

叶甲科昆虫的定殖机制

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摘要: 在复杂的生态环境中, 叶甲科昆虫利用寄主植物的挥发物作为嗅觉信号, 并协同视觉信号共同作用以提高其远距离搜寻和定位寄主的效率。叶甲科昆虫也释放信息素来调节同种或者异种个体的行为反应; 找到寄主植物后, 叶子的形态学特性和化学组分的浓度等接触性因素就会影响叶甲科昆虫对寄主植物的最终选择。叶甲对上述这些信号物质的反应也受叶甲本身状态的影响, 如生殖、滞育、饥饿、交配以及取食等。叶甲科昆虫对寄主植物的搜寻、辨识和接受、取食以及繁殖的过程受一种或多种因素协同影响。从嗅觉、视觉和触觉等方面对叶甲科昆虫的定殖机制做一综述。

关键词: 叶甲; 寄主挥发物; 信息素; 触觉; 视觉; 嗅觉

The colonizing mechanism of Chrysomelidae

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Abstract: In this paper, the main factors related to the host colonization of leaf beetles in Chrysomelidae were reviewed. In the host location process of the beetles, plant volatiles, especially herbivore-infested plant volatiles play an important role. Up to now, several Chrysomelids have been shown to orient preferably to herbivore-infested plants whose volatiles differ qualitatively and quantitatively from the undamaged plants and generally are much larger than the latter. Beetle pheromones can also regulate conspecific and heterospecific behavioral responses. Both male and female adults in this family produce long-range pheromones, which include sex and aggregation pheromones. The pheromones are chemically diverse and consist of either single compound or a blend. Recent studies on Chrysomelid chemical communication have revealed that only male adults produced aggregation pheromones attractive to both sexes and that specific host plant volatiles have a synergistic role with sex or aggregation pheromones. In addition to chemical signals stated as above, the shape and color of the host plants are also the distant signals by which the beetles locate the host. These visual cues have a synergistic role with olfactory cues when Chrysomelids locate the hosts. Once landing on the host plant, the leaf traits, such as morphological characteristics and chemical composition, will influence whether the beetle accepts the host plant or not. The morphological characteristics of the leaves affect the attachment ability of the beetle to the leaf surface. Generally, Chrysomelids like smooth leaf surface. The leaf beetles can also estimate the host suitability by perceiving leaf chemicals, which are mainly secondary metabolites of host plants. Host-specific compounds are sufficient to stimulate feeding. Behavior of Chrysomelids in response to these above signals may be affected by numerous factors, including the physiological status of the beetles, such as reproduction, diapause, hungry, mating or feeding experience. These factors have integrated effects on the host colonization of leaf

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beetles. For a better understanding of host plant colonization by Chrysomelid, future studies need address, in addition to ecological and behavioral aspects, the molecular mechanisms underlying interactions between host plants and the leaf beetles.

Key Words: Chrysomelidae leaf beetle; volatiles; pheromone; touch; vision; olfaction

植食性昆虫要成功地定殖于寄主植物,取决于其定位寄主、利用植物的营养以及抵御植物防御反应的能力,这种能力由昆虫^[1-3]和植物^[4]的表型和基型的适应协调性所决定。

叶甲科(Chrysomelidae)隶属于鞘翅目,近40000种,几乎都是植食性的昆虫^[5]。一般成虫食叶,幼虫或土中食根,或潜生食茎、食叶柄、花芽和叶肉等,或露生食叶,许多种类的叶甲的蛹期也在寄主植物上完成。叶甲科昆虫与寄主植物在长期协同进化过程中形成了极为密切的系统关系,叶甲可根据寄主植物在生长过程中的变化而改变自身的产卵和取食行为^[6-7]。

叶甲科昆虫能感知来自种内和寄主植物的各种化学信息,并由此做出相应的行为反应,即寻找适宜的食物、配偶以及生存与繁殖场所^[8-9]。为了找到和识别寄主植物,叶甲科昆虫可利用单一或者多个感觉系统协同作用,这些感觉系统包括视觉^[10]、嗅觉^[11-13]、味觉^[14-15]和触觉等。但是这些感觉系统所利用的信号在识别寄主的准确性方面有所不同,有些可能更为可信^[16]。根据近年来的研究进展,本文从寄主植物挥发物、信息素、视觉和接触信号等多个方面对影响叶甲科昆虫定殖的几种主要因素作一系统性综述。

1 寄主植物挥发物

植物释放的挥发性有机化合物(volatile organic compounds, VOCs)既是植物间信息交流的信号物质^[17-18],也是植食性昆虫用以识别和定位寄主植物的重要信息^[19]。在复杂的生态环境中,昆虫中枢神经系统以高等级的时空分辨率接收挥发物信息,从而使植食性昆虫可准确地定位到寄主植物^[20-21]。寄主植物释放的挥发性化学信息的特殊性可通过挥发物在质上^[22-23]或者量上^[24-25]的不同来体现,也可通过寄主和非寄主植物组成成分的相对变化来体现^[26]。

植物VOCs的单一或者混合组分为叶甲在复杂的生态环境中找寻和识别寄主发挥着重要的作用。在叶甲科昆虫中,最早发现寄主植物挥发物对其具有吸引活力的是马铃薯叶甲 *Leptinotarsa decemlineata* 成虫^[5,27],之后很多野外和室内的研究均证实马铃薯叶甲受马铃薯挥发物的引诱^[28-30]。VOCs吸引叶甲科昆虫的现象还在很多研究中得到了证实,如:叶甲 *Trirhabda Canadensis*^[31-32]、玉米根甲虫 *Diabroticites* spp.^[33-35]、叶甲 *Agelastica coeruleae*^[36]。Garcia-Robledo 等^[37]测试了4种同域的叶甲 *Cephaloleia dorsalis* Baly, *C. erichsonii* Baly, *C. fenestrata* Weise 和 *C. placida* Baly 对4种寄主植物的选择作用,结果显示叶甲在寄主挥发物和空气之间选择时,4种叶甲均能选择其对应的寄主植物。

植物VOCs信号可以自发产生,也可多种因素诱导产生。机械损伤、昆虫产卵或取食等因素诱导之后,植物挥发物的组成或比例都会发生变化。各种损伤诱导的植物挥发物与健康植物挥发物相比,无论在质上还是量上都有很大差异,所以更易成为植食性昆虫远距离识别寄主植物的信号物质^[38-39]。诱导挥发物的释放具有系统性,可使邻近未受害的植物改变其挥发物的组成相,从而改变邻近植物对叶甲科昆虫的吸引力,如杨毛臀萤叶甲 *Agelastica alni* 着陆在被其为害过的赤杨树上后,邻近未受害的赤杨树对这种叶甲的吸引力减小^[40]。

虫害诱导的植物挥发物(Herbivore-induced plant volatiles, HIPVs)吸引同种^[12,41-47]或异种叶甲^[48]的现象已被广泛证实。如被雄性茄子叶甲 *Epitrix fuscula* Crotch 取食后,寄主植物释放的(2E,4E,6Z)-2,4,6-nonatrienal 和(2E,4E,6E)-2,4,6-nonatrienal 在挥发物中所占的比例最高,生测结果显示这2种物质对雌雄两性均有引诱作用^[49];叶甲 *Chrysomela scripta* 可被虫害诱导的寄主挥发物所吸引,而对未受害的寄主植物、叶甲本身和粪便没反应^[42]。Cossé 等^[50]的试验结果也表明叶甲取食为害诱导怪柳 *Tamarix* spp. 释放的3Z-6:

Ald, 2E-6: Ald, 3Z-6: OH, 2E-6: OH, 3Z-6: OAc, 1-己醇、庚醛、辛醛、苯甲醇、壬醛、吲哚、(2E, 6Z)-2, 6-壬二醛、(E, E)-法尼烯、(2E, 4E)-2, 4-庚二烯醛对桤柳条叶甲 *Diorhabda elongata* Brullé 具有触角电位活性, 而健康木中这些物质含量很少; 3Z-6: Ald, 2E-6: Ald, 3Z-6: OH, 2E-6: OH 这 4 种物质在虫害后释放量增大了大约 50 倍, 在桤柳受害后的 30 min 内这些物质最易被检测到。

HIPVs 的组成十分复杂, 包括萜类化合物、绿叶性气味、含氮化合物和除绿叶性气味以外的醛、醇、酮、酯及一些呋喃衍生物^[51]。不同的叶甲为害寄主植物后, HIPVs 中有一种或者几种物质是相同的, 这些相同的化学信息物质对不同种类的叶甲均具引诱活性。吲哚是许多种叶甲诱导后产生的一种典型的化学信息物质, 单独或作为混合成分中的一种可吸引多种叶甲。吲哚单独就能吸引黄瓜色条叶甲 *Acalymma vittatum*^[52], 吲哚和 1, 2, 4-三甲氧基苯、反-肉桂醛等比例混合能吸引西方玉米根虫 *Diabrotica virgifera virgifera* 和北方玉米根虫 *Diabrotica barberi*^[53]。南瓜属 *Cucurbita* spp. 花释放的苯甲醇和吲哚均可吸引十一星根萤叶甲 *Diabrotica undecimpunctata* howard 和西方玉米根虫^[54-55]。此外, 吲哚也是吸引西方玉米根虫的单一物质 4-甲氧基肉桂醛的增效剂^[56-57]。

绿叶性气味 (GLVs) 是 HIPVs 中很重要的组成部分, 是指植物挥发物中 6 个碳的醛、醇及其酯类, 这些物质大部分是己烯醇、己烯醛或者乙酸叶醇酯的同分异构体。植物叶片遭受到机械损伤^[50]、虫害诱导^[12]或茉莉酸诱导后^[58]会立即释放 GLVs, GLVs 是植物伤反应信号, 其混合气味能够吸引叶甲科昆虫^[50], 但对一些种类的叶甲在区分寄主和非寄主植物时, GLVs 不能起到信息化合物的作用, 当与寄主植物释放的挥发物混合后则提高了叶甲对寄主的选择能力^[5, 37, 59]。例如: 单一的 GLVs 不能吸引马铃薯叶甲, 但 GLVs 和其它的寄主挥发物混合就能起到引诱马铃薯叶甲的作用^[29, 60]; 顺-3-己烯醇对龟甲 *Cassida denticollis* 无引诱作用, 但是这种绿叶气味的存在可以提高叶甲对寄主和非寄主植物的分辨能力^[61]; 顺-3-乙酸叶醇酯在黑角负泥虫 *Oulema melanopus* 取食后诱导寄主植物产生的挥发物中所占比例较大, 亦能引起黑角负泥虫的触角电位反应, 但在野外单独使用却不能吸引黑角负泥虫, 和信息素混用也不能提高对黑角负泥虫的引诱力^[62], 但当和苯甲醛、壬醛以及水杨酸甲酯混用之后, 对雌雄两性黑角负泥虫均具引诱活性^[45]。

HIPVs 对叶甲科昆虫行为的影响依赖于寄主植物受害程度的轻重, 这是因为寄主植物受害程度的差异, 直接影响挥发物的组成和含量。室内嗅觉仪试验结果表明较轻的用剪刀剪的机械伤害仅在 15 min 内对马铃薯叶甲具有引诱作用, 而更严重的用金刚砂粉摩擦造成的伤害在 1 h 内都对叶甲具有引诱作用^[43]。榆叶甲 *Xanthogaleruca luteola* 会依据产卵诱导的寄主挥发物调整其产卵密度, 当榆树枝上有少量卵着生, 产卵诱导的挥发物吸引雌性甲虫继续产卵; 当枝上布满卵粒, 诱导的挥发物就会驱避甲虫产卵^[63]而吸引其卵寄生蜂——寡节小蜂 *Oomyzus gallerucae*^[64]。玉米根甲虫的幼虫在低虫口密度下很少或根本不再移动, 而在高虫口密度下则明显从被害植株移向邻近未受害的植株^[65]。

2 信息素

昆虫种内信息素包括性信息素、聚集信息素、踪迹信息素、标记信息素和告警信息素等。叶甲科昆虫信息素的研究多集中在聚集信息素^[42, 45, 62, 66-68]和性信息素^[69-71]等方面。雄性和雌性叶甲产生的远距离信息素在叶甲科昆虫中都有发现, 它们是由各种单一或者混合的化学物质组成。

2.1 结构和成分

叶甲科昆虫的信息素由酮、酯、萜烯和呋喃类组成。带斑黄瓜叶甲 *Diabrotica balteata* 雌性产生的性信息素最先被发现^[5, 72], 随后 7 种玉米根甲虫 (种和亚种) 的信息素相继被鉴定出来, 它们由甲基仲醇酯类组成, 结构类似酮类^[73]。手性或非手性的大环内酯类也能作为叶甲科的信息素, 如锯谷盗 *Oryzaephilus surinamensis* (L.)^[74] 和锈赤扁谷盗 *Cryptolestes ferrugineus* (Stephens)^[75]。雄性黄曲条跳甲 *P. cruciferae* Goeze 产生的 6 种特有的倍半萜类物质以一定比例混合后, 在田间具有引诱力, 其中 4 种已被合成应用^[44, 66, 76-78]。马铃薯叶甲释放的二羟基酮^[42, 67]、叶甲 *Aphthona* 和 *Phyllotreta* 释放的一系列雪松烯、杜松烯等^[76-77, 79, 80]、桤柳条叶甲 *Diorhabda elongata* Brullé 释放的一种 7-碳二烯醛和乙醇^[81] 以及黑角负泥虫 *Oulema melanopus* 释放的羟基

酮^[45,62]都被证实对叶甲有引诱作用。Bartelt 等^[82]首次发现取食千屈菜的叶甲 *Galerucella californiensis* 和 *G. pusilla* 的信息素是呋喃结构。叶甲科昆虫的信息素成分详见表 1。

表 1 叶甲科昆虫的信息素成分
Table 1 Components of pheromone in Chrysomelidae

物种 Species	信息素成分 Components of pheromone	参考文献 Reference
跳甲 <i>Aphthona</i> spp.	(9 <i>R</i> , 9 <i>aS</i>)-2, 3, 5, 6, 7, 8, 9, 9 <i>a</i> -octahydro-5, 5, 9-trimethyl-3-methylene-1 <i>H</i> -benzocycloheptene (9 <i>R</i> , 9 <i>aS</i>)-5, 6, 7, 8, 9, 9 <i>a</i> -hexahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocycloheptene; (3 <i>R</i> , 9 <i>R</i> , 9 <i>aS</i>)-2, 3, 5, 6, 7, 8, 9, 9 <i>a</i> -octahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocyclohepten-3-ol (3 <i>S</i> , 9 <i>R</i> , 9 <i>aS</i>)-2, 3, 5, 6, 7, 8, 9, 9 <i>a</i> -octahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocyclohepten-3-ol	[76]
黄曲条跳甲 <i>Phyllotreta cruciferae</i>	(9 <i>R</i> , 9 <i>aS</i>)-5, 6, 7, 8, 9, 9 <i>a</i> -hexahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocycloheptene;	[80, 83]
<i>Galerucella pusilla</i> <i>Galerucella californiensis</i>	12, 13-dimethyl-5, 14-dioxabicyclo[9.2.1]-tetradeca-1(13), 11-dien-4-one	[82]
马铃薯叶甲 <i>Leptinotarsa decemlineata</i>	(<i>S</i>)-3, 7-dimethyl-2-oxo-oct-6-ene-1, 3-diol	[84]
玉米根虫 <i>Diabrotica</i> spp.	1, 2, 4-trimethoxybenzene, indole, (<i>E</i>)-cinnamaldehyde	[85]
西方玉米根虫 <i>Diabrotica virgifera virgifera</i>	4-methoxycinnamaldehyde; syn-benzaldoxime; 1, 2, 4-trimethoxybenzene, indole, (<i>E</i>)-cinnamaldehyde 或者 (<i>E</i> , <i>E</i>)-3, 5-octadien-2-on	[53, 86]
带斑黄瓜叶甲 <i>Diabrotica balteata</i>	6, 12-dimethylpentadecan-2-one	[69]
北方玉米根虫 <i>Diabrotica barberi</i>	syn-benzaldoxime; 1, 2, 4-trimethoxybenzene, indole, (<i>E</i>)-cinnamaldehyde 或者 (<i>E</i> , <i>E</i>)-3, 5-octadien-2-one	[86]
桤柳条叶甲 <i>Diorhabda elongata</i>	(2 <i>E</i> , 4 <i>Z</i>)-2, 4-heptadienal (2 <i>E</i> , 4 <i>Z</i> -7: Ald), (2 <i>E</i> , 4 <i>Z</i>)-2, 4-heptadien-1-ol (2 <i>E</i> , 4 <i>Z</i> -7: OH); 3 <i>Z</i> -6: Ald, 2 <i>E</i> -6: Ald, 3 <i>Z</i> -6: OH, 2 <i>E</i> -6: OH	[50, 81]
南美叶甲 <i>Diabrotica speciosa</i>	1, 4-dimethoxybenzene	[87]
黑角负泥虫 <i>Oulema melanopus</i>	(<i>E</i>)-8-hydroxy-6-methyl-6-octen-3-one	[45]
茄子叶甲 <i>Epitrix fuscata</i>	(2 <i>E</i> , 4 <i>E</i> , 6 <i>Z</i>)-2, 4, 6-nonatrienal; (2 <i>E</i> , 4 <i>E</i> , 6 <i>E</i>)-2, 4, 6-nonatrienal; (9 <i>R</i> , 9 <i>aS</i>)-5, 6, 7, 8, 9, 9 <i>a</i> -hexahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocycloheptene; (3 <i>R</i> , 9 <i>R</i> , 9 <i>aS</i>)-2, 3, 5, 6, 7, 8, 9, 9 <i>a</i> -octahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocyclohepten-3-ol (3 <i>S</i> , 9 <i>R</i> , 9 <i>aS</i>)-2, 3, 5, 6, 7, 8, 9, 9 <i>a</i> -octahydro-3, 5, 5, 9-tetramethyl-1 <i>H</i> -benzocyclohepten-3-ol	[49]

2.2 释放和作用对象

早期发现的叶甲科昆虫的信息素属性信息素类,基本是由雌性产生,只吸引雄性,如:带斑黄瓜叶甲 *Diabrotica balteata*^[85]、取食欧洲狗舌草的叶甲 *Longitarsus jacobaea*^[70]、马铃薯叶甲^[71]。后来发现的叶甲科信息素多是由雄性释放的长距离信息素,属聚集信息素类,对雌雄两性都有吸引作用。如:叶甲 *Phyllotreta cruciferae* Goeze^[44,66,74-76]、桤柳条叶甲 *Diorhabda elongata* Brullé^[81]、马铃薯叶甲^[67,84]、取食千屈菜 *Lythrum salicaria* 的叶甲 *Galerucella californiensis* 和 *G. pusilla*^[82]。雄性黑角负泥虫 *Oulema melanopus* 释放的信息素-羟基酮,均能引起两性的触角电位反应^[45],这种信息素在白天的释放速率是晚上的 5 倍,1 头雄虫能持续 28 d 释放^[62]。由雄性叶甲释放信息素,吸引二性的现象可能是由于雄性对寄主植物和扩散转移的信号更敏感,而雌性对聚集信号更敏感^[46]。Szentesi 等^[10]也通过比较雄性马铃薯叶甲在辨别不同颜色的色板的表现优于雌

性,而认为雄性叶甲在寄主和交配选择中占主导地位。

2.3 来源

叶甲科昆虫信息素来源于叶甲的粪便、异性表皮的分泌物以及虫害诱导挥发物等。雄性叶甲产生的聚集信息素有两个来源,一是粪便中的混合物^[49,76,81,84],二是寄主植物受叶甲为害诱导产生的挥发物^[80,83];而马利筋叶甲 *Chrysochus cobaltinus* 和叶甲 *C. auratus* 雄性选择配偶是受到雌性表皮的碳氢化合物所吸引^[88]。

2.4 和寄主挥发物交互作用

植物挥发物和昆虫释放的信息素是植物与植食性昆虫之间、植食性昆虫个体之间信息交流的重要信号物质。植物源挥发物能增强叶甲科昆虫对信息素的反应^[68,80,83,89],这种植物挥发物与信息素之间的增效作用在叶甲科昆虫寻找寄主和配偶的过程中具有积极作用^[13]。对马铃薯叶甲最有效的引诱剂就是由3种寄主植物挥发物((*Z*)-3-乙酸叶醇酯、(±)-芳樟醇、水杨酸甲酯)和信息素((*S*)-3,7-dimethyl-2-oxo-oct-6-ene-1,3-diol)混合而成^[90]。Cossé 等^[50]证实了桤柳条叶甲 *D. elongata* Brullé 信息素和绿叶气味混合的引诱力,比单独的绿叶气味高6倍左右,比单独使用信息素诱集高4倍左右。

叶甲科昆虫许多信息素的发现就是在对虫害诱导挥发物的分析和生物测定中发现的。通过比较雌性和雄性桤柳条叶甲 *Diorhabda elongata* Brullé 取食诱导的寄主挥发物以及健康寄主植物挥发物的组成,发现(2*E*,4*Z*)-2,4-庚二烯醛和(2*E*,4*Z*)-2,4-庚二烯-1-醇这2种物质是雄性叶甲取食诱导寄主释放的挥发物中所特有的,并能引起触角电位反应,野外生测也表明这两种物质能吸引雌雄两性^[81]。

3 视觉

取食绣线菊的单食性叶甲 *Altica engstroemi* Sahlberg 即使饥饿24 h,对受为害前后的寄主挥发物都没有反应,因此,推测视觉信号在其寄主搜寻过程中起的作用可能比气味信号更大^[91]。*Cassida canaliculata* Laich. 是草地鼠尾草 *Salvia pratensis* L. 的单食性害虫,主要通过爬行来找到复杂的寄主栖息地,嗅觉在其找寻寄主的过程中可能不起主要作用,主要是依靠视觉来定位其寄主^[92]。Garcia-Robledo 等^[37]也发现专食性最强的叶甲 *C. fenestrata* 却不能区分寄主和非寄主植物挥发物,并推测其寄主定位过程中不仅仅需要嗅觉信号还需要辅以视觉信号,或者是单纯依靠视觉信号来找寻寄主。叶甲科昆虫利用视觉信号来进行寄主定位的现象在很多研究中已经得到证实。当叶甲找寻食物时,通过辨别植物的轮廓^[14]和色彩^[10]来区分寄主和非寄主。依赖视觉定位的叶甲,可根据一天中的不同时间段光的波长和方向的变化来判断选择寄主植物,因为叶甲对不同波长光的敏感性不同,如黄曲条跳甲 *P. striolata* 就能利用这种光波的变化来选择寄主^[93]。

颜色对叶甲科昆虫的选择寄主行为也有很大影响,如马铃薯叶甲偏爱黄黑条纹和黄色、浅绿色的色板^[10]。田间的诱捕实验很多也证实了不同颜色的诱捕器具诱捕到的叶甲数量也有很大差异。如:Arruda-Gatti 等^[94]在野外诱捕实验中证实南美叶甲 *Diabrotica speciosa* (Germar) 雌雄两性对绿色诱捕器比黄色和白色更敏感,雌虫对黄色的反应比白色更强烈;黄色诱捕器诱到的黑角负泥虫 *Oulema melanopus* 最多^[62];黄色诱捕器诱集到的取食棉白杨的叶甲 *Chrysomela scripta* 也比黑色诱捕器多^[42]。

4 触觉

叶甲科昆虫通过视觉、嗅觉找到寄主植物后,植物的表皮构造和理化性质(叶子的形态学特性、表皮蜡质的化学成分以及植物组织内的营养和次生代谢产物等接触性因素)都影响着叶甲科昆虫的定殖^[2,14]。

4.1 寄主植物性状

植物的表面性状很大程度地影响昆虫的附着。许多昆虫能利用足部特殊的附着结构来成功地附着在不同物质上,附着力因附着表面的几何形状和性状及理化性质的不同而变化^[14,95-97]。有研究发现昆虫喜欢附着在光滑的表面而非凹凸不平的表面,如马铃薯叶甲更喜欢在光滑表面上着陆,这是因为其刚毛末端能有效接触寄主植物的叶表面^[14]。叶甲 *Gastrophysa viridula* Degeer 对抛光纸表面的附着力比9 μm 粗糙度的纸要大,在叶表面和抛光纸上的附着力比玻璃要低,测试结果表明叶甲在粗糙不平的表面上的附着力降低了4倍^[97]。有学者认为细胞的疏水性可以解释叶甲在粗糙表面上附着力的减小^[14]。另有研究发现植物叶表面的毛状体

对叶甲的定殖也有很大影响,如:马铃薯 *Solanum tarijense* 叶子表面密被的毛状体阻碍了马铃薯叶甲的取食,在机械拔除毛状体后,明显减少了叶甲从叶上的掉落^[98]。

4.2 次生代谢物质

叶表面的毛状体存在与否,马铃薯叶甲对马铃薯 *Solanum tarijense* 都很少取食^[98];昆虫能成功附着在光滑的植物表面,但在透明的蜡质覆盖的植物表面则不能附着,这些都可能是叶表面的挥发性和非挥发性的化学组分的影响^[99-103]。寄主植物是否适宜,最准确、最可信赖的是接触化学感应。影响叶甲科昆虫接触感应的信息物质主要是植物的次生物质。植物次生物质,是指与糖、脂肪、蛋白质和核酸等植物基础代谢物质相对而言的众多类群化合物,诸如像醇醛类、萜烯类、黄酮类和单宁类等。基础代谢物质对植物的生长发育和维持生命必不可少,而次生代谢物质在植物体内是否存在对植物的生长发育不受影响,但却是植物体抵御病虫害侵袭的重要物质基础。不同种植物具有特异的次生物质组成。

寄主植物的不同部位所含的化学营养物质的成分或比例不同,适合不同虫态的生长发育。叶甲科昆虫多喜食近老熟叶片和茎,而喜欢产卵在新长出的叶片上,如:以桉树为食的叶甲 *Chrysophtharta agricola*^[104]。取食柳树的叶甲 *Plagioderia versicolora* 在实验室则喜欢产卵在新鲜的嫩叶子上,可能是因为新叶片所含有的防御物质少,适宜卵的发育;但在田间喜欢枝杈中心附近的老熟叶子上产卵,可能由于田间光线或者捕食性天敌的存在等因素影响其产卵选择^[105]。

在接触化学感应中,叶甲主要通过对寄主植物中不同化学物质的感知来定殖,化学物质的相对比例可能对叶甲定殖不是很重要^[21]。在生测实验中,寄主植物的茎对以草地鼠尾草为食的叶甲 *Cassida canaliculata* Laich 没有吸引力,叶子对其有很小的吸引力;但是当叶甲接触寄主植物后,就比较喜欢寄主植物的茎。经过分馏法提取了茎的成分对叶甲进行生测,发现有两种非极性接触刺激物对叶甲来说有引诱作用^[106]。

叶甲咬食寄主植物,只有验证特有物质的存在后才能有效地刺激其取食。叶甲的取食刺激物可能是几种物质的混合物^[106],一种物质单独对叶甲来说可能没有活性^[107-108]。如,取食草地鼠尾草的叶甲 *C. canaliculata* 对单独使用 1 种接触刺激没有反应,至少需要 2 种接触刺激物来刺激其取食。用 100% 正己烷提取液和 50% 正己烷加上 50% 二氯甲烷混合提取液比单独使用正己烷提取液吸引力要明显增强,这种混合活性说明至少 2 种或更多种物质包含在内。这是因为如果 1 种刺激物不是寄主植物所特有的,就可能被其它种类昆虫所误解^[92],这也是植食性昆虫与寄主植物在漫长的协同进化过程中获得的一种生存本能。

5 叶甲本身的状态

叶甲科昆虫可能因本身的状态不同,对寄主的选择性也有所不同,这主要受以下两方面因素的影响:一是叶甲的内状态,如:虫龄、激素水平、饥饿状态和经历等因素。Cossé 等^[50]用寄主挥发物合成的引诱剂在野外诱捕桉柳条叶甲 *Diorhabda elongata* 时,发现对照和处理捕获到的雄性叶甲比例都较大,这可能是和叶甲的行为、生理和生态背景有关系,如交配和产卵后雌虫的死亡导致雄虫的比例增高。二是叶甲的生理状态,如繁殖、滞育、饥饿或者取食也能改变叶甲对活性物质的反应。许多叶甲产卵在非寄主植物上,一方面可能增加叶甲繁殖的成功性,一方面减少寄生蜂的取食,如多食性叶甲 *Galeruca tanacetii* L. 优先选择产卵到草等非寄主植物上^[109]; *Galerucella tenella* 在原产地取食草莓,但是在测试中,叶甲却也取食绣线菊,甚至优先选择绣线菊,这可能是密度制约策略,上一代避免用尽植物的营养源,使它们的后代不存在竞争者^[110]。此外,叶甲科昆虫的交配或性接触也能影响到叶甲的定殖。马铃薯叶甲交配后的 24 h 内引诱剂对叶甲的引诱力降低,72 h 后才恢复;异性接触后引诱剂对叶甲的引诱力也降低,同性接触则不发生这样的反应^[47]。交配降低了引诱剂的引诱作用,可能是为确保交配,减少雌性在雄性着生的寄主植物上的活动;嗅觉在交配 72 h 后恢复,可能是产卵的需要或者是增加重复交配的可能性。

6 结语

叶甲科昆虫从不同的营养层面出发,来选择和定殖于寄主植物。在这个过程中,可能某一种因素起主要作用,其他一种或几种因素起协同作用。在远距离找寻寄主的过程中,VOCs 和 HIPVs 发挥着重要的嗅觉信

号的作用,植物的大小、颜色等视觉信号也给叶甲提供了重要的信息。叶甲也会在这一过程中释放信息素吸引同种叶甲来交配或取食。当叶甲到达寄主植物后,植物表皮性状和次生代谢物质等接触性信息就影响着叶甲的取食和产卵等行为。另外,植物的高度和密度等环境因素^[111-115]以及叶甲本身的状态都影响其对寄主植物的定殖。这些因素不是单独起作用,而是相互协调,相互促进,如寄主挥发物和信息素混用、植物次生物质和信息素混用^[80]都能提高对叶甲科昆虫的引诱作用。

确定何种因素在叶甲科昆虫的定殖中起主导作用,并对各种影响因素进行综合考虑,对利用诱捕手段监测和防治叶甲科昆虫具有及其重要的意义。在实践中,利用 HIPVs 或信息素合成引诱剂,充分考虑诱捕器的颜色、形状和表面光滑度等定殖要素,可最大程度地提高诱捕效果。此外,在叶甲科昆虫的防治过程中,引诱剂的应用还可以配合无公害农药一起使用。将叶甲科昆虫诱集后杀死,可减少化学农药的使用量和施药范围,实现成功防治的同时减少了环境污染。尽管目前对某些叶甲科昆虫的定殖机制在生态和行为学方面已有了比较系统的研究,未来还需要在分子、生理学和化学生态学等领域来进一步深入的研究,以确定影响叶甲科昆虫定殖的主要影响因素,为野外监测和防治叶甲提供理论基础和实践经验。

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