

化学信息介导的昆虫产卵行为及机制研究进展*

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摘要 产卵行为是昆虫完成个体发育、繁衍后代、维持种群稳定的重要行为活动之一, 化学信息在昆虫产卵选择行为中发挥着重要作用。昆虫在识别和定位产卵位点时会受到来自植物、昆虫本身以及微生物释放的挥发性有机化合物等因素的影响, 合理应用这些化学信息调控昆虫行为是实现害虫绿色防控的重要方式。本文综述了昆虫多样的产卵策略及其影响的主要因素, 详述了调控昆虫产卵行为的化学信息的来源, 论述了植物、昆虫信息化合物和微生物释放的挥发物对昆虫行为的调控作用, 从昆虫外周神经系统中重要化学感受蛋白的作用机制为切入点阐述了昆虫的产卵机制与研究现状, 及其在害虫绿色防控中的应用, 并对未来重点研究的方向进行了分析和展望。

关键词 挥发物; 产卵行为; 植食性昆虫; 天敌昆虫; 化学感受; 行为调控

Research progress on semiochemicals-mediated egg-laying behavior and mechanism in insects

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Abstract Egg-laying behavior of insect is critical for completing their ontogeny, reproduction, and maintaining population stability. Chemical cues play a dominant role in regulating insect oviposition. Volatile organic compounds released by plants, insects, and microorganisms influence the detection and localization of insect oviposition sites. Exploiting and rationally applying these chemical cues to regulate insect behaviors is an important strategy for environmentally friendly pest control. This article summarizes the diverse egg-laying strategies of insects and their contributing factors, details the sources of chemical information that regulate insect oviposition behavior, and lists the regulatory effects of volatiles released by plants, insect semiochemicals and microorganisms on insect behaviors. The mechanism and research status of oviposition selection mediated by chemical cues are illustrated on the mechanism of the important chemoreceptor proteins in the insect peripheral nervous system, and applications in environmentally friendly prevention and control of agricultural pests are reviewed. Finally, future research directions are prospected.

Key words volatile organic compounds; egg-laying behavior; herbivore; natural enemy; chemical detection; behavioral regulation

产卵行为作为昆虫最重要的行为活动之一, 具有重要的意义 (Lu *et al.*, 2011; Anholt, 2020; 对昆虫的个体发育、种群动态、物种繁衍具有非 Anholt *et al.*, 2020)。昆虫对产卵位点的选择具

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有多样性,包括土壤,植物的根、茎、叶以及果实,腐烂的木材,昆虫幼虫,以及水等基质(Kambysellis and Heed, 1971; Carson and Kaneshiro, 1976; Becher *et al.*, 2012; Günther *et al.*, 2019)。昆虫产卵涉及一系列复杂的行为过程,一般包括寄主定位、接触试探、识别、接受、产卵及清洁等步骤(Smedley *et al.*, 2002; Yang *et al.*, 2008)。一般而言,昆虫首先利用视觉和嗅觉系统远距离搜寻产卵位点;当靠近产卵位点时,昆虫会综合利用触角、唇瓣、足跗节和产卵器等组织上的化学传感器和机械传感器对产卵位点的物理结构以及化学性质等进行评估,从而完成对产卵位点的识别与接受(Yang *et al.*, 2008; Cury *et al.*, 2019)。昆虫对这些化学或物理线索的识别与评估离不开昆虫的嗅觉、味觉和触觉等感觉的输入(Hussain *et al.*, 2016; Rimal *et al.*, 2019; Auer *et al.*, 2020; Zhang *et al.*, 2020),其中化学线索起到了先决和主导的作用(Leroy *et al.*, 2011a, 2012; Abraham *et al.*, 2018; Cury *et al.*, 2019; Anholt, 2020; Tait *et al.*, 2020)。本文对昆虫产卵决策以及影响昆虫产卵选择的化学线索进行综述,对昆虫产卵选择机制、研究现状及其应用进行归纳与总结,以期对昆虫产卵信息化合物产品的研发以及害虫的绿色防控提供一定的借鉴作用和理论指导。

1 昆虫的产卵策略

昆虫的产卵选择行为是昆虫对环境适应的结果,由于幼虫改变其栖息地的能力有限,怀卵雌虫需要寻找到合适的位点并产卵,从而减少后代遇到捕食或饥饿风险,最大限度地提高胚胎存活率以及保证后代正常生长发育,对昆虫完成生活史而言非常重要(Refsnider and Janzen, 2010)。不同昆虫对产卵基质的偏好多种多样,例如,在果蝇科昆虫中,已报道的产卵基质包括植物的叶片、水果、腐烂的仙人掌、真菌、甚至螃蟹体表等(Markow, 2019),即使在亲缘关系很近的物种之间,彼此对产卵基质的偏好也不尽相同。

为了最大限度地提高后代的存活率,昆虫往往选择在捕食风险较低的位点产卵(Petranka

and Fakhoury, 1991; Kacsoh *et al.*, 2013)。绝大多数雌性昆虫都具有这样的产卵策略,例如,长纹脉毛蚊 *Culiseta longiareolata* 不会在具有捕食者存在的环境周围产卵,以确保它们的后代可以生存下来(Eitam and Blaustein, 2004)。另外,避免种间竞争也是昆虫的一种重要的产卵决策,在植食性昆虫和捕食性昆虫中都很常见。例如,地中海粉螟 *Anagasta kuehniella* 雌虫避免在具有一定种群密度的同种或异种昆虫定殖的植株上产卵(Corbet, 1971),而捕食性昆虫亮带食蚜蝇 *Epistrophe nitidicollis* 和黑带食蚜蝇 *Episyrphus balteatus* 雌虫也具有相似的产卵决策,以降低种内或种间竞争(Hemphill *et al.*, 1993; Amorós-Jiménez *et al.*, 2015)。

具有较好营养条件的产卵基质也是昆虫选择理想产卵位点的一种策略,可加快后代在适宜生境下快速的生长发育(Refsnider and Janzen, 2010)。植食性昆虫的“选择-表现”假说指出,雌性更倾向于在对其幼虫具有最高营养效益的寄主植物上产卵(Pöykkö, 2006),在理想的寄主植物上生存能够大幅缩短幼虫阶段的发育时间,可以有效地降低被捕食或寄生的风险。例如,北美瓶草蚊 *Wyeomyia smithii* 喜欢在一种较大的猪笼草紫瓶子草 *Sarracenia purpurea* 上产卵,是因为北美瓶草蚊幼虫能够以紫瓶子草捕捉的其他昆虫残体为食。这种产卵位点的选择机制间接地利用了猪笼草与猎物结构关系,使北美瓶草蚊后代能轻松获得充足的食物,促进幼虫生长发育,并降低被取食的风险(Heard, 1994)。

在复杂多变的外界环境中,昆虫往往会在风险与食物之间做出权衡。果蝇的雌虫会将卵产在营养丰富的食物周围,或营养并不丰富的位点,以避免食物招致有害微生物或捕食者威胁子代生存(Miller *et al.*, 2011; Yang *et al.*, 2015; Sumethasorn and Turner, 2016)。Sumethasorn 和 Turner (2016) 研究发现黑腹果蝇 *Drosophila melanogaster* 偏好在含有乙醇的基质上产卵,而不是营养物质丰富的位点,以保护幼虫免受寄生蜂的危害。Yang 等(2008)发现黑腹果蝇雌虫偏好在苦味基质上产卵,不选择蔗糖基质,但仅存在苦味或甜味一种基质时,雌虫产卵数量基本

相等,且果蝇对苦味基质的产卵偏好随着苦味与甜味基质之间距离的增加而减少。该研究结果表明当雌虫可以评估后代将面临的觅食成本并做出产卵决策时,仅仅是选择营养丰富的产卵位点;当雌虫存在多种选择时,则优先选择对子代生存更安全的产卵位点(Miller *et al.*, 2011; Becher *et al.*, 2012)。这些研究结果进一步揭示了昆虫对产卵选择的决策过程不仅仅是由雌虫感知周围环境后的个体感官输入决定的,而是雌性个体整合各种感觉输入,评估产卵基质上的各种条件对后代生存的影响后作出的判断。

2 化学线索影响昆虫产卵选择

昆虫的产卵选择具有定位、识别和接受等一般过程,主要受到物理信号和化学信号的调节,其中化学信号起着先决和主导作用(图 1),昆虫的产卵选择行为很大程度上取决于化学感受引起的神经信号输入(Abraham *et al.*, 2018; Cury *et al.*, 2019; Anholt, 2020; Tait *et al.*, 2020)。

2.1 来自植物的挥发性化合物

植物释放的挥发性化合物在植食性昆虫寄主的选择定位中起着非常重要的作用。这些植物源的挥发性化合物可以为植食性昆虫定位食物和产卵位点提供指示,帮助它们做出寄主选择的第一步(Bruce, 2015)。研究发现这些化合物主要是萜烯类、烯烃、醇类、酮类、醛类和酯类等化合物(Paré and Tumlinson, 1999)。根据化合物的来源,可将这些化合物进一步分为寄主植物挥发物和非寄主植物挥发物。

2.1.1 寄主植物挥发物

2.1.1.1 植食性昆虫对普通植物挥发物的产卵选择 植食性昆虫对普遍存在于寄主植物挥发物中的醇、醛和酯类等衍生物有较为强烈的趋向性反应(Huang *et al.*, 2021; Jacobsen and Raguso, 2021)。例如,茶小绿叶蝉 *Empoasca vitis* 能够识别茶树品系 Enbiao 和 Banzhuyuan 释放的挥发物顺-3-己烯乙酸酯和顺-3-己烯醇,并表现出明显的产卵偏好性(Xin *et al.*, 2017)。烟草 *Nicotiana tabacum* 挥发物壬醛、烟碱和茄酮能够激活烟青

虫 *Helicoverpa assulta* 触角的 EAG 反应,并显著吸引雌成虫产卵(Wang *et al.*, 2020)。另有研究显示,植物挥发物顺-3-己烯基丁酯也是吸引烟青虫雌虫产卵的关键成分(Li *et al.*, 2020)。行为学和双向产卵选择试验表明,玉米花粉挥发物苯甲醛、壬醛、对伞花烃、柠檬烯和 α -蒎烯对阿拉伯按蚊 *Anopheles arabiensis* 怀卵雌虫有显著吸引作用,并可刺激雌虫产卵(Wondwosen *et al.*, 2017)。

2.1.1.2 植食性昆虫对虫害诱导的植物挥发物的产卵决策 植物受到虫害胁迫后会启动一系列防御反应,释放出有别于健康植物所释放的植物挥发物,即虫害诱导植物挥发物(Herbivore-induced plant volatiles, HIPVs),HIPVs 的主要成分是一些萜烯类化合物、绿叶挥发物(Green leaf volatile, GLV)以及一些含氮/硫化化合物(Engelberth *et al.*, 2004)。为了提高同种后代的存活率,降低后代生存竞争,植食性昆虫往往会避免在已被为害的植物上定殖和产卵。研究显示,虫害诱导的烟草植株挥发物法尼烯的同分异构体(反式,反式)- α -法尼烯(49%)、(反式)- β -法尼烯(26%)、(顺式)- β -法尼烯(18%)以及(顺式,反式)- α -法尼烯(7%)能显著抑制烟青虫雌成虫的产卵行为,同时对其幼虫内寄生蜂齿唇姬蜂 *Campoletis chloridae* 有显著的引诱作用,表明植物释放的 HIPVs 能够调控三级营养级间的作用模式(Wu *et al.*, 2019)。研究发现海灰翅夜蛾 *Spodoptera littoralis* 取食棉花后诱导的挥发物 4,8-二甲基-1,3,7-壬三烯(DMNT)能抑制同种个体对其主要性信息素组分(顺式)-9-(反式)-11-十四碳烯-1-醇的选择,从而影响交配和产卵行为(Hatano *et al.*, 2015)。类似地,海灰翅夜蛾取食玉米后诱导的挥发物吲哚能够驱避雌成虫产卵,达到直接防御的作用(Veyrat *et al.*, 2016)。由此可见, HIPVs 驱避某些植食性昆虫是植物在长期进化过程中产生的防御反应,以减少对植物自身的危害。而有些植食性昆虫进化出了对抗植物防御反应的策略,可利用 HIPVs 定位寄主植物并产卵。芥子油苷(Glucosinolate, GS)是十字花科植物典型的含

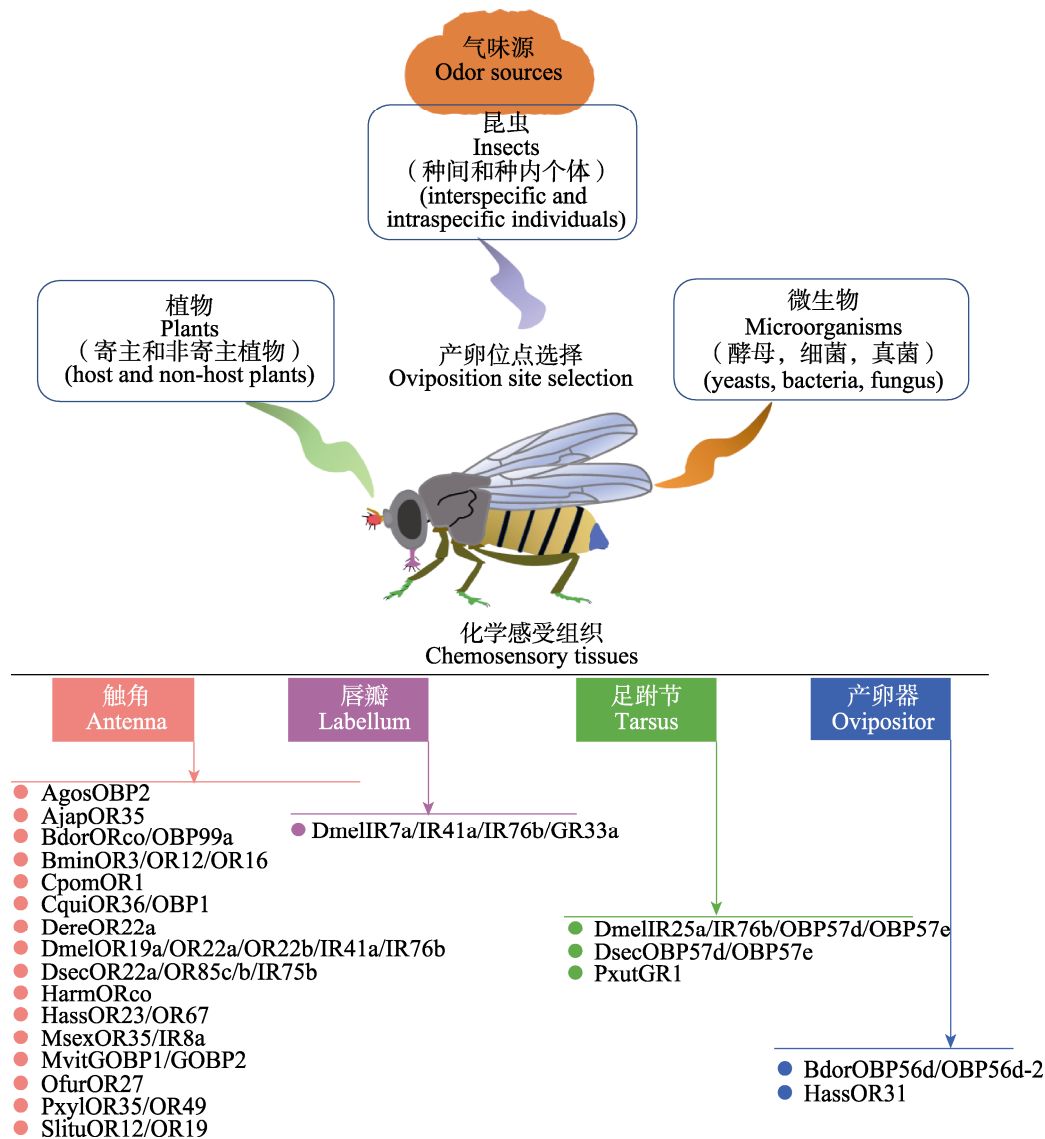


图 1 昆虫产卵位点选择机制示意图

Fig.1 Schematic diagram of mechanism on oviposition site selection in insects

来自植物、昆虫以及微生物释放的挥发性有机化合物在昆虫产卵选择行为中发挥着重要的调控作用，昆虫主要通过触角、唇瓣、足跗节和产卵器上表达的多种化学感受蛋白（气味受体、离子型受体、味觉受体和气味结合蛋白）对产卵位点的化学性质进行评估，从而完成对产卵位点的识别与接受。Volatile organic compounds released by plants, insects, and microorganisms play a crucial role in regulating insect oviposition. Insects predominantly assess the chemical properties of oviposition sites through various chemosensory proteins, including odorant receptors (ORs), ionotropic receptors (IRs), gustatory receptors (GRs), and odorant binding proteins (OBPs), which are expressed in their antenna, labellum, tarsus, and ovipositors. This enables insects to recognize and accept suitable oviposition sites. 图中示例引用文献 Reference: AgosOBP2 (Rebijith *et al.*, 2016); AjapOR35 (Wang *et al.*, 2017b); BdorORco/OBP99a (Zhang *et al.*, 2018; Xu *et al.*, 2022); BminOR3/OR12/OR16 (Liu *et al.*, 2020b); CpomOR1 (Garczynski *et al.*, 2017); CquiOR36/OBP1 (Xu *et al.*, 2009; Choo *et al.*, 2018); DereOR22a (Linz *et al.*, 2013); DmelOR19a/OR22a/OR22b/IR41a/IR76b (Dweck *et al.*, 2013; Hussain *et al.*, 2016; Mansourian *et al.*, 2018); DsecOR22a/OR85c/b/IR75b (Prieto-Godino *et al.*, 2017; Auer *et al.*, 2020); HarmORco (Fan *et al.*, 2022); HassOR23/OR67 (Wu *et al.*, 2019; Wang *et al.*, 2020); MsexOR35/IR8a (Zhang *et al.*, 2019, 2022b); MvitGOBP1/GOBP2 (Zhou *et al.*, 2015); OfurOR27 (Yu *et al.*, 2020); PxylOR35/OR49 (Liu *et al.*, 2020a); SlituOR12/OR19 (Zhang *et al.*, 2013); DmelIR7a/IR41a/IR76b/GR33a (Hussain *et al.*, 2016; Poudel and Lee, 2016; Rimal *et al.*, 2019); DmelIR25a/IR76b/OBP57d/OBP57e (McKenna *et al.*, 1994; Chen and Amrein, 2017; Scheuermann and Smith, 2019); DsecOBP57d/OBP57e (Matsuo *et al.*, 2007); PxutGR1 (Ozaki *et al.*, 2011); BdorOBP56d/OBP56d-2 (He *et al.*, 2022); HassOR31 (Li *et al.*, 2020).

硫次生代谢产物,一些十字花科植物被咀嚼式口器的昆虫取食后,会大量产生异硫氰酸酯(Isothiocyanate, ITC)等有毒物质以抵御昆虫为害;同时,害虫取食也可以启动植物茉莉酸等信号通路的防御系统,进一步促进 GS 的合成及黑芥子酶的活性,提高植物的防御水平。然而,小菜蛾 *Plutella xylostella* 在进化过程中形成了应对 GS 的策略,其幼虫消化道内存在一种特殊的硫酸酯酶,能快速降解 GS,以免受毒害。最近的研究发现,小菜蛾不仅能够抵御 ITC,还可利用 ITC 作为关键的化学线索定位十字花科寄主植物,其中 3 种 ITCs(3-甲基丙基异硫氰酸酯、4-戊烯基异硫氰酸酯和苯乙基异硫氰酸酯)可引起小菜蛾雌虫较强的触角电位反应,并显著地吸引其产卵(Liu *et al.*, 2020a)。

2.1.1.3 天敌昆虫对植物挥发物的产卵选择 对于天敌昆虫而言,HIPVs 能够使天敌昆虫在复杂的环境中更容易地找到猎物,植物也可以间接达到自我防御的目的(Paré and Tumlinson, 1999)。研究表明在虫害诱导植物挥发物中对天敌昆虫起到引诱作用的组分主要是萜类化合物和 GLVs(Conchou *et al.*, 2019)。Verheggen(2008)以及 Leroy 等(2010)研究发现被蚜虫为害后的植株释放出的 HIPVs,如(顺)-3-己烯醇和(反)- β -法尼烯(EBF),能够引起食蚜蝇对寄主植物的定位并刺激黑带食蚜蝇产卵。最新的研究显示,虫害诱导植物挥发物中的 EBF 组分也能被大灰优蚜蝇 *Eupeodes corollae* 成虫识别,作为远距离定位蚜虫的化学线索(Wang *et al.*, 2022)。另有研究显示,蚜虫为害金盏花植物释放的吲哚和 4-松油醇可显著吸引异色瓢虫 *Harmonia axyridis* 对其进行远距离定位,为天敌昆虫精准防控提供了重要的化学线索(Zhang *et al.*, 2022a)。

2.1.1.4 植物表面蜡质化合物对昆虫的产卵作用 寄主植物叶片表面蜡质化合物能够作为短距离线索吸引和刺激植食性昆虫产卵。叶片表面蜡质化合物组分因植物种类而异,主要包括长链烷烃、游离脂肪酸、醇类、醛类和酯类。研究发现,植物齿果酸模 *Rumex dentatus* 单叶表面蜡质

成分十八烷(2.44 $\mu\text{g/mL}$)、二十七烷(35.57 $\mu\text{g/mL}$)和二十九烷(23.58 $\mu\text{g/mL}$)的混合物,或者植物光蓼 *Polygonum glabrum* 单叶表面蜡质成分十八烷(4.08 $\mu\text{g/mL}$)、9-十六碳烯酸(19.54 $\mu\text{g/mL}$)和二十二酸(23.58 $\mu\text{g/mL}$)的混合物可作为一种萤叶甲 *Galerucella placida* 的近距离吸引线索和产卵刺激信息素(Koner *et al.*, 2022)。此外,白云杉 *Picea glauca* 角质层蜡质中单萜类混合物能够协同刺激云杉卷叶蛾 *Choristoneura fumiferana* 雌蛾产卵和幼虫取食行为(Ennis *et al.*, 2015)。

2.1.2 非寄主植物挥发物 越来越多的研究显示,一些非寄主植物的挥发物对植食性昆虫的产卵有抑制作用。如非寄主罗勒属 *Ocimum* 植物释放的萜烯类化合物和精油组分可显著驱避番茄潜叶蛾 *Tuta absoluta*、马铃薯块茎蛾 *Phthorimaea operculella* 和小地老虎 *Agrotis ipsilon* 雌蛾产卵,降低产卵量(AbdEl-Aziz *et al.*, 2007; Sharaby *et al.*, 2009; Yarou *et al.*, 2018)。丁香罗勒 *Ocimum gratissimum* L.、罗勒 *Ocimum basilicum* 和圣罗勒 *Ocimum sanctum* 提取物及相关精油对于一些象鼻虫科 Dryophthoridae、象甲科 Curculionidae、长蠹虫科 Bostrichidae、拟步甲科 Tenebrionidae、豆象科 Bruchidae 等仓储害虫也具有驱避和产卵忌避作用,这些研究结果证实了罗勒属植物对许多昆虫的驱避效果具有广谱性,在生产上具有很好的应用潜力(Asawalam *et al.*, 2008; Ogendo *et al.*, 2008; Kiradoo and Srivastava, 2010)。最新的研究显示,非寄主植物天竺葵 *Pelargonium* $\times$ *hortorum* 叶片挥发物月桂烯、 γ -萜品烯、芳樟醇、樟脑和萜品烯-4-醇以相对比例 1 : 5 : 3 : 4 : 3 构成的混合物对小菜蛾雌成虫有最强的产卵驱避作用,可显著降低卵量。网罩试验发现缓释该混合物具有 0.9 m 的有效驱避距离和长达 26 d 的有效驱避时长,并进行了田间验证。因此这 5 种驱避化合物以特定比例组成的混合物有望成为小菜蛾驱避行为调控剂,并可能成为“推-拉”防治策略中“推”成分的潜在候选物质(Song *et al.*, 2022)。

2.2 来自昆虫种间或种内的信息化合物

昆虫在产卵过程中会在卵表或产卵位点处

分泌化学信息物质,能够影响昆虫种间或种内的产卵行为。释放的信息素包括产卵刺激素 (Oviposition stimulants) 以及产卵忌避素 (Oviposition deterring pheromones, ODPs) 等,这些标记信息化合物能够刺激或抑制雌成虫产卵,调节昆虫产卵决策以保证后代的适合度。

2.2.1 产卵刺激素 产卵刺激素可以刺激雌成虫的产卵行为并促使卵的聚集,保护卵块内部的卵免受天敌寄生,有利于形成良好的生存环境,同时聚集在同一位点的卵块增加了幼虫的局部密度,从而最大限度地提高种群对食物的利用率,促进个体生长和种群扩大。如巴氏白蛉 *Phlebotomus papatasi* 的卵和 1 龄幼虫表面提取物中低剂量的月桂酸可刺激雌虫产卵,而雌成虫对高龄幼虫的识别作用降低 (Kowacich *et al.*, 2020)。家蝇 *Musca domestica* 卵巢提取物中的正二十三烷和 (顺)-9-二十三烯可吸引雌蝇产卵 (Jiang *et al.*, 2002)。研究表明食物气味促使黑腹果蝇雄虫分泌的 9-二十三烯具有增加求偶机会、影响雌虫产卵决定和聚集等作用,这可能是果蝇雄虫用来提高子代生存适合度的一种机制 (Lin *et al.*, 2015),这说明除了“mother-knows-best”机制以外 (Thompson, 1988; Mayhew, 1997; Gripenberg *et al.*, 2010),“father”也能影响雌虫的产卵决定,从而最大限度地提高子代的存活率。另外,已交配果蝇雌虫排出的粪便中含有雄虫在交配过程中转移而来的性信息素 (顺式)-十八碳烯醇醋酸酯 (cis-11-vaccenyl acetate, cVA),该化合物通过标记食物作为其他已交配雌虫的产卵聚集信息素 (Wertheim *et al.*, 2002; Sarin and Dukas, 2009)。同时,已交配雌虫自身也会释放挥发性表皮碳氢化合物,吸引其他雌虫并刺激产卵 (Duménil *et al.*, 2016)。

研究表明植食性昆虫挥发物及其信息素组分也可以作为天敌昆虫的产卵刺激素。具有代表性的研究是蚜虫天敌对蚜虫报警信息素等化学线索的精准识别。Verheggen 等 (2008) 研究显示蚜虫报警信息素 EBF 能被黑带食蚜蝇识别,并引诱雌虫产卵。蚜虫表皮碳氢化合物二十三烷和二十六烷等,也能够吸引大灰食蚜蝇 *Syrphus*

corollae 并刺激产卵 (Shonouda *et al.*, 1998)。另外,天敌昆虫也可通过植食性昆虫释放的性信息素定位寄主。例如麦蛾茧蜂 *Bracon hebetor* 雌虫能识别寄主大蜡螟 *Galleria mellonella* 雄虫释放的性信息素壬醛和十一醛混合物,将其作为寻找产卵场所的直接线索 (Dweck *et al.*, 2010)。有性蚜的性信息素荆芥内酯和荆芥醇也可以作为七点草蛉 *Chrysopa cognata* 和菜蚜茧蜂 *Diaeretiella rapae* 识别寄主的关键化学线索 (Vet and Dicke, 1992; Boo *et al.*, 1998)。由此可见,天敌昆虫识别植食性昆虫释放的信息素具有普遍性和特殊性,但目前有关天敌昆虫产卵选择的嗅觉识别机制研究还比较匮乏。

2.2.2 产卵忌避素 产卵忌避素抑制雌虫的产卵行为,降低种群的聚集程度,避免同种或近缘种竞争有限的资源,为后代占有适宜的小生境。雌成虫在产卵时在寄主或卵上分泌一类标记信息化合物,以避免再回到同一位点产卵,或者用以警告同种或近缘种雌虫不要在该寄主及其附近产卵。昆虫的产卵忌避素可由卵、幼虫和成虫产生。

卵自身携带的产卵忌避素可由卵本身产生,如葡萄花翅小卷蛾 *Lobesia botrana* 卵提取物中的直链脂肪酸和脂肪酸酯可抑制雌成虫产卵 (Thiéry *et al.*, 1992a)。欧洲玉米螟 *Ostrinia nubilalis* 卵表面的 5 种甲酯 (棕榈酸甲酯、亚油酸甲酯、棕榈油酸甲酯、油酸甲酯和硬脂酸甲酯) 是其近缘种 *Aphomia sociella* 和地中海玉米螟 *Sesamia nonagrioides* 的产卵抑制剂 (Thiéry *et al.*, 1992b)。棉铃虫 *Helicoverpa armigera* 卵表的 4 种脂肪酸 (豆蔻酸、棕榈酸、油酸和硬脂酸) 也可显著抑制雌虫的产卵行为 (Liu *et al.*, 2008)。

幼虫携带的产卵忌避素主要由肠道分泌通过粪便释放,多见于鳞翅目种类中,如马铃薯块茎蛾幼虫粪便挥发物中的正构烷烃,尤其是二十五烷强烈驱避雌成虫产卵 (Zhang *et al.*, 2019a)。棉铃虫幼虫粪便中鉴定到的棕榈酸和油酸可显著抑制雌成虫产卵 (Xu *et al.*, 2006)。烟草天蛾 *Manduca sexta* 幼虫粪便释放的 3-甲基戊酸和己酸可抑制雌虫的产卵行为 (Zhang *et al.*, 2019b)。

海灰翅夜蛾幼虫粪便中的苯甲醛和 5 种萜烯类化合物(香芹酚、丁香酚、橙花叔醇、绿叶醇和百里香酚)组成的混合物可强烈抑制雌虫产卵,而缺失任一组分都不再具有抑制效果(Anderson *et al.*, 1993),同时该幼虫粪便挥发物也是其近缘种小地老虎的产卵抑制素(Hashem *et al.*, 2013)。类似的研究发现,一种秆野螟 *Ostrinia zealis* 幼虫粪便释放的 5 种脂肪酸混合物(棕榈酸、硬脂酸、油酸、亚油酸和亚麻油酸)可显著驱避 4 种秆野螟属雌虫(秆野螟、玉米螟 *Ostrinia furnacalis*、麻田豆秆野螟 *Ostrinia scapularis* 和 *Ostrinia latipennis*)产卵(Li and Ishikawa, 2004)。另有研究显示,怀卵雌虫避免在同种幼虫爬过的区域产卵。例如,六斑月瓢虫 *Cheilomenes sexmaculata* 1 龄幼虫爬过的区域会抑制同种雌虫产卵,鉴定到该瓢虫产卵忌避素活性组分为幼虫表皮碳氢化合物(Z)-pentacos-12-ene(Klewer *et al.*, 2007)。二星瓢虫 *Adalia bipunctata* 幼虫取食蚜虫时,其第十腹节臀板可分泌以烷烃为主要成分的信息素,抑制同种雌虫在蚜虫种群区域内产卵(Laubertie *et al.*, 2006; Martini *et al.*, 2013)。黑带食蚜蝇幼虫爬痕释放的挥发性化合物 3-甲基丁酸、2-甲基丁酸、2-甲基丙酸、3-羟基-2-丁酮、己酸和石碳酸可显著抑制雌虫产卵,且随着幼虫爬痕挥发物释放量增加,对雌虫产卵抑制作用增大(Almohamad *et al.*, 2010)。由此可见,怀卵雌虫识别产卵忌避素这种行为构成了一种生存策略,优化产卵位点,以减少后代竞争。

成虫产卵忌避素一般产生或贮存于外分泌腺、消化系统或生殖系统,主要见于鞘翅目、鳞翅目和双翅目等昆虫种类。研究显示大菜粉蝶 *Pieris brassicae* 和菜粉蝶 *Pieris rapae* 雌成虫附腺能产生产卵忌避素,后分泌到卵壳上,从而抑制同种雌虫产卵(Klijnstra and Schoonhoven, 1987; Schoonhoven *et al.*, 1990)。蓝橘绕实蝇 *Rhagoletis mendax* 的寄生性茧蜂 *Diachasma alloeum* 产卵后,用产卵器在果实表面摩擦,将产卵忌避素涂抹在果实表面,避免其他怀卵雌虫在同一果实内产卵减少种内竞争(Stelinski *et al.*, 2007)。非洲芒果实蝇 *Ceratitis cosyra* 雌

成虫粪便中的抗氧化剂谷胱甘肽可抑制同种其他个体和近缘种纳塔尔实蝇 *Ceratitis rosa*、地中海实蝇 *Ceratitis capitata* 和瓜实蝇 *Zeugodacus cucurbitae* 雌虫的产卵行为,且该信息素含量随着雌虫龄期增长而增加(Cheseto *et al.*, 2017)。随后的研究发现,该实蝇产卵雌虫粪便中的谷氨酸组分也可作为同种雌虫的产卵忌避素(Cheseto *et al.*, 2018)。为避免在同一油菜豆荚 *Brassica napus* 内重复产卵,白菜籽龟象 *Ceutorhynchus assimilis* 雌虫产卵后,会在寄主豆荚上涂抹腹节分泌的接触性产卵忌避素(Ferguson *et al.*, 1999)。另有研究表明,天敌昆虫释放的信息素可调控寄主的产卵行为。例如,黑腹果蝇寄生蜂布拉迪小环腹瘿蜂 *Leptopilina boulardi* 释放的猕猴桃碱和荆芥内酯可显著驱避黑腹果蝇雌虫产卵(Ebrahim *et al.*, 2015)。

2.3 来自微生物的产卵线索

微生物产生的挥发性有机化合物也是调控昆虫产卵行为的重要化学信号。昆虫根据微生物释放的挥发物图谱来识别和区分不同的环境微生物。根据微生物对昆虫自身的作用方式,分为有益微生物和有害微生物。

2.3.1 有益微生物的挥发物对昆虫产卵的影响

昆虫与环境有益微生物之间存在相互适应关系。一方面,有益微生物可以给昆虫提供营养,帮助解毒和消化食物,因而昆虫对有益微生物保持特定的偏好(Davis and Landolt, 2013; Angleró-Rodríguez *et al.*, 2016);另一方面,有益微生物产生的挥发性化合物可以操纵昆虫媒介的行为,促进其传播(Keesey *et al.*, 2017; Flury *et al.*, 2019; Kandasamy *et al.*, 2019)。最典型的例子就是酵母与黑腹果蝇之间的相互作用(Ganter, 2006; Becher *et al.*, 2012)。经酵母菌侵染的果实具有更高的营养价值,可促进果蝇感官和生理适应,有助于果蝇取食和产卵。Becher 等(2012)鉴定了一种酿酒酵母 *Saccharomyces cerevisiae* 挥发物,包括乙醇、乙酸、羟基丁酮、2-苯基乙醇和异戊醇,行为学研究结果显示,酵母挥发物与发酵葡萄汁或发酵酵母培养基对果蝇有同样

的引诱效果,表明酿酒酵母本身足以吸引果蝇产卵并促进幼虫发育。此外,由于大多数酵母缺乏活跃的孢子传播机制,因此果蝇媒介在真菌的繁殖过程中起着不可或缺的作用,这有利于果蝇与酵母的互惠共生 (Starmer and Fogleman, 1986; Günther *et al.*, 2019; Luo *et al.*, 2021)。

除酵母外,细菌也很容易在过熟的果实上生长,分解消耗糖类合成必需的营养物质(如对寄主至关重要的细菌蛋白和维生素),降低腐烂果实中蔗糖的浓度,而果蝇可以通过味觉系统探测蔗糖浓度来区分腐烂水果和新鲜水果,在细菌丰富的低糖位点产卵。另外,发酵细菌可刺激果蝇的消化系统,刺激肠道内促进营养消化和吸收的酶的分泌,维持肠道内稳态从而促进幼虫的发育。该研究揭示了一个自然生态现象,即昆虫的产卵行为需要固有的微生物群来调节,同时也解释了一个相互矛盾的现象,即果蝇会偏好选择那些能量匮乏但有大量细菌的位点产卵 (Liu *et al.*, 2017)。研究显示,果蝇还可以被腐烂水果的气味吸引,其嗅觉系统能够感受水果上生长的微生物所产生的各种代谢化合物,包括乙醇、乙酸及多胺等,可强烈吸引果蝇取食和产卵 (Joseph *et al.*, 2009; Azanchi *et al.*, 2013; Hussain *et al.*, 2016)。

来自昆虫肠道或粪便中的有益微生物群落发酵产生的挥发性物质,也是调控寄主或天敌昆虫产卵行为的重要化学线索。例如,桔小实蝇 *Bactrocera dorsalis* 肠道微生物柠檬酸杆菌 *Citrobacter* sp. 可进入雌虫卵巢进行垂直传播并显著影响实蝇的产卵量 (Cheng *et al.*, 2017; Guo *et al.*, 2017)。最新的研究发现,该柠檬酸杆菌随实蝇产卵进入果实后可发酵产生乙酸叶醇酯,该物质可显著引诱实蝇产卵 (He *et al.*, 2022)。蚜虫取食植物产生的蜜露包含多种糖类、氨基酸、有机酸等构成了微生物生长的极佳环境 (Hussain *et al.*, 1974; Leroy *et al.*, 2011b), 促进挥发性化合物的产生,释放出的挥发物可作为天敌昆虫的利它素 (Leroy *et al.*, 2012; Pinheiro *et al.*, 2015; Vosteen *et al.*, 2016)。Leroy 等 (2011a) 发现食蚜蝇可以识别蚜虫蜜露中微生物

的发酵产物,用于自身产卵选择的参考,蜜露中微生物松鼠葡萄球菌 *Staphylococcus sciuri* 发酵产生的 3-甲基-2-丁烯醛、2-甲基丁酸和丁酸可以显著吸引食蚜蝇产卵。

2.3.2 有害微生物的挥发物对昆虫产卵的影响
除了有益的酵母和细菌,环境中还存在着大量危险的微生物。青霉菌 *Penicillium* 是水果上常见的一种菌群,其中许多类群可产生有杀虫活性的次生代谢产物 (Castillo *et al.*, 1999)。这些霉菌、蓝藻和细菌会产生挥发性化合物土臭素,从而指示有害微生物的存在。对不同昆虫的行为调控具有多样性。研究发现该化合物会抑制黑腹果蝇产卵和取食行为 (Stensmyr *et al.*, 2012), 但蓝藻产生的土臭素可引诱埃及伊蚊 *Aedes aegypti* 雌虫产卵,田间试验表明土臭素可作为产卵引诱剂诱捕埃及伊蚊 (Melo *et al.*, 2020)。最新的研究发现,青霉菌挥发物土臭素可驱避未怀卵的桔小实蝇;相反,怀卵雌虫更加偏好选择在含有青霉菌的基质上产卵。这种现象与黑腹果蝇和埃及伊蚊的情况截然不同。进一步研究发现,青霉菌产生的芳樟醇、3-萜烯、右旋柠檬烯和 6-戊基-2H-吡喃-2-酮混合物能够显著吸引桔小实蝇怀卵雌虫产卵。同时,青霉菌可为桔小实蝇提供 B 族维生素吡哆醇,促进幼虫的生长发育,提高成虫羽化率并缩短羽化时间。而且青霉菌孢子也充分利用了桔小实蝇产卵器对柑橘果实造成的损伤而加速萌发,促使实蝇成为了青霉菌的潜在传播媒介。该研究结果揭示了青霉菌与桔小实蝇在柑橘果实上建立了互利互惠的新模式 (Gu *et al.*, 2022)。类似地,桃蛀螟 *Conogethes punctiferalis* 偏好在青霉菌侵染的苹果上产卵,尤其对指状青霉菌 *Penicillium digitatum* 侵染的苹果的产卵选择率更高,是因为被青霉菌侵染的苹果释放了更多的己酸乙酯和 (顺式, 反式) - α -法尼烯。由此可见,青霉菌可以通过改变寄主植物挥发物的释放而调控桃蛀螟的寄主选择行为 (Guo *et al.*, 2022)。另有研究发现,鸡粪中茎点霉菌 *Phoma* spp.、镰刀菌 *Fusarium* spp. 及根霉菌 *Rhizopus* spp. 释放的挥发物二甲基三硫醚和苯乙醇显著抑制家蝇产卵,表明真菌来源的挥发物可以帮助家蝇

避免在竞争性真菌占据的资源上繁殖,从而有利于子代幼虫的生存 (Lam *et al.*, 2010)。

3 昆虫产卵选择机制

昆虫通过高度发达且灵敏的化学感受系统在复杂的自然环境中精准识别产卵线索,并做出正确的产卵决策 (Lin *et al.*, 2015; Anholt, 2020; Tait *et al.*, 2020; 李慧等, 2021)。这一识别过程非常复杂,可以简要地分为两个步骤,首先在外周神经水平上,昆虫通过化学感受系统对化学线索进行识别,并将化学信号转换成电信号传导至中枢神经系统 (Amin and Lin, 2019; Pannunzi and Nowotny, 2019; Anholt, 2020);其次是在中枢神经系统水平上,中枢神经系统通过对外周神经系统的电信号输入进行整合与加工,使昆虫产生相应的行为反应 (Schultzhaus *et al.*, 2016; Chin *et al.*, 2018; Anton and Rössler, 2021; Patel and Rangan, 2021)。整个化学感受过程离不开多种化学感受组织中多种类型的基因参与 (图 1),主要包括气味受体 (Odorant receptors, ORs) (Clyne *et al.*, 1999)、离子型受体 (Ionotropic receptors, IRs) (Benton *et al.*, 2009)、味觉受体 (Gustatory receptors, GRs) (Clyne *et al.*, 2000)、气味结合蛋白 (Odorant binding proteins, OBPs) (Vogt and Riddiford, 1981)、化学感受蛋白 (Chemosensory proteins, CSPs) (McKenna *et al.*, 1994) 和感觉神经元膜蛋白 (Sensory neuron membrane proteins, SNMPs) (Vogt *et al.*, 2009) 等。对这些蛋白功能的研究是解析昆虫产卵选择机制的前提和基础。

3.1 气味受体参与昆虫对化学线索的识别与定位

气味受体在昆虫触角外周嗅觉系统识别气味分子的过程中起着关键作用,对其功能鉴定有助于揭示昆虫触角外周神经系统的嗅觉识别机制。目前,研究人员利用转录组或基因组测序技术鉴定出了鳞翅目、双翅目、鞘翅目、半翅目和膜翅目等许多植食性昆虫的全部或部分的气味受体基因库 (de Fouchier *et al.*, 2017; Yan *et al.*, 2020)。其中对鳞翅目和双翅目昆虫的气味受体

功能研究较为广泛,一些研究揭示了气味受体的功能在植食性昆虫产卵选择等行为活动中发挥着重要作用。例如,烟青虫气味受体 *HassOR67* 能够特异性识别其栽培寄主烟草植物挥发物壬醛,引诱雌蛾产卵 (Wang *et al.*, 2020); 气味受体 *HassOR23* 识别虫害诱导的烟草植物挥发物法尼烯同分异构体及其结构类似物,抑制雌成虫产卵 (Wu *et al.*, 2019); 在雌虫产卵器中高表达的气味受体 *HassOR31* 能够感受顺 3-己烯基丁酯等 12 种寄主植物气味分子,而切除触角的雌蛾仍偏好在放置植物挥发物的地方产卵,进一步表明 *HassOR31* 参与雌虫的产卵选择行为 (Li *et al.*, 2020)。另外,研究显示,小菜蛾气味受体 *PxylOR35* 和 *PxylOR49* 能特异性感受拟南芥挥发物 ITCs 类气味,通过 CRISPR/Cas9 技术对 *PxylOR35*/*PxylOR49* 单敲除和双敲除后的产卵行为试验表明,单敲除品系导致小菜蛾雌蛾的触角电位反应及对拟南芥植株的产卵偏好性降低,双敲除品系直接导致此行为丧失。证实了小菜蛾对拟南芥植株的产卵偏好是由两种高度特异的气味受体 *PxylOR35* 和 *PxylOR49* 共同调控的,且 *PxylOR35* 的作用更大 (Liu *et al.*, 2020a)。在斜纹夜蛾 *Spodoptera litura* 成虫触角的长毛形感器、短毛形感器和锥形感器神经元中表达的 *SlituOR12* 可以识别植物挥发物乙酸叶醇酯, *SlituOR19* 可以识别 4'-乙基苯乙酮,这 2 个 ORs 可能在斜纹夜蛾搜寻寄主植物和产卵位点过程中起作用 (Zhang *et al.*, 2013)。亚洲玉米螟雌虫触角偏好表达的气味受体 *OfurOR27* 可感受植物挥发物壬醛、辛醛和正辛醇从而介导雌虫的产卵驱避行为,推测 *OfurOR27* 是一个特异性感受驱避剂的气味受体 (Yu *et al.*, 2020)。在野外,烟草天蛾和一种甲虫 *Lema daturaphila* 可以同时为害共同寄主植物曼陀罗 *Datura wrightii*, 研究显示被甲虫取食后的曼陀罗植株释放的 α -古巴烯能够激活烟草天蛾的气味受体 *MsexOR35*,从而介导了烟草天蛾雌虫对寄主曼陀罗的产卵偏好行为。虽然烟草天蛾幼虫在被甲虫为害过的植物上生长速度相对缓慢,但却能降低被寄生的概率。由此可见,烟草天蛾能够有效地权衡种间竞

争与产卵适合度,为后代提供一个风险较低的生活环境(Zhang *et al.*, 2022b)。最新的研究显示,棉铃虫 *HarmORco*^{-/-} 纯合突变体丧失了生殖、产卵选择、性信息素交流以及幼虫趋化等多种行为,揭示了气味受体共受体 ORco 在棉铃虫化学通讯和生殖过程中起到了至关重要的作用(Fan *et al.*, 2022)。另外,鳞翅目昆虫的性信息素受体基因也参与昆虫的产卵行为。研究显示,利用 CRISPR/Cas9 技术敲除苹果蠹蛾 *Cydia pomonella* 性信息素受体基因 *CpomOR1*, 突变体雌虫的产卵量及卵孵化率均显著下降,证明了 *CpomOR1* 与雌虫的产卵行为和生殖能力密切相关(Garczynski *et al.*, 2017)。

目前,双翅目昆虫黑腹果蝇的产卵选择行为机制研究的比较全面。果蝇主要利用触角上表达的 ORs 感受植物挥发物进行寄主定位。例如,黑腹果蝇喜欢在柑橘类水果上产卵,其主要活性物质是柠檬烯,能够激活触角上锥形感器 ab3A 神经元上表达的 *DmelOR19a* 受体,并将信号投递到脑部的 DC1 嗅小球来介导果蝇对柑橘的产卵偏好(Dweck *et al.*, 2013)。另有研究显示,非洲特有果蝇种类 *Drosophila erecta* 已经进化出对露兜树属 *Pandanus candelabrum* 植物果实的寄主特化,气味受体-神经元-嗅小球(*DereOR22a/ab3A/DM2*)参与了对露兜树果实成熟过程中产生的挥发物 3-甲基-2-丁烯乙酸酯的识别并引起显著地产卵引诱行为(Linz *et al.*, 2013)。同样,津巴布韦的黑腹果蝇几乎只在马鲁拉果 *Sclerocarya birrea* 上觅食和产卵,马鲁拉果产生的 3-甲基丁酸乙酯通过激活 *DmelOR22a-DmelOR22b/ab3A/DM2* 神经通路而成为产卵位点偏好的嗅觉线索(Mansourian *et al.*, 2018)。单食性的塞席尔果蝇 *Drosophila sechellia* 完全以海巴戟科的诺丽果 *Morinda citrifolia* 为食,挥发物己酸甲酯可以显著吸引塞席尔果蝇,而对其他的果蝇没有显著的吸引力(Prieto-Godino *et al.*, 2017),研究发现塞席尔果蝇的气味受体 *DsecOR22a* 和 *DsecOR85c/b* 介导了对诺丽果挥发性化合物特异性识别,从而实现对寄主的远距离定位(Auer *et al.*, 2020)。由此可见,萜烯类

化合物以及脂肪族化合物可以通过果蝇触角外周神经系统中的气味受体识别从而介导果蝇的产卵选择行为。

除果蝇外,柑橘大实蝇 *Bactrocera minax* 气味受体 *BminOR3* 可专一性识别植物挥发物 1-辛烯-3-醇, *BminOR12* 可识别植物挥发物顺-3-己烯基乙酸酯、丙烯酸丁酯、正辛醇、丙酸丁酯、苯甲醇、(S)-(+) -香芹酮、水杨酸甲酯和苯甲醛, *BminOR16* 可特异性识别植物挥发物十一醇,推测这 3 个 OR 参与调控柑橘大实蝇的寄主定位和产卵选择行为(Liu *et al.*, 2020b)。最新的研究,利用 CRISPR/Cas9 技术敲除桔小实蝇气味受体共受体基因 *BdorORco*, 突变体雌蝇对苯并噻唑和 1-辛烯-3-醇的产卵偏好行为丧失,对甲基丁香酚、 β -石竹烯和乙酸乙酯的感受能力显著降低,觅食时间显著增加,揭示了 *BdorORco* 参与调控桔小实蝇的多种行为和生理过程(Xu *et al.*, 2022)。另有研究人员利用反向化学生态学的方法,在非洲爪蟾 *Xenopus laevis* 卵母细胞中表达了 7 个致倦库蚊 *Culex quinquefasciatus* 的气味受体,筛选了 230 种气味分子后,明确了乙醛能够激活在雌虫触角高表达的气味受体 *CquiOR36*, 且证实了该化合物可作为致倦库蚊的产卵引诱剂,具有潜在的应用价值(Choo *et al.*, 2018)。

3.2 离子型受体和味觉受体参与昆虫的近距离产卵

关于昆虫产卵选择机制的研究主要集中在果蝇,研究显示黑腹果蝇主要通过唇瓣、足跗节、产卵器上的多种化学感觉通路,对产卵基质的化学和物理性质进行评估,涉及对酸类、多胺及糖类等化合物的感受与基质软硬度的评估(Hussain *et al.*, 2016; Chen and Amrein, 2017; Rimal *et al.*, 2019)。过熟或发酵水果中富含的酸类和胺类化合物能够激活离子型受体 IRs 与味觉受体 GRs 从而介导果蝇产卵引诱(Yadav and Borges, 2017)。水果自然发酵挥发物乙酸是引诱黑腹果蝇产卵的主要化学线索,通过果蝇遗传操作方法结合行为学研究证实雌虫利用唇瓣上的味觉神

神经元识别乙酸, 将其作为产卵引诱的主要化学线索 (Joseph *et al.*, 2009)。Rimal 等 (2019) 进一步发现在黑腹果蝇唇瓣苦味受体神经元中表达的 *DmelIR7a* 也能特异性识别乙酸, 并参与果蝇的产卵决策。另有研究揭示了黑腹果蝇前足跗节上存在专门的酸味感受神经元, 依靠 2 个离子型受体 *DmelIR25a* 和 *DmelIR76b* 来感知产卵基质中的乙酸和柠檬酸, 介导果蝇对含酸基质的产卵偏好 (Chen and Amrein, 2017)。另外, 巴戟天属 *Morinda* 水果挥发物富含中链脂肪酸, 以己酸和辛酸为主, 可特异性吸引塞席尔果蝇, 通过对酸敏感通路的研究显示在腔锥形感器 *ac3I* 中表达离子型受体 *DsecIR75b* 的神经元对己酸敏感, 并且通过 *DsecIR75b* 单个氨基酸突变进一步验证了该结果, 与黑腹果蝇相比该神经元的数量显著地扩增, 并且信号投递到脑部的 *DL2d* 嗅小球也伴随扩张, 从生理和神经解剖学水平阐明了塞席尔果蝇对巴戟天属水果的寄主特化机制 (Prieto-Godino *et al.*, 2017)。

同样地, 挥发性多胺可强烈吸引果蝇取食和产卵也是通过多种感官系统探测和评估实现的。产卵位点的长距离定位是通过嗅觉系统中表达的离子型受体 *DmelIR76b* 和 *DmelIR41a* 感受与识别多胺气味; 当到达或接近产卵位点时, 雌蝇利用味觉系统中表达 *DmelIR76b* 和 *DmelGR66a* 苦味受体神经元感受多胺来诱导产卵, 并且这一结果在埃及伊蚊中也得到证实, 推测对多胺的行为识别机制在物种间可能是保守的 (Hussain *et al.*, 2016)。此外, 黑腹果蝇苦味受体 *GR33a* 也可感受寄主植物产生的有毒代谢物香豆素, 从而介导雌虫的产卵驱避行为 (Poudel and Lee, 2016)。

除果蝇外, 其他昆虫的产卵研究逐渐增多。在鳞翅目昆虫烟草天蛾中, Zhang 等 (2019b) 利用 CRISPR/Cas9 技术分别敲除共受体 *MsexORco*、*MsexIR8a* 和 *MsexIR25a*, 证实了 IR 通路介导了烟草天蛾成虫对同种幼虫粪便释放的挥发物 3-甲基戊酸和己酸的识别, 显著抑制雌蛾的产卵行为。研究显示柑橘凤蝶 *Papilio xuthus* 仅在少数几种植物上产卵, Ozaki 等 (2011) 发

现雌虫跗节上表达的 *PxutGR1* 可能参与产卵选择, 将该受体在 *Sf9* 细胞体外表达并进行功能研究, 结果显示产卵刺激素辛弗林能够特异性激活该受体。随后利用 RNAi 技术沉默 *PxutGR1* 后, 柑橘凤蝶跗节味觉感器对辛弗林的敏感性和产卵行为显著降低, 表明 *PxutGR1* 是柑橘凤蝶寄主特化的关键因子。在半翅目昆虫褐飞虱 *Nilaparvata lugens* 中, 注射糖受体 *NlugGR11* 双链 dsRNA 后, 褐飞虱产卵量显著降低, 表明 GR 参与调节褐飞虱的繁殖能力 (Chen *et al.*, 2017)。

3.3 气味结合蛋白在昆虫产卵过程中的作用

气味结合蛋白在气味受体与气味分子之间起着十分重要的连接作用, 即与气味分子或信息素结合协助向气味受体运输 (Pelosi *et al.*, 2018)。目前, 已有研究揭示了气味结合蛋白在植食性昆虫寄主定位和产卵选择等生理活动中发挥着重要作用。例如鳞翅目昆虫豆野螟 *Maruca vitrata* 的 *MvitGOBP1* 和 *MvitGOBP2* 对丁酸丁酯、柠檬烯、4-乙基苯丙酮、1H-吡啶-4-醇、丁酸辛酯和 2-甲基-3-苯丙醛等寄主植物花的挥发物具有高亲和力, 推测 *MvitGOBPs* 在豆野螟识别寄主植物气味信号转导中起关键作用 (Zhou *et al.*, 2015), 而 *MvitOBP3* 也能高度结合上述这些化合物, 推测可能对豆科蔬菜上的雌蛾具有产卵引诱作用 (Ai *et al.*, 2021)。双翅目昆虫桔小实蝇雌虫产卵器中特异表达的 *BdorOBP56d* 和 *BdorOBP56d-2* 对其肠道微生物挥发物乙酸叶醇酯具有高度亲和力, 并且对该化合物具有强烈的产卵趋向性; 利用 RNAi 技术沉默气味结合蛋白 *BdorOBP56d* 或 *BdorOBP56d-2* 后, 没有降低桔小实蝇对乙酸叶醇酯的产卵偏好, 当两个气味结合蛋白同时沉默后, 乙酸叶醇酯对桔小实蝇的产卵引诱效果消失, 表明 *BdorOBP56d* 和 *BdorOBP56d-2* 参与调控桔小实蝇产卵行为 (He *et al.*, 2022)。类似地, 桔小实蝇气味结合蛋白 *BdorOBP99a* 表达量敲低后, 雌蝇对寄主植物香蕉的产卵偏好性丧失, 表明 *BdorOBP99a* 也参与调控桔小实蝇的产卵选择行为 (Zhang *et al.*, 2018)。另有研究显示, 致倦

库蚊的 *CquiOBP1* 能结合蚊子产卵信息素 6-乙酰氧基十六碳烷酸-5-内酯, 促使产卵信息素运输至膜结合的气味受体 (Xu *et al.*, 2009), 沉默 *CquiOBP1* 后, 致倦库蚊对产卵引诱剂的 EAG 反应显著降低, 表明 *CquiOBP1* 参与致倦库蚊对产卵信息素的识别且 OBPs 的高水平表达对昆虫嗅觉系统的敏感性至关重要 (Pelletier *et al.*, 2010)。半翅目昆虫棉蚜 *Aphis gossypii* 的 *AgosOBP2* 基因沉默后, 触角对寄主棉花提取物和产卵引诱剂吡啶的电生理反应显著降低, 证实了 *AgosOBP2* 在棉蚜寄主定位和识别产卵线索过程中发挥重要作用, 同时 *AgosOBP2* 有可能成为 RNAi 介导的基因沉默防治半翅目昆虫的一个有效靶点 (Rebijith *et al.*, 2016)。

此外, 气味结合蛋白也参与昆虫对味觉线索的吸引和驱避。研究表明黑腹果蝇的 *DmelOBP57d* 和 *DmelOBP57e* 参与味觉感受, 黑腹果蝇足上味觉感器中表达的两个气味结合蛋白 *DmelOBP57d* 和 *DmelOBP57e* 参与对主碳链为 6~9 个碳原子的脂肪酸介导的产卵驱避反应 (McKenna *et al.*, 1994; Scheuermann and Smith, 2019)。而塞席尔果蝇足的味觉感器中表达的 *DsecOBP57d* 和 *DsecOBP57e* 则发生了改变 (Tomioka *et al.*, 2012), 其中 *DsecOBP57e* 基因上游的一个 4 bp CCAT 插入导致了功能丧失 (Matsuo *et al.*, 2007); *DsecOBP56e* 基因中存在一个过早终止密码子, 导致等位基因的功能缺失 (Dworkin and Jones, 2009)。因此, 塞席尔果蝇可能进化出了多个 OBPs 等位基因, 丧失了对己酸和辛酸的识别, 促成对寄主诺雨果的产卵偏好行为 (Matsuo *et al.*, 2007)。

有关天敌昆虫产卵选择的嗅觉编码机制研究尚甚少。尽管随着组学技术的发展, 已在膜翅目、鞘翅目和双翅目中分析鉴定出了多种寄生性天敌和捕食性天敌的化学感受基因 (Wang *et al.*, 2017a; Liu *et al.*, 2018, 2020c; Jia *et al.*, 2019, 2020; Rondoni *et al.*, 2021; Ma *et al.*, 2022a, 2022b), 但是对于基因功能的研究还相当匮乏。研究显示, 寄主挥发物 β -石竹烯、十一烷、(反式)- α -金合欢烯、(+)-香橙烯和(顺式)-3-己烯醇能

够显著引诱荔枝椿象 *Tessaratoma papillosa* 寄生性天敌平腹小蜂 *Anastatus japonicus* 产卵; 利用 RNAi 技术沉默气味受体 *AjapOR35* 后, β -石竹烯和(反式)- α -金合欢烯对平腹小蜂的产卵引诱效果消失, 表明 *AjapOR35* 可能参与调控平腹小蜂的产卵行为 (Wang *et al.*, 2017b)。天敌昆虫的化学感受基因在外周嗅觉系统识别 HIPV 和寄主挥发物过程中发挥关键作用, 参与天敌昆虫寄主定位、取食、交配和产卵选择等重要生命活动。目前, 天敌昆虫化学感受基因的功能研究仍然较少, 深入揭示天敌昆虫外周和中枢嗅觉系统对害虫相关气味分子的编码机制, 将有助于筛选天敌昆虫行为调节剂, 用于开发对靶标害虫的精准防控。

4 应用

研究化学线索介导的昆虫产卵行为主要目的是寻找对害虫产卵有引诱或驱避作用的活性组分, 即产卵信息化合物, 进而研究信息化合物对产卵行为的触发和指导作用。利用各种气味化合物来特异性调节靶标害虫的行为对于农业害虫的绿色防控而言是重要的研究领域。目前, 利用一些生态植物调控昆虫行为的应用在害虫无公害综合治理中已取得一定成效。

4.1 信息化化合物的应用

人工合成来源于昆虫、植物等的信息化合物用释放器缓释到田间, 在吸引害虫取食、产卵、干扰交配, 直接诱杀成虫或吸引天敌方面已经取得了成功 (James, 2003; Kaplan, 2012; Uefune *et al.*, 2012)。目前, 以鳞翅目昆虫的性信息素及其类似物为主要组分的昆虫行为调控产品居市场首位, 而关于植食性昆虫和天敌昆虫的产卵行为调控产品则较少。

越来越多的研究证实, 挥发性植物次生代谢产物精油对许多害虫起到毒杀、拒食和产卵忌避的作用, 这种对害虫产卵的天然抗性在农作物害虫治理方面具有巨大应用价值 (Kumari and Kaushik, 2016)。例如, 香茅草 *Cymbopogon nardus* 中 $4\,000\,\mu\text{g}\cdot\text{g}^{-1}$ 香茅油可使棉铃虫的产卵率降低

53%-66%, 田间施用香茅油可降低 72% 的果实损伤率, 显著提高辣椒品质 (Setiawati *et al.*, 2011)。薄荷属植物 *Minthostachys spicata* 和 *Minthostachys glabrescens* 精油对马铃薯块茎蛾的产卵行为有显著抑制作用, 使其产卵量减少约 80% (Guerra *et al.*, 2007)。与冬葱 *Allium ascalonicum*、薄荷 *Mentha haplocalyx* 相比, 香樟 *Cinnamomum camphora* 的乙醇提取精油抑制温室烟粉虱 *Bemisia tabaci* 产卵效果最好 (Wagan *et al.*, 2022)。田间笼罩试验结果显示, 蓖麻 *Ricinus communis* 提取物和油乳剂混合对小菜蛾表现出较强的杀幼和产卵忌避效果 (Kodjo *et al.*, 2011)。

根据植物挥发物组分合成的产卵引诱剂已成功应用于苹果绕实蝇 *Rhagoletis pomonella* 的防治。该实蝇将卵产于寄主植物的果实内, 以果实形状及果实中挥发的特殊气味作为产卵导向物。将人工合成的苹果绕实蝇产卵引诱剂丁醇己酸酯涂抹在小木球上, 悬挂在果园四周, 可显著引诱苹果绕实蝇将卵全部产在这些小球上, 成功降低了苹果绕实蝇对寄主植物的危害 (Prokopy *et al.*, 1990)。有研究发现一种生物类黄酮类色素的廉价降解产物为 2,4-二羟基苯甲酸 (2,4-dihydroxybenzoic acid, DHBA), 当斑点瓢虫 *Coleomegilla maculata* 接触或取食 DHBA 后会刺激雌虫产卵, 因此该化合物可作为捕食性瓢虫的产卵刺激素应用于天敌昆虫大规模的饲养系统 (Riddick *et al.*, 2019)。Choo 等 (2018) 利用反向化学生态学的方法筛选到了致倦库蚊产卵引诱剂乙醛, 有效性超过三个数量级, 在监测致倦库蚊种群和病原菌的传播中具有巨大的实际应用潜力。Melo 等 (2020) 研究发现蓝藻产生的土臭素可作为产卵引诱剂诱捕埃及伊蚊, 由于土臭素价格高昂且难以获得, 因此甜菜根皮提取物作为土臭素的替代品被开发出来, 已在巴西开展了田间应用研究, 证实了甜菜根皮提取物能够显著引诱埃及伊蚊产卵。该研究结果为发展一种切实可行的埃及伊蚊生物防控策略提供了直接证据。目前, 产卵引诱剂在田间应用仍较为有限, 其主要问题是它们仅在很小的浓度范围内

有效, 而野外条件下, 产卵引诱剂的浓度会因高温和降雨等环境条件变化产生较大的波动。

4.2 推-拉策略的应用

Pyke 等 (1987) 在澳大利亚首次提出害虫控制的推-拉策略, 研究利用驱避剂和引诱剂来调控棉田中棉铃虫的分布。1990 年推-拉策略的理论由 Miller 和 Cowles (1990) 正式提出并完善, 已成功应用于葱地种蝇 *Delia antiqua* 的防治。该策略目的是通过干扰害虫的行为来控制或消灭害虫, 主要方法就是将特殊植物挥发物和植物种植方式结合起来, 即利用驱避物质 (或间作) 驱离主要作物上的害虫 (推), 并将天敌吸引到田间, 同时利用引诱物质 (如诱捕器或陷阱植物) 将害虫从田间引出来 (拉) 集中消灭, 通过这样的“推-拉”组合, 减少害虫对农作物的危害, 减少杀虫剂的使用 (Cook *et al.*, 2007; Khan *et al.*, 2016)。目前, 推-拉策略已被证明可以有效抑制田间多种害虫种群增长, 如玉米和高粱田中的玉米禾螟 *Chilo partellus* (Khan *et al.*, 2016)、棉田中的棉铃虫 (Pyke *et al.*, 1987)、油菜田中的油菜花露尾甲 *Meligethes aeneus* (Mauchline *et al.*, 2005)、豆田中的条纹根瘤象 *Sitona lineatus* (Smart *et al.*, 1994) 和麦田中的麦长管蚜 *Sitobion avenae* (Xie *et al.*, 2012)。研究证实基于间作体系的“推-拉”策略可有效控制玉米田中草地贪夜蛾 *Spodoptera frugiperda* 为害。在乌干达, 间作食用豆科作物的玉米田中草地贪夜蛾的为害水平明显低于单作玉米 (Hailu *et al.*, 2018)。在东非和墨西哥, 基于玉米与耐旱植物扭曲山蚂蝗 *Desmodium intortum* 间作, 同时在这种间作作物周围种植臂形草 *Brachiaria cv Mulato II* 作为边界作物, 可大大减少草地贪夜蛾造成的损失 (Midega *et al.*, 2018; Guera *et al.*, 2021; Scheidegger *et al.*, 2021)。最新的研究发现, 蚕豆可作为忌避植物驱避草地贪夜蛾产卵和取食, 玉米可作为陷阱植物引诱成虫产卵和幼虫取食, 两者可引入小麦间作系统中用于草地贪夜蛾的防控 (Liu *et al.*, 2022)。推-拉策略也已成功应用到其他谷类作物的害虫防控 (Pickett *et al.*,

2014), 未来仍需进一步筛选、培育和改造对植食性害虫有引诱作用或者驱避作用的植物, 与产卵忌避素、报警信息素、拒食剂等驱避剂以及产卵刺激素、聚集信息素、性信息素和食诱剂等引诱剂相结合, 以期实现对植食性害虫的高效、绿色防控。

5 展望

随着化学生态学的发展, 利用基因编辑技术和神经电生理技术等多技术手段, 解析了模式昆虫果蝇和一些重要农业昆虫感受化学信号从而产生产卵选择行为的生化机制(图 1), 为昆虫化学生态学研究成果广泛应用于害虫的绿色防控提供参考。

虽然化学线索介导的昆虫产卵选择行为的研究取得了一些突破性进展, 但仍需从以下几个方面开展深入研究: 1) 自然界中, 植物、昆虫及微生物等释放的气味分子通常是十分复杂的, 那么对这些气味分子的分离与鉴定需要有更高的要求。发展高灵敏度、操作简捷的化合物收集、鉴定、分析技术以及昆虫电生理技术仍是化学生态学领域未来研究的主要方向。2) 尽管已有大量研究鉴定出了驱避植食性昆虫、引诱天敌昆虫的昆虫行为调控化合物, 但如何将这些化学信息素进行整合加工, 搭配合适的缓释材料进行商业化生产, 并科学合理地应用于害虫的综合治理还需要进一步的系统性研究。3) 有关化学线索在寄生性和捕食性天敌昆虫寻找产卵位点方面的作用机制等相关研究还比较匮乏, 深入探究天敌昆虫气味编码及神经感受机制, 解析调节天敌昆虫产卵选择行为的重要靶标及机理, 可为进一步筛选高效稳定的天敌昆虫产卵调节剂提供理论依据, 为产生抗药性的植食性害虫防治提供新的思路与途径。4) 近年来, 关于调节昆虫产卵选择的化学线索和感受机制主要在模式昆虫中开展, 对于果蝇的产卵选择研究主要涉及化学线索的来源、挥发性气体成分分析、行为学实验、相关的感觉神经和相应的分子机制, 研究重点还集中在嗅觉和味觉对产卵选择的影响上。实际上, 昆虫的产卵选择过程非常复杂, 涉及视觉和触觉

等众多感受器官, 需要各器官相互交叉配合, 还可能更复杂的产卵决策机制需要进一步探索。深入研究昆虫产卵选择机制, 可为防治植食性害虫和更好的发挥寄生性和捕食性天敌昆虫的生物控害作用提供理论依据。

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