

信息化学物质在寄生蜂寻找配偶和寄主中的作用及其应用潜力*

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摘要 寄生蜂是重要的生物防治因子, 对田间害虫数量具有明显的控制作用。交配和寄生是寄生蜂最重要的两个行为, 对维持寄生蜂种群数量和控制害虫发生至关重要。因此, 研究寄生蜂交配和寄生行为相关的信息化学物质一直是生物互作和化学生态学领域的热点。过去几十年, 随着触角电位-气相色谱联用(Gas chromatography-electroantennographic detection, GC-EAD)等活性化合物鉴定技术的广泛应用, 多种调节寄生蜂行为的信息化学物质得到鉴定。其中, 虫害诱导的植物气味挥发物(Herbivory-induced plant volatiles, HIPVs)和寄主释放的信息素(Pheromone)是寄生蜂定向和定位寄主的重要嗅觉信号。在此基础上建立的三级营养关系(植物-害虫-寄生蜂)理论(Tritrophic interactions)促进了我们对寄生蜂寄生机制的认识。另外, 由于寄生蜂个体小, 性信息素释放量低, 寄生蜂性信息素鉴定工作是化学生态学研究领域的一个挑战。近期, 寄生蜂性信息素通信机制的研究有所突破, 我国重要寄生蜂——棉铃虫齿唇姬蜂(*Campoletis chloridae*)的性信息素和感受机制得到系统性的研究, 相关结果证明性信息素可以通过促进交配来提高寄生蜂的寄生效率。本文将综述与寄生蜂寄生和交配行为相关的关键信息化学物质, 探讨利用这些化合物进行害虫防治所面临的机遇和挑战。

关键词 寄生蜂; 寄生率; 交配; 信息化学物质; 害虫防治

Infochemicals used by parasitoids to find mates and hosts and their application in pest control

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Abstract Parasitoids are important biological control agents for many agricultural pests. Mating and parasitizing hosts are the two most prominent behaviors of parasitoids and are essential for their reproduction and survival. Therefore, the identification of the infochemicals involved in mating and parasitizing is an important first step to understanding the chemical ecology of these species. In recent decades, state-of-the-art chemical analysis techniques, such as gas chromatography-electroantennographic detection (GC-EAD), has resulted in the identification of an increasing number of infochemicals that regulate parasitoid behavior. Herbivore-induced plant volatiles (HIPVs) and host-derived kairomones are two major categories of chemical cues guiding host detection. Based on this, the concept of “tritrophic” (plant-pest-parasitoid) interactions has been developed, significantly deepening our understanding of the mechanisms underlying host identification by parasitoids. Identification of parasitoid sex pheromones has been challenging due to their small body size and the correspondingly small amounts of sex pheromones released. The sex pheromone communication mechanism in a parasitoid, *Campoletis chloridae*,

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has recently been elucidated. The results indicate that sex pheromones can enhance the parasitizing capacity of parasitoids by facilitating mating. In this review we summarize the infochemicals that regulate parasitoid behaviors and discuss the prospects and challenges of applying these infochemicals to control insect pests.

Key words parasitoids; infochemicals; parasitism; mating; pest management

寄生昆虫 (Parasitoids) 物种丰富, 超过 10 万种, 约 78% 物种属于膜翅目 (Hymenoptera), 20% 属于双翅目 (Diptera), 其它寄生昆虫属于鞘翅目 (Coleoptera)、鳞翅目 (Lepidoptera)、脉翅目 (Neuroptera) (Heyneman, 1972; Eggleton and Belshaw, 1992; Feener and Brown, 1997;)。可见, 寄生蜂的种类在寄生昆虫中占大多数。因为寄主多为重要经济作物害虫, 所以寄生蜂被认为是一种重要的生物防治因子, 得到广泛的关注 (王琛柱和钦俊德, 2007; 陈学新等, 2017; 时敏等, 2020)。例如, 赤眼蜂类 *Trichogramma* spp. 寄生蜂, 可寄生数百种昆虫的卵, 特别是鳞翅目昆虫的卵, 对蛾类害虫的防治具有重要意义 (Zang *et al.*, 2021)。在我国黄河流域和长江流域的农田中, 多达 40% 的棉铃虫 *Helicoverpa armigera* 幼虫会被棉铃虫齿唇姬蜂 *Campoletis chloridae* 寄生并被杀死 (戴小枫, 1990)。寄生蜂的寄生模式多种多样, 根据产卵位置, 可分为内寄生 (卵产在寄主体内) 和外寄生 (卵产在寄主体表); 根据寄生时寄主的发育阶段可分为卵寄生、幼虫寄生和蛹寄生; 根据寄主范围, 可分为广寄生 (寄生几种或多种寄主) 和专寄生 (寄生一种或少数几种寄主) 等 (侯照远和严福顺, 1997)。

寄生蜂利用信息化学物质 (Semiochemicals 或 Infochemicals) 快速定向、定位合适的配偶和寄主是交配和寄生成功的关键。交配和寄生都是链式行为反应的过程, 根据环境信号而逐步递进。环境信号的可检测性 (Detectability) 和可靠性 (Reliability) 是寄生蜂要面对的问题 (Vet and Dicke, 1992)。与配偶或者寄主间接相关的信号, 如植物挥发物等, 多而繁杂, 可检测性高但是可靠性低; 与配偶或者寄主位置相关的直接信号, 如昆虫释放的信息素, 量少且随风扩散, 可检测性低, 但是可靠性高 (Vet *et al.*, 1991;

Fernández-Grandon and Poppy, 2015)。寄主昆虫取食诱导植物产生的挥发物兼具检测性强和可信度高的特点, 是寄生蜂搜寻寄主的重要线索。过去几十年, 与寄生蜂定向和定位寄主相关的信息化学物质不断被鉴定出来。本文将综述与寄生蜂交配和寄生行为相关的信息化学物质, 对重要化合物的行为调节能力和应用前景进行重点介绍和讨论。

1 配偶定位

性信息素的种属特异性是昆虫识别配偶的关键。自第一种昆虫的性信息素——蚕蛾醇被鉴定以来 (Butenandt *et al.*, 1959), 昆虫性信息素鉴定和相关感受机制研究一直是化学生态学领域的研究热点。其中报道最多的是鳞翅目昆虫的性信息素, 组分多为 10-18 碳的不饱和醛、醇、酯 (Ando and Yamakawa, 2011)。由于寄生蜂个体通常较小, 释放的性信息素量低, 寄生蜂性信息素的鉴定工作相对落后, 相关的报道也缺乏分子和生理层面的实验证据 (Ayasse *et al.*, 2001)。寄生蜂的性信息素一般由雌性释放, 雄性感受 (Godfray *et al.*, 1994)。寄生蜂的挥发性性信息素包括醛、酮、酯、烯炔类化合物等, 结构多种多样, 有的含有较复杂的甲基侧链和苯环结构 (表 1)。近期, 十四醛 Tetradecanal 和十七烷酮 2-heptadecanone (1 : 4.6) 被鉴定为棉铃虫齿唇姬蜂雌蜂释放的性信息素, 把这两个化合物按比例添加到被正己烷清洗过的雌性蜂体上后可以恢复对雄蜂的吸引力并引起雄蜂振翅这一经典的求偶行为 (图 1) (Guo *et al.*, 2022)。在分子层面发现, 表达在棉铃虫齿唇姬蜂雄性触角中两个气味受体 CchOR18 和 CchOR47 是分别感受十四醛和十七烷酮的受体, 这两个受体是首次被鉴定的寄生蜂的性信息素受体 (图 1) (Guo *et al.*, 2022)。除了雌性性信息素

外,有些寄生蜂是由雄性释放性信息素来吸引雌性。例如,丽蛹金小蜂雄性释放(4R,5R)-5-羟基-4-癸内酯 (4R,5R)-5-hydroxy-4-decanolide 和 (4R,5S)-5-羟基-4-癸内酯 (4R,5S)-5-hydroxy-4-decanolide 来吸引雌性,这两个化合物是首次被鉴定的寄生蜂雄性性信息素(Ruther *et al.*, 2007) (表 1)。

除了挥发性的性信息素外,表皮烷烃(Cuticle hydrocarbons, CHCs)被认为是寄生蜂的接触性信息素。例如,在黑青小蜂 *Dibrachys cavus* 中,处女蜂体表的 3-甲基二十九烷 3-methylnonacosane 和 3-甲基三十一烷 3-methylhentriacontane 可是接触性信息素组分(Ruther *et al.*, 2011)。7-甲基二十四烷 7-methyltetracosane 和 3-甲基二十七

烷 3-methylheptacosane 被证明分别是金小蜂 *Urolepis rufipes* 和米象金小蜂 *Lariophagus distinguendus* 的接触性信息素组分(Kühbandner *et al.*, 2013; Würf *et al.*, 2020)。因为挥发性的差异,挥发性信息素和 CHCs 可能在求偶的不同阶段发挥作用。挥发性信息素主要介导寄生蜂长距离搜寻配偶,而 CHCs 则在近距离提供配偶适合度的关键信息。迄今为止,挥发性信息素和接触性信息素还没有同时在一个寄生蜂物种中得到系统的研究,这很可能是由于研究方法的局限性和不同的研究侧重点造成的。因此,在未来的研究工作中,我们应当同时研究挥发和接触性信息素的作用,这样会对寄生蜂性信息素通信机制有一个全面的认识。

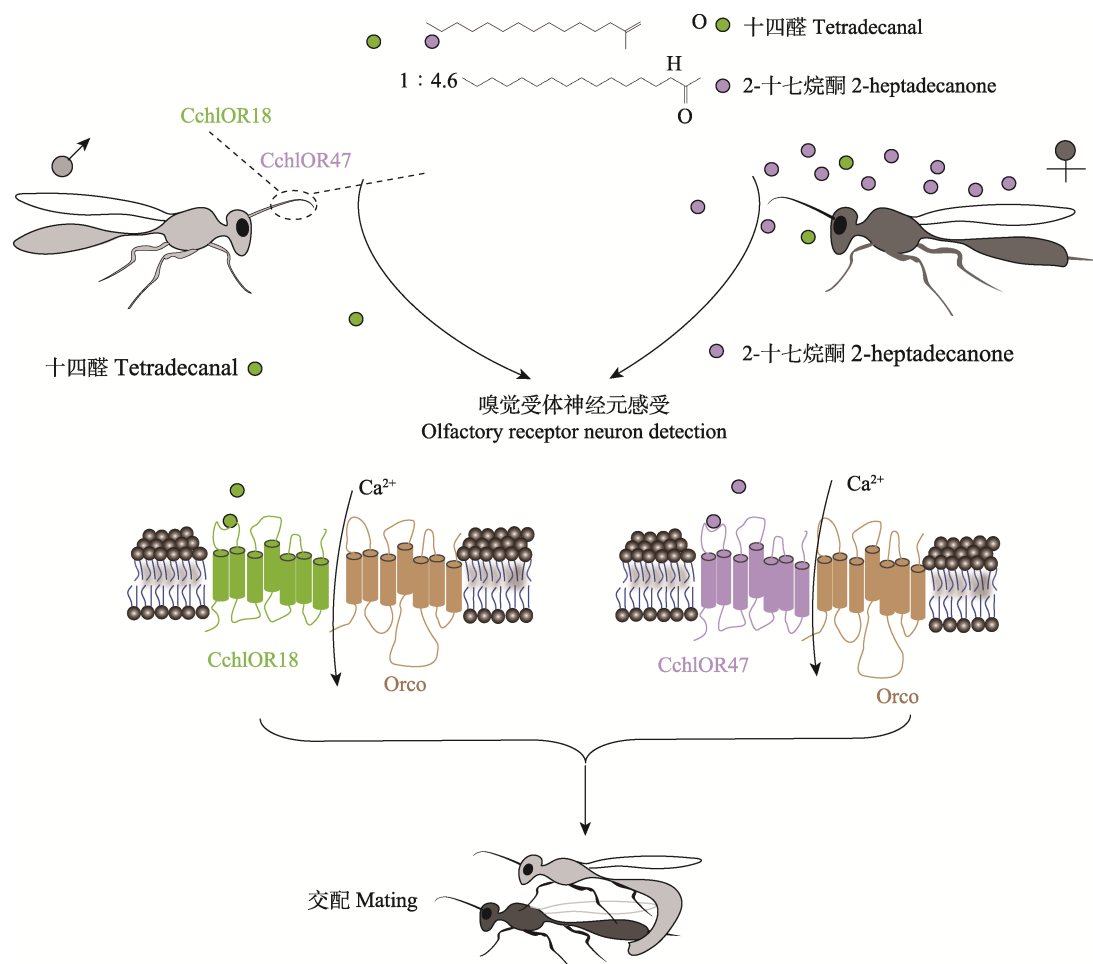


图 1 棉铃虫齿唇姬蜂性信息素通信机制模式图 (Guo *et al.*, 2022)

Fig. 1 Schematic representation of sex pheromone communication in *Campoplex chorideae* (Guo *et al.*, 2022)

表 1 寄生蜂的挥发性性信息素

Table 1 Reported airborne sex pheromones of parasitoids

寄生蜂 Parasitoids	性信息素组分 Sex pheromones	来源 Resources	实验方法 Methods	参考文献 References
内拟寄生瘤姬蜂 <i>Itoplectis conquisitor</i>	香叶醛 Geranial; 柠檬醛 Neral	雌性体表无水乙醚提取物 Anhydrous ether extracts of female bodies	GC-MS; 笼式选择实验 Cage preference	Robacker and Hendry, 1977
网皱革腹茧蜂 <i>Ascogaster reticulatus</i>	顺-9-十六醛 (Z)-9-hexadecenal	雌性体表正己烷提取物 Hexane extracts of female bodies	GC-MS; 培养皿搜寻实验 Host localization in a Petri dish	Kainoh <i>et al.</i> , 1991
<i>Macrocentrus grandii</i>	顺-4-十三醛 (Z)-4-tridecenal	雌性体表正己烷提取物 Hexane extracts of female bodies	GC-MS; 风洞实验 Wind tunnel; 田间实验 Field test	Swedenborg and Jones, 1992
四齿革腹茧蜂 <i>Ascogaster quadridentata</i>	顺,顺-9,12-十八碳二烯醛 (Z,Z)-9,12-octadecadienal	雌性 Porapak Q 收集物 Porapak Q collection of female body volatiles	GC-EAD; GC-MS; Y 型管 Y-tube olfactometer; 田间实验 Field test	DeLury <i>et al.</i> , 1999
<i>Melittobia digitata</i>	反-香柠檬烯 (E)-bergamotene	雄性体表二乙醚提取物 Diethyl ether extracts of male bodies; 雄性 SPME 收集物 SPME collection of male volatiles	GC-MS; 选择实验 Preference test	Cônsoli <i>et al.</i> , 2002
丽蝇蛹集金小蜂 <i>Nasonia vitripennis</i>	(4R,5R)-5-羟基-4-癸内酯 (4R,5R)-5-hydroxy-4-decanolide; (4R,5S)-5-羟基-4-癸内酯 (4R,5S)-5-hydroxy-4-decanolide; 4-甲基喹唑啉 4-methylquinazoline	雄性腹部二氯甲烷提取物 Dichloromethane extracts of male abdomens	GC-MS; 四腔嗅觉仪 Four-chamber olfactometer	Ruther <i>et al.</i> , 2007
红跗头甲肿腿蜂 <i>Cephalonomia tarsalis</i>	十二醛 Dodecanal	雌性二氯甲烷提取物 Dichloromethane extracts of female bodies	GC-MS; 四腔嗅觉仪 Four-chamber olfactometer	Collatz <i>et al.</i> , 2009
蝇蛹俑小蜂 <i>Spalangia endius</i>	6-甲基水杨酸甲酯 Methyl 6-methylsalicylate	雌性 SPME, SuperQ 收集物 SPME and SuperQ collection of female volatiles	GC-MS; GC-EAD; 培养皿搜寻实验 Host localization in a Petri dish	Nichols <i>et al.</i> , 2010
<i>Leptopilina heterotoma</i>	伊蚊内酯 (-)-iridomyrmecin	雌性体表二氯甲烷提取物 Dichloromethane extracts of female bodies	GC-MS; Y-型管 Y-tube olfactometer; 交配实验 Mating assay	Weiss <i>et al.</i> , 2013; Böttinger <i>et al.</i> , 2019
<i>Leptopilina rykyuensis</i>	伊蚊内酯 (-)-iridomyrmecin	雌性体表二氯甲烷提取物 Dichloromethane extracts of female bodies	GC-MS; 培养皿交配实验 Mating assay in a Petri dish	Böttinger <i>et al.</i> , 2019
<i>Leptopilina japonica</i>	伊蚊内酯 (-)-iridomyrmecin	雌性体表二氯甲烷提取物 Dichloromethane extracts of female bodies	GC-MS; 培养皿交配实验 Mating assay in a Petri dish	Böttinger <i>et al.</i> , 2019

续表 1 (Table 1 continued)

寄生蜂 Parasitoids	性信息素组分 Sex pheromones	来源 Resources	实验方法 Methods	参考文献 References
菜粉蝶盘绒茧蜂 <i>Cotesia glomerata</i>	壬醛 Nonanal	雌雄体表二氯甲烷提取物 Dichloromethane extracts of female and male bodies	GC-EAD; 四臂嗅觉仪 Four-arm olfactometer	Xu <i>et al.</i> , 2019
边室盘绒茧蜂 <i>Cotesia marginiventris</i>	庚醛 Heptanal	雌性 SuperQ 收集物 SuperQ collection of female volatiles; 雌性体表二氯甲烷提取物 Dichloromethane extracts of female bodies	GC-EAD; GC-PFC; 四臂嗅觉仪 Four-arm olfactometer	Xu <i>et al.</i> , 2020
白蜡吉丁啮小蜂 <i>Tetrastichus planipennis</i>	(6S,10S)-(2E,4E,8E)-4,6,8,10- tetramethyltrideca-2,4,8-triene	雌性 HayeSep-Q 收集物 HayeSep-Q collection of female volatiles	GC-MS; NMR; 风洞实验 Wind tunnel; 田间实验 Field test	Cossé <i>et al.</i> , 2020
棉铃虫齿唇姬蜂 <i>Campoletis chlorideae</i>	十四醛 Tetradecanal; 2-十七烷酮 2-heptadecanone	雌性体表正己烷提取物 Hexane extraction of female bodies	GC-EAD; GC-MS; EAG; Y 型管 Y-tube olfactometer; 培养皿交配实验 Mating assay in a Petri dish	Guo <i>et al.</i> , 2022

气相色谱-质谱联用 GC-MS: Gas chromatography coupled with mass spectrometry; 触角电位-气相色谱联用 GC-EAD: Gas chromatography coupled with electroantennogram detection; 触角电位 EAG: Electroantennogram; 二乙稀基-乙基乙稀苯型高分子多孔小球 PorapakQ; 气相色谱制备馏分收集器 GC-PFC: Gas chromatography-preparative fraction collector; 固相微萃取 SPME: Solid phase micro extraction; 核磁共振 NMR: Nuclear magnetic resonance.

1 寄主搜寻

1.1 寄主栖境定位 (Host habitat localization)

在自然界中,新羽化的寄生蜂往往处于一个全新的环境,面临的首要问题是寄主栖境定位。另外,当种群密度过高或者寄主数量过少的情况下,寄生蜂也会选择新的寄主栖境 (French and Travis, 2001)。在野外,寄主的栖境充斥着植物散发的多种多样的挥发物,这些植物挥发物对寄生蜂嗅觉系统而言可检测性高,可在长距离范围上引导寄生蜂向寄主栖境靠近 (Read *et al.*, 1970),但是植物挥发物只能指示寄生蜂潜在寄主存在的可能性,其可靠性低。在寄生蜂定向寄主生境过程中,虽然视觉可能会通过感知寄主栖境的物理特点如叶片形状的不同来提供一些辅助信息 (Mackauer, 1965),但是嗅觉起决定性的主导作用。在此过程中,雌蜂和雄蜂都可以利

用寄主植物气味来定位寄主的栖境,但生理意义不同,雌蜂主要目的是寻找寄主,而雄性主要是通过寻找寄主栖境中的雌蜂来进行交配。

1.2 寄主定位 (Host localization)

当寄生蜂到达寄主栖境后,雌蜂的首要任务是定位寄主。寄主的栖境由多种生物群落组成,通常雌蜂会在寄主所在植物周围 1-2 cm 进行搜寻,用触角等化学感觉器官对寄主损伤的植物组织进行试探,就近搜索寄主,然后依靠直接或间接的信号定位寄主 (Vinson, 1975, 1976)。进入寄主栖境后,寄主位置相关的化学信号多种多样,但基本可分为两类,第一类是寄主侵害的植物释放的“求救信号”,第二类是寄主本身释放的利他素,有可能是寄主的性信息素、聚集信息素、粪便及鳞片气味等。这些化学物质释放量相对较低,但是具有较高的种属特异性,对寄生蜂而言可检测性低,但是可靠性高。因为寄生是雌

蜂的特异行为,所以雌蜂感受 HIPV 和寄主利他素的能力强,而雄蜂的感受能力相对较弱。

1.2.1 虫害诱导植物气味挥发物 当被植食性昆虫损伤后,植物会释放一定比例的气味化合物来吸引植食者的天敌寄生蜂,这些化合物通称为植食者诱导的植物气味挥发物 (Herbivore-induced plant volatiles, HIPVs)。早在 20 世纪 80 年代初科学家就提出植物被害虫侵害后会释放气味化合物来招募寄生蜂进行间接防御 (Price *et al.*, 1980)。从 20 世纪 80 年代到 90 年代,通过研究不同的三级营养关系 (植物-害虫-天敌寄生蜂)证明植物被害虫侵害后释放气味化合物具有种属特异性,是寄生蜂定位寄主的可靠信号。因此,20 世纪 90 年代初, HIPVs 概念被正式提出,被认为是介导三级营养关系的主要信息化学物质 (Dicke *et al.*, 1990; Turlings *et al.*, 1990)。不同植物挥发的 HIPVs 组分通常不同,而且同类植物被不同害虫侵害后释放的 HIPVs 也可能不同 (Guo and Wang, 2019; Takabayashi, 2022)。HIPVs 主要包括 6 个碳的绿叶气味 (Green leaf volatiles, GLVs)、脂肪族化合物 (Aliphatic compounds)、萜烯类化合物 (Terpenoids) 及芳香族化合物 (Aromatic compounds) 等 (Guo and Wang, 2019)。过去几十年,通过质谱分析对比健康的植株和害虫危害的植物的挥发物组成,多种植物的 HIPV 组分得到鉴定,包括棉花 (Loughrin *et al.*, 1994, 1995; McCall *et al.*, 1994; Rose *et al.*, 1996; Röse and Tumlinson, 2004)、玉米 (Turlings *et al.*, 1990, 1991; Turlings and Tumlinson, 1992; Yan and Wang, 2006a, 2006b)、烟草 (De Moraes *et al.*, 1998, 2001; Yan *et al.*, 2005)、芸豆 (Birkett *et al.*, 2003) 和西红柿 (Silva *et al.*, 2017) 等。其中,绿叶气味顺-3-己烯醇(Z)-3-hexen-1-ol 和顺-3-己烯乙酸酯(Z)-3-hexenyl acetate、单萜类化合物反- β -罗勒烯(E)- β -ocimene 和芳樟醇 Linalool、倍半萜类化合物 α -法呢烯(E,E)- α -farnesene 和反- β -石竹烯(E)- β -caryophyllene、萜烯同系物反-4,8-二甲基-1,3,7-壬三烯(E)-4,8-dimethyl-1,3,7-nonatriene (DMNT) 和反,反-4,8,12-三甲基-1,3,7,11-十三碳四烯(E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) 是

常见的 HIPV 组分 (McCormick *et al.*, 2012; Guo and Wang, 2019)。虽然 HIPVs 含有多种组分,但是寄生蜂可能只利用其中一部分来定位寄主,所以活性 HIPV 组分的鉴定对提高寄生蜂防治害虫的效率至关重要。然而,以往的研究基本侧重于 HIPVs 的化学鉴定和寄生蜂对总体 HIPVs 的行为反应,研究单一组分对寄生蜂行为的调节作用还非常少。表 2 列举了已报道的对寄生蜂具有明显吸引力或者可以提高其寄生效率的 HIPV 组分。这些研究基本利用传统的行为学实验,如风洞试验、Y 型管选择实验等,逐一分析 HIPV 组分对寄生蜂行为的调控作用,耗时耗力。近年来,随着测序技术的应用,大量寄生蜂的化学感受相关基因得到鉴定,为利用“反向化学生态学”鉴定 HIPV 活性组分提供了基础。例如,在棉铃虫齿唇姬蜂中,转录组测序鉴定到一个只在雌性触角中表达的气味受体——CchlOR62 (Sun *et al.*, 2019)。功能研究发现 CchlOR62 的配体是一种棉花和烟草的 HIPV 组分——顺-茉莉酮(Z)-jasmone; 行为实验表明顺-茉莉酮对雌蜂有强烈的吸引力,而且能明显地提高雌蜂对棉铃虫低龄幼虫的寄生效率,表明反向化学生态学是鉴定 HIPV 活性组分的一种快速可靠的方法 (Sun *et al.*, 2019)。有意思的是,并不是所有的 HIPV 组分都对寄生蜂有吸引力,例如拟南芥释放的 HIPV 组分水杨酸甲酯 Methyl salicylate 对半闭弯尾姬蜂 *Diadegma semiclausum* 有趋避作用 (Snoeren *et al.*, 2010),说明了营养级之间互作的复杂性。

1.2.2 寄主性信息素 性信息素是昆虫求偶的决定性信号,具有很高的物种特异性,这也给了天敌“可乘之机”。行为实验说明寄生蜂可以“监听”寄主的性信息素来定位寄主。在风洞实验中,异利匙胸瘿蜂 *Leptopilina heterotoma* 明显趋向寄主果蝇 *Drosophila melanogaster* 的性信息素顺 11-十八乙酸酯(Z)-11-vaccenyl acetate(cVA),在笼罩实验中也明显选择含有 cVA 的诱芯 (Wertheim *et al.*, 2003)。螟黄赤眼蜂 *Trichogramma chilonis* 和菜蛾绒茧蜂 *Cotesia plutellae* 是小菜蛾 *Plutella xylostella* 的天敌寄生蜂,它们在 Y 型嗅觉仪中对小菜蛾的性信息素顺 11-十六醛(Z)-11-hexadecenal、顺 11-十六乙

表 2 吸引寄生蜂的虫害诱导植物气味挥发物组分
Table 2 Active components of herbivore-induced plant volatiles

三级营养关系 Tritrophic interactions	有效挥发物 Effective volatiles	实验方法 Methods	效果 Effects	参考文献 References
棉花-棉铃虫- 棉铃虫齿唇姬蜂 <i>Cotton-Helicoverpa armigera-Campoletis chloridae</i>	顺-3-己烯乙酸酯 (Z)-3-hexenyl acetate; 顺-茉莉酮(Z)-jasmane	Y-型管 Y-tube olfactometer; 笼罩实验 Cage experiment	吸引雌蜂 Attracting females; 提高寄生率 Enhancing parasitism	Loughrin <i>et al.</i> , 1995; Sun <i>et al.</i> , 2019, 2020
芸豆-白粉虱- 丽蚜小蜂 <i>Phaseolus vulgaris-Trialeurodes vaporariorum-Encarsia formosa</i>	顺-3-己烯醇(Z)-3-hexen-1-ol; 3-辛酮 3-octanone; DMNT	GC-MS; 风洞实验 Wind tunnel	吸引雌蜂 Attracting females	Birkett <i>et al.</i> , 2003
玉米-东方粘虫- 棉铃虫齿唇姬蜂 <i>Maize- Mythimna separata-Campoletis chloridae</i>	顺-3-己烯乙酸酯(Z)-3-hexenyl acetate; 芳樟醇 Linalool	GC-MS; Y 型管 Y-tube olfactometer	吸引雌蜂 Attracting females	Yan and Wang, 2006b; Sun <i>et al.</i> , 2020
豆科植物-南美斑潜蝇- 离潜蝇茧蜂 <i>Fabaceae spp.-Liriomyza huidobrensis-Opius dissitus</i>	顺-3-己烯醇(Z)-3-hexen-ol	GC-MS; Y 型管 Y-tube olfactometer	吸引雌蜂 Attracting females	Wei <i>et al.</i> , 2007
棉花-棉铃虫- 中红侧沟茧蜂 <i>Cotton-Helicoverpa armigera-Microplitis mediator</i>	壬醛 Nonanal; DMNT; 顺-3-己烯乙酸酯(Z)-3-hexenyl acetate	GC-EAD; Y 型管(+)-; 笼罩实验 Cage experiment	吸引雌蜂 Attracting females; 提高寄生率 Enhancing parasitism	Yu <i>et al.</i> , 2010
玉米-粉红禾草螟- 布氏赤眼蜂 <i>Maize-Chilo partellus-Trichogramma bournieri</i>	反-(1R,9S)-石竹烯 (E)-(1R,9S)-caryophyllene; DMNT; TMTT	GC-MS; Y 型管 Y-tube olfactometer	吸引雌蜂 Attracting females	Tamiru <i>et al.</i> , 2011
荔枝-荔枝平腹小蜂 <i>Litchi-Tessaratoma papillosa-Anastatus japonicus</i>	β -石竹烯 β -caryophyllene; 十一烷 Undecane; 反- α -法尼烯(E)- α -farnesene; (+)- 香橙烯 (+)-aromadendrene; 顺-3-己烯醇(Z)-3-hexen-ol	GC-MS; 选择实验 Preference test; 卵寄生实验 Oviposition choice	吸引雌蜂 Attracting females; 提高定位寄主卵的效率 Facilitating host egg localization	Wang <i>et al.</i> , 2017

气相色谱-质谱联用 GC-MS: Gas chromatography coupled with mass spectrometry; 反-4,8-二甲基-1,3,7-壬三烯 DMNT: (E)-4,8-dimethyl-1,3,7-nonatriene; 反,反-4,8,12-三甲基-1,3,7,11-十三碳四烯 TMTT: (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene.

酸酯(Z)-11-hexadecenyl acetate、顺-11-十六醇(Z)-9-hexadecenol(1:1:0.01)有明显的趋向反应(Reddy *et al.*, 2002)。田间引诱实验发现茶毒蛾黑卵蜂 *Telenomus euproctidis* 明显趋向其寄主台湾黄毒蛾 *Euproctis taiwana* 的主要性信息素组分顺-16-甲基-9-十七碳烯基异丁酸酯(Z)-16-methyl-9-heptadecenyl isobutyrate(Arakaki *et al.*, 1996)。同样,田间引诱实验发现 *Wroughtonia*

ligator 明显选择含有其寄主黑腹尼虎天牛 *Neoclytus acuminatus* 性信息素组分 2,3-二甲基环己醇(2,3)-hexanediol 的粘板(Johnson *et al.*, 2021)。麦蛾柔茧蜂 *Bracon hebetor* 是一种外寄生蜂,以螟蛾科昆虫为寄主,GC-EAD 和 Y 型嗅觉仪实验表明交配的但没有寄生经验的雌性麦蛾柔茧蜂对蜡螟 *Galleria mellonella* 的雄性性信息素壬醛 Nonanal 和十一醛 Undecanal(7:3)

有明显的电生理和行为趋向反应 (Dweck *et al.*, 2010)。在 Y 型嗅觉仪中, 黑卵蜂 *Telenomus busseolae* 对处于召唤期的甘蔗螟虫 *Sesamia nonagrioides* 释放的性信息素, 顺 11-十六乙酸酯、顺 11-十六醇、顺 11-十六醛和乙酸十二酯 Dodecyl acetate (8.5 : 1 : 1 : 2) 有明显的趋向反应 (Colazza *et al.*, 1997)。在一个聚丙烯笼 (24 cm × 24 cm × 8 cm) 中, 寄足黑卵蜂 *Telenomus podisi* 明显趋向寄主褐蝽 *Euschistus heros* 雄性释放的性信息素 2,6,10-三甲基十三烷酸甲酯 methyl 2,6,10-trimethyltridecanoate (Silva *et al.*, 2006)。四臂嗅觉仪行为实验发现, 红金姬小蜂 *Chrysonotomyia ruforum* 行为趋向赤松叶蜂 *Diprion pini* 和松锈叶蜂 *Neodiprion sertifer* 的主要性信息素组分 (2S,3R,7R)-3,7-二甲基-2-十三烷基乙酸酯 (2S,3R,7R)-3,7-dimethyl-2-tridecyl acetate 和松锈叶蜂的性信息素组分 (2S,3S,7S)-3,7-二甲基-2-十五烷基乙酸酯 (2S,3S,7S)-3,7-dimethyl-2-pentadecyl acetate, 且这种行为选择不受寄生经历的影响 (Hilker *et al.*, 2000)。田间引诱和室内选择实验发现无花果粉蚧 *Planococcus ficus* 的性信息素 (S)-(+)-lavandulyl senecioate 可吸引天敌寄生蜂 *Anagyrus pseudococchi* (Franco *et al.*, 2008)。桃蚜 *Myzus persicae* 的性信息素组分 (4aS,7S,7aR)-荆芥内酯 (4aS,7S,7aR)-nepetalactone 可以刺激其天敌寄生蜂 *Aphidius colemani* 的触角产生强烈的电生理反应, 而且引起天敌的驻留行为 (Fernández-Grandon and Poppy, 2015)。此外, 触角电位分析发现棉铃虫齿唇姬蜂对棉铃虫的性信息素组分顺 11-十六醛和顺 9-十六醛的有较强的电生理反应, 说明棉铃虫齿唇姬蜂可以感受寄主的性信息素组分 (颜增光等., 2006)。最近, Shan 等 (2019) 通过反向化学生态学研究发现中红侧沟茧蜂 *Microplitis mediator* 的离子型受体 IR64a2 对寄主棉铃虫的性信息素组分顺 9-十四醛 (Z)-9-tetradecenal 起反应, 说明中红侧沟茧蜂可以感受寄主性信息素组分从而准确定位寄主。

寄生蜂多在白天活动, 而寄生蜂的寄主多在夜间活动, 取食、求偶和交配, 这为寄生蜂利用寄主的信息素定位寄主造成困难。那么, 这种时

间差会不会导致寄生蜂很难接触到寄主的性信息素? 其实不然, 有研究表明寄主成虫在夜间召唤 (Calling) 时释放的性信息素会被周围植物组织吸附 (Wall *et al.*, 1981; Noldus *et al.*, 1991)。另外, 寄主在产卵时, 因为产卵器与性信息素腺体位置靠近, 也会遗留部分性信息素在卵或植物组织上。这些残留在环境介质上的寄主性信息素组分为寄生蜂提供了寄主的位置 (Poivet *et al.*, 2012)。

1.2.3 寄主聚集信息素 寄主的聚集信息素 (Aggregation pheromone) 也是寄生蜂定位寄主的信号源之一。例如, 点蜂缘椿 *Riptortus clavatus* 雄性释放 (反, 顺)-2-己烯基-3-己烯酸酯 (E)-2-hexenyl (Z)-3-hexenoate 作为聚集信息素组分, 这个化合物不仅可以聚集点蜂缘椿象还对寄生蜂黑蝽卵跳小蜂 *Ooencyrtus nezarae* 有较强的吸引力, 还能在田间显著提高黑蝽卵跳小蜂对点蜂缘椿象卵的寄生率 (Masuta *et al.*, 2001; Son *et al.*, 2009; Alim and Taek Lim, 2011)。另外, 四臂嗅觉仪行为实验表明谷蠹 *Rhyzopertha dominica* 的聚集信息素 Dominicalure 对米象金小蜂 *Lariophagus distinguendus* 有较强的吸引力 (Steidle *et al.*, 2003)。

1.2.4 寄主成虫鳞片 很多寄生蜂以鳞翅目昆虫作为寄主, 鳞翅目昆虫鳞片中的化合物可能被寄生蜂利用来定位寄主。早在 1972 年, Lewis 等 (1972) 利用温室和田间行为实验发现粉斑螟蛾 *Cadra cautella* 成虫鳞片的正己烷提取物可以明显提高广赤眼蜂 *Trichogramma evanescens* 对粉斑螟蛾卵的寄生效率, 第一次证明寄主鳞片也是寄生蜂定位寄主的信号源。随后在 1973 年, 他们在美洲棉铃虫 *Helicoverpa zea* 成虫鳞片的正己烷提取物中分离到 4 种活性成分, 分别为二十二烷 Docosane、二十三烷 Tricosane、二十四烷 Tetracosane 和二十五烷 Pentacosane, 可以提高广赤眼蜂对美洲棉铃虫卵的寄生效率, 其中二十三烷的效果最好 (Jones *et al.*, 1973)。

1.2.5 寄主粪便 20 世纪 70 年代, 化学生态学家发现寄主的粪便挥发物是寄生蜂搜寻寄主的信号源之一。在 1971 年, Jones 等 (1971) 利用培养皿 (9 cm 直径) 选择实验发现藏红足侧沟

茧蜂 *Microplitis croceipes* 趋向其寄主美洲棉铃虫幼虫粪便中的化合物, 十三甲基三十烷 13-methylhentriacontane, 这个化合物是第一个被报道的与寄生蜂寄生相关的昆虫利它素。随后, Hendry 等 (1973) 利用同样的行为实验发现 *Orgilus lepidus* 明显地选择含有马铃薯块茎蛾 *Phthorimaea operculella* 幼虫的粪便组分庚酸 n-heptanoic acid 的滤纸片。通过对比微红盘绒茧蜂 *Cotesia rubecula* 对主要寄主菜粉蝶 *Pieris rapae*、次要寄主大菜粉蝶 *Pieris brassicae* 和非寄主暗脉菜粉蝶 *Pieris napi* 2 龄幼虫粪便的偏好, 研究人员发现微红盘绒茧蜂明显更喜欢主要寄主菜粉蝶的粪便, 也选择大菜粉蝶的粪便, 但是对非寄主的粪便没有选择性, 这个对比研究说明寄主粪便是有效的寄主定位信号 (Agelopoulos *et al.*, 1995)。美洲蟑螂 *Periplaneta americana* 的粪便组分顺, 顺-6,9-十七碳二烯 (Z,Z)-6,9-heptacosadiene 也对蜚卵啮小蜂 *Aprostocetus hagenowii* 有明显的吸引力 (Suiter *et al.*, 1996)。此外, 从 2 龄小菜蛾的粪便分离出的异硫氰酸丙烯酯 Allyl isothiocyanate 对螟黄赤眼蜂 *Trichogramma chilonis* 和菜蛾绒茧蜂 *Cotesia plutellae* 有明显的吸引力, 异硫氰酸丙烯酯是十字花科植物释放的标记化合物, 说明寄主粪便对寄生蜂的吸引力部分来自于植物 (Reddy *et al.*, 2002)。

1.2.6 其它寄主定位信号 有些寄生蜂寄主的生存策略比较特殊, 但是寄生蜂恰恰利用这种特殊性来搜寻合适的寄主。寄生蜂 *Pseudacteon tricuspis* 专性寄生红火蚁, 它可以感受工蚁释放的警戒信息素来定向和定位寄主 (Morrison and King, 2004)。另外, *P. tricuspis* 对红火蚁毒液中的生物碱组分 2,6-二烷基哌啶 2,6-dialkylpiperidine 有明显的触角电生理反应和行为趋向, 说明红火蚁的毒液生物碱是 *P. tricuspis* 定位红火蚁的嗅觉信号之一 (Chen *et al.*, 2009)。此外, 鳞翅目昆虫幼虫的上颚腺 (Mandibular gland) 组分也是寄生蜂定位寄主的嗅觉信号。例如, 地中海粉螟 *Ephestia kuehniella* 5 龄幼虫的上颚腺组分 2-酰基环己烷-1,3-二酮 2-acylcyclohexane-1,3-diones

可以刺激麦蛾茧蜂 *Bracon hebetor* 的触角电位反应和产卵器的试探行为 (Strand *et al.*, 1989)。同样, 烟芽夜蛾 *Heliothis virescens* 幼虫上颚腺中的 32 碳、33 碳、34 碳饱和碳水化合物对黑头折脉茧蜂 *Cardiochiles nigriceps* 有吸引力, 能够明显增加雌蜂触角试探含有这些化合物的滤纸片的频次 (Vinson *et al.*, 1975)。另外, 大蜡螟 *Galleria mellonella* 和猫儿眼白眼眉天蛾 *Celerio euphorbiae* 淋巴液中的己糖和氨基酸组分可以有效地激发埃姬蜂 *Itopectis conquisitor* 的寄生行为 (Hegdekar and Arthur, 1973)。

2 信息化学物质在生物防治上的应用潜力

在害虫生物防治方面, 信息化学物质的应用主要有以下几个方向: (1) 监测寄生蜂种群动态, 为人工释放寄生蜂提供科学依据 (Suckling *et al.*, 2002); (2) 优化交配条件, 利用性信息素可增加雌雄寄生蜂交配的机会, 有可能使寄生蜂的饲养种群有一个比较理想的性比, 促进室内大规模繁育寄生蜂 (Ruther, 2013); (3) 促进寄生蜂定向和定位寄主的效率, 有效提高寄生蜂的寄生效率 (Peñaflor and Bento, 2013)。

上述寄生蜂搜寻寄主所利用的信息化学物质和性信息素均可在害虫推拉防治策略中发挥作用。但是, 现阶段信息化学物质对寄生蜂行为的调节作用还基本停留在室内或者野外小范围验证阶段, 实际应用还非常有限。在未来, 我们需要在田间扩大行为测试的范围, 促进实验室结果的应用转化。在进行田间实验时, 除了测试信息化学物质对寄生蜂寄生效率的影响外, 也要关注以下问题。第一, 植物-害虫-寄生蜂之间的互动可能远比我们想象的复杂。例如, 玉米等植物释放的 HIPV 组分吲哚 Indole 招募红腹侧沟茧蜂 *Microplitis rufiventris* 的同时也可以改变寄主海灰翅夜蛾 *Spodoptera littoralis* 幼虫体表的挥发物谱, 使其失去对红腹侧沟茧蜂的吸引力, 降低了寄生蜂的寄生效率 (Ye *et al.*, 2018)。另外, 通常情况下海灰翅夜蛾幼虫趋避吲哚, 而当寄生

蜂存在时则不再趋避,说明害虫也会利用 HIPV 组分进行自我防护 (Ye *et al.*, 2018)。第二,信息化学物质之间存在拮抗作用。在室内笼罩实验中,顺-茉莉酮和顺-3-己烯乙酸酯单独使用时均能明显提高棉铃虫齿唇姬蜂寄生棉铃虫幼虫的效率,但是二者的混合物却没有效果 (Sun *et al.*, 2020)。第三,信息化学物质可能产生迷向效果。田间环境条件与室内实验条件不同,室内有效的化合物在田间不一定有效,有的情况下可能还会起到迷向寄生蜂的作用,使寄生效率下降 (Guo *et al.*, 2022)。第四,重寄生蜂 (Hyperparasitoid) 也可以利用 HIPV 来定位寄生蜂进行寄生,从而削弱寄生蜂对害虫种群的控制力度 (Poelman *et al.*, 2012; Li *et al.*, 2020), 而重寄生的影响往往在实验设计时被我们忽视。

3 展望

过去几十年,与寄生蜂寄生相关的信息化学物质,包括多种植物源气味挥发物和寄主昆虫的信息素得到鉴定,提供了新的害虫防治思路。例如,室内选择实验表明顺-茉莉酮和性信息素可以分别吸引棉铃虫齿唇姬蜂雌蜂和雄蜂从而提高雌性定位寄主和雄蜂定位配偶的效率,二者同时使用可以明显地提高棉铃虫齿唇姬蜂的寄生效率 (Sun *et al.*, 2019; Guo *et al.*, 2022)。但是,室内的行为实验有其局限性,人为设定的条件与田间条件的复杂度相差较大。在未来的研究中,我们在室内行为学研究的基础上,应当尽量模拟田间条件,有条件可利用真实植物和大空间温室来测试化合物对寄生蜂行为的调节作用,这样得到的结果会更加符合实际情况。另外,我们也应当重视开发田间释放信息化化合物的方法。传统喷洒和悬挂缓释诱芯的方法简单易行,但化合物耗费量大,且使用失当易产生迷向作用。利用转基因植物来释放关键化学信息物质可能是未来的发展方向之一,特别是基因编辑技术在植物中的应用为这个方向提供了很多可能性 (Brillada *et al.*, 2013)。在化学生态学领域,越来越多的研究通过研究气味受体的功能来鉴定活性化合物。寄生蜂的基因组含有多达几百个气味受体基

因,而这些基因基本还都是孤儿受体,功能没有得到鉴定,因此寄生蜂气味受体的功能研究是一个挑战 (Zhou *et al.*, 2015)。最近,机器学习 (Quantitative-structure-activity relationship, QSAR) 被用来预测果蝇、蚊子和鳞翅目昆虫气味受体的配体,成功率在 70% 以上 (Boyle *et al.*, 2013; Tauxe *et al.*, 2013; Caballero-Vidal *et al.*, 2021)。鉴于寄生蜂庞大的气味受体数量,利用 QSAR 来快速预测寄生蜂气味受体的配体并结合功能验证可能是一种快速有效的鉴定活性信息化学物质的方法。

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