Rubus idaeus* L. *Zeitschrift für Lebensmittel-Untersuchung und-Forschung* **171**, 180–182.

Howlett, F.M. (1912) The effect of citronella oil in two species of *Dacus*. *Transactions of the Entomological Society, London* **60**, 412–418.

Howlett, F.M. (1915) Chemical reactions of fruit flies. *Bulletin of Entomological Research* **6**, 297–305.

Janssen, A., Bruin, J., Jacobs, G., Schraag, R. & Sabelis, M.W. (1997) Predators use volatiles to avoid prey patches with conspecifics. *Journal of Animal Ecology* **66**, 223–232.

Judd, W.S., Campbell, C.S., Kellogg, E.A. & Stevens, P.F. (1999) *Plant systematics – a phylogenetic approach*. Sunderland, Massachusetts, Sinauer Associates, Inc.

Karlson, P. & Butenandt, A. (1959) Pheromones (ectohormones) in insects. *Annual Review of Entomology* **4**, 39–58.

Kitching, W., Lewis, J.A., Perkins, M.V., Drew, R.A.I., Moore, C.J., Schurig, V., Konig, W.A. & Francke, W. (1989) Chemistry of fruit flies. Composition of the rectal gland secretion of (male) *Dacus cucumis* (cucumber fly) and *Dacus halfordiae*. Characterization of (Z,Z)-2,8-dimethyl-1,7-dioxaspiro[5.5]undecane. *Journal of Organic Chemistry* **54**, 3893–3902.

Knudsen, J.T., Tollsten, L. & Gunnar Bergström, L. (1993) Floral scents – a checklist of volatile compounds isolated by head-space techniques. *Phytochemistry* **33**, 253–280.

Korneyev, V.A. (2000) Morphological features of the Tribe Dacini (Dacinae): their significance to behaviour and classification. pp. 3–22 *in* Aluja, M. & Norrbom, A. (*Eds*) *Fruit flies: phylogeny and evolution of behaviour*. Boca Raton, Florida, CRC Press.

Koyama, J. (1989) Mating pheromones: tropical dacines. pp. 165–168 *in* Robinson, A.S. & Hooper, G. (*Eds*) *Fruit flies: their biology, natural enemies and control*. Amsterdam, Elsevier.

Krohn, S., Fletcher, M.T., Kitching, W., Drew, R.A.I., Moore, C.J. & Francke, W. (1991) Chemistry of fruit flies: nature of glandular secretion and volatile emission of *Bactrocera cacuminatus* (Hering). *Journal of Chemical Ecology* **17**, 485–495.

Labandeira, C.C. (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics* **28**, 153–193.

Landolt, P.J. & Phillips, T.W. (1997) Host plant influences on sex pheromone behaviour of phytophagous insects. *Annual Review of Entomology* **42**, 371–391.

Lewis, J.A., Moore, C.J., Fletcher, M.T., Drew, R.A.I. & Kitching, W. (1988) Volatile compounds from the flowers of *Spathiphyllum cannaefolium*. *Phytochemistry* **27**, 2755–2757.

Marco, J.A., Barbera, O., Rodriguez, S., Domingo, C. & Adell, J. (1988) Flavonoids and other phenolics from *Artemisia hispanica*. *Phytochemistry* **27**, 3155–3159.

Matsuki, M. (1996) Regulation of plant phenolic synthesis: from biochemistry to ecology and evolution. *Australian Journal of Botany* **44**, 613–634.

Mazomenos, B.E. (1989) *Dacus oleae*. pp. 169–178 *in* Robinson, A.S. & Hooper, G. (*Eds*) *Fruit flies: their biology, natural enemies and control*. Amsterdam, Elsevier.

McKey, D. (1979) The distribution of secondary compounds within plants. pp. 56–133 *in* Rosenthal, G. & Janzen, D. (*Eds*) *Herbivores: their interactions with plant secondary metabolites*. New York, Academic Press.

Meats, A. & Hartland, C.L. (1999) Upwind anemotaxis in response to cue-lure by the Queensland fruit fly, *Bactrocera tryoni*. *Physiological Entomology* **24**, 90–97.

Meats, A. & Osborne, A. (2000) Dose-related upwind anemotaxis and movement up odour gradients in still air in the presence of methyl eugenol by the wild tobacco fruit fly, *Bactrocera cacuminata*. *Physiological Entomology* **25**, 41–47.

Metcalf, R.L. (1979) Plants, chemicals and insects. Some aspects of coevolution. *Bulletin of the Entomological Society of America* **25**, 30–35.

Metcalf, R.L. (1987) Plant volatiles as insect attractants. *CRC Critical Reviews in Plant Sciences* **5**, 251–301.

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

Metcalf, R.L. & Metcalf, E.R. (1992) *Plant kairomones in insect ecology and control*. New York, Chapman and Hall.

Metcalf, R.L., Metcalf, E.R., Mitchell, W.E. & Lee, L.W.Y. (1979) Evolution of the olfactory receptor in the oriental fruit fly, *Dacus dorsalis*. *Proceedings of the National Academy of Sciences, USA* **76**, 1561–1565.

Metcalf, R.L., Metcalf, E.R. & Mitchell, W.C. (1981) Molecular parameters and olfaction in the oriental fruit fly *Dacus dorsalis*. *Proceedings of the National Academy of Sciences, USA* **78**, 4007–4010.

Metcalf, R.L., Mitchell, W.C. & Metcalf, E.R. (1983) Olfactory receptors in the melon fly *Dacus cucurbitae* and the oriental fruit fly *Dacus dorsalis*. *Proceedings of the National Academy of Sciences, USA* **80**, 3143–3147.

Mori, K. (1997) Pheromones: synthesis and bioactivity. *Journal of the Chemical Society, Chemical Communications* **1997**, 1153–1158.

Muraji, M. & Nakahara, S. (2001) Phylogenetic relationships among fruit flies, *Bactrocera* (Diptera, Tephritidae), based on the mitochondrial rDNA sequences. *Insect Molecular Biology* **10**, 549–559.

Nakagawa, S., Farias, G.J. & Steiner, L.F. (1970) Response of female Mediterranean fruit flies to male lures in the relative absence of males. *Journal of Economic Entomology* **63**, 227–229.

Nation, J.L. (1981) Sex-specific glands in tephritid fruit flies of the genera *Anastrepha*, *Ceratitis*, *Dacus* and *Rhagoletis* (Diptera: Tephritidae). *Journal of Insect Morphology and Embryology* **10**, 121–129.

Niklas, K.J. (1982) Chemical diversification and evolution of plants as inferred from paleobiochemical studies. pp. 29–91 *in* Nitecki, M.H. (*Ed.*) *Biochemical aspects of evolutionary biology*. Chicago, University of Chicago Press.

Nishida, R. & Fukami, H. (1990) Sequestration of distasteful compounds by some pharmacophagous insects. *Journal of Chemical Ecology* **16**, 151–164.

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

Nishida, R., Iwahashi, O. & Tan, K.H. (1993) Accumulation of *Dendrobium superbum* (Orchidaceae) fragrance in the rectal glands by males of the melon fly, *Dacus cucurbitae*. *Journal of Chemical Ecology* **19**, 713–722.

Nishida, R., Shelly, T.E. & Kaneshiro, K. (1997) Acquisition of female-attracting fragrance by males of the oriental fruit fly from a Hawaiian lei flower, *Fagraea beteriana*. *Journal of Chemical Ecology* **23**, 2275–2285.

Nursten, H.E. (1970) Volatile compounds: the aroma of fruits. pp. 239–268 *in* Hulme, A.C. (*Ed.*) *The biochemistry of fruits and their products*. London, Academic Press.

Paterson, H.E.H. (1993) *Evolution and the recognition concept of species*. Baltimore, Johns Hopkins University Press.

Pellmyr, O. & Thien, L.B. (1986) Insect reproduction and floral fragrances: keys to the evolution of the angiosperms. *Taxon* **35**, 76–85.

Perkins, M.V., Fletcher, M.T., Kitching, W., Drew, R.A.I. & Moore, C.J. (1990) Chemical studies of the rectal gland secretions of some species of *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae). *Journal of Chemical Ecology* **16**, 2475–2487.

Pichersky, E. & Gershenzon, J. (2002) The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Current Opinion in Plant Biology* **5**, 237–243.

Poramarcom, R. & Boake, C.R. (1991) Behavioural influences on male mating success in the Oriental fruit fly, *Dacus dorsalis* Hendel. *Animal Behaviour* **42**, 435–460.

Raghu, S. (2003) *The autecology of* Bactrocera cacuminata *(Hering) (Diptera: Tephritidae: Dacinae): functional significance of resources*. PhD thesis. Griffith University, Brisbane.

Raghu, S. & Clarke, A.R. (2003a) Sexual selection in a tropical fruit fly: role of a plant derived chemical in mate choice. *Entomologia Experimentalis et Applicata* **107**, 53–58.

Raghu, S. & Clarke, A.R. (2003b) Spatial and temporal partitioning of behaviour by adult fruit flies: direct evidence for methyl eugenol as a mate rendezvous cue for *Bactrocera cacuminata*. *Physiological Entomology* **28**, 175–184.

Raghu, S. & Lawson, A.E. (2003) Feeding behaviour of *Bactrocera cacuminata* (Hering) (Diptera: Tephritidae) on methyl eugenol: a laboratory assay. *Australian Journal of Entomology* **42**, 149–152.

Raghu, S., Clarke, A.R. & Bradley, J. (2002a) Microbial mediation of fruit fly – host plant interactions: is the host plant the 'centre of activity'? *Oikos* **97**, 319–328.

Raghu, S., Clarke, A.R. & Yuval, B. (2002b) Investigation of physiological consequences of feeding on methyl eugenol by *Bactrocera cacuminata* (Diptera: Tephritidae). *Environmental Entomology* **31**, 941–946.

Rohdendorf, B.B. (1974) *The historical development of Diptera*. Edmonton, University of Alberta.

Schmid, J. & Amrhein, N. (1999) The shikimate pathway. pp. 147–160 *in* Singh, B.K. (*Ed.*) *Plant amino acids: biochemistry and biotechnology*. New York, Marcel Dekker.

Severin, H.P. & Severin, H.S. (1913) A historical account on the use of kerosene to trap the Mediterranean fruit fly. *Journal of Economic Entomology* **6**, 347–351.

Shelly, T.E. (2000) Flower-feeding effects mating performance in male oriental fruit flies *Bactrocera dorsalis*. *Ecological Entomology* **25**, 109–114.

Shelly, T.E. & Dewire, A.M. (1994) Chemically mediated mating success in male oriental fruit flies. *Annals of the Entomological Society of America* **87**, 375–382.

Shelly, T.E. & Villalobos, E.M. (1995) Cue lure and the mating behaviour of male melon flies (Diptera: Tephritidae). *Florida Entomologist* **78**, 473–482.

Shelly, T.E., Whittier, T.E. & Villalobos, E.M. (1996b) Trimedlure affects mating success and mate attraction in male Mediterranean fruit flies. *Entomologia Experimentalis et Applicata* **78**, 181–185.

Shelly, T.E., Resilva, S., Reyes, M. & Bignayan, H. (1996a) Methyl eugenol and mating competitiveness of irradiated male *Bactrocera philippinensis*. *Florida Entomologist* **79**, 481–488.

Smith, P.T., McPheron, B.A. & Kambhapati, S. (2002) Phylogenetic analysis of mitochondrial DNA supports the monophyly of Dacini fruit flies (Diptera: Tephritidae). *Annals of the Entomological Society of America* **95**, 658–664.

Smith, P.T., Kambhapati, S. & Armstrong, K.A. (2003) Phylogenetic relationship among *Bactrocera* species (Diptera: Tephritidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **26**, 8–17.

Steiner, L.F., Mitchell, W.C., Harris, E.J., Kozuma, T.T. & Fujimoto, M.S. (1965) Oriental fruit fly eradication by male annihilation. *Journal of Economic Entomology* **58**, 961–964.

Stewart, W.N. (1983) *Paleobotany and the evolution of plants*. Cambridge, Cambridge University Press.

Stok, J.E., Lang, C., Schwartz, B.D., Fletcher, M.T., Kitching, W. & De Voss, J.J. (2001) Carbon hydroxylation of alkyltetrahydropyranols: a paradigm for spiroacetal biosynthesis in *Bactrocera* sp. *Organic Letters* **3**, 397–400.

Swain, T. (1977) Secondary compounds as protective agents. *Annual Review of Plant Physiology* **28**, 479–501.

Tallamy, D.W., Mullin, C.A. & Frazier, J.L. (1999) An alternate route to insect pharmacophagy: the loose receptor hypothesis. *Journal of Chemical Ecology* **25**, 1987–1997.

Tan, K.H. (2000) Sex pheromone components in defense of melon fly, *Bactrocera cucurbitae* against Asian house gecko, *Hemidactylus frenatus*. *Journal of Chemical Ecology* **26**, 697–704.

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

Tan, K.H. & Nishida, R. (2000) Mutual reproductive benefits between a wild orchid, *Bulbophyllum patens*, and *Bactrocera* fruit flies via a floral synomone. *Journal of Chemical Ecology* **26**, 533–546.

Tan, K.H., Nishida, R. & Toong, Y.C. (2002) Floral synomone of a wild orchid, *Bulbophyllum cheiri*, lures *Bactrocera* fruit flies for pollination. *Journal of Chemical Ecology* **28**, 1161–1172.

Thien, L.B., Heimermann, W.H. & Holman, R.T. (1975) Floral odours and quantitative taxonomy of *Magnolia* and *Liriodendron*. *Taxon* **24**, 557–568.

van Buren, J. (1970) Fruit phenolics. pp. 269–304 *in* Hulme, A.C. (*Ed.*) *The biochemistry of fruits and their products*, London, Academic Press.

Van der Pijl, L. (1960) Ecological aspects of flower evolution. I. Phyletic evolution. *Evolution* **14**, 403–416.

Van der Pijl, L. (1961) Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* **15**, 44–59.

Walker, J.R.L. (1975) *The biology of plant phenolics*. London, Edward Arnold.

White, I.M. (2000) Morphological features of the Tribe Dacini (Dacinae): their significance to behaviour and classification. pp. 505–533 *in* Aluja, M. & Norrbom, A. (*Eds*) *Fruit flies: phylogeny and evolution of behaviour*. Boca Raton, Florida, CRC Press.

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