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绿叶挥发物及其生态功能研究进展

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摘 要: 系统总结了绿叶挥发物的释放规律、代谢途径和对不同生物群落的生态调控功能,包括能诱导植物生成相关防御基因和防御化合物,自身及其诱导生成的虫害诱导植物挥发物和花外蜜露能够在植株间传递预警信号、吸引和驱避植食性昆虫、协同或抑制昆虫信息素、招引寄生蜂,还能影响病原微生物的生长。指出了在田间条件下天敌因受到背景气味、气象条件、害虫种群分布和数量等诸多因素的影响,很难达到理想的生物防治效果。因此仍需对植食性昆虫与天敌的化学遗传学和生态学、不同植物—植食性昆虫—天敌三重营养间的互作关系,以及不同植食性昆虫虫口密度对田间防效的影响等诸多方面进行深入研究,以明确虫害诱导挥发物中关键物质的多重生态功能,并确定虫害诱导挥发物的田间应用技术。

关键词: 绿叶挥发物;释放规律;代谢途径;生态功能;植食性昆虫;寄生蜂
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Advances in Green Leaf Volatiles and Its Ecological Functions

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Abstract: Green leaf volatiles (GLV) play an important role in the chemical information network among plants, pest insects and natural enemies. That the release disciplines, metabolic pathways and the ecological functions on different biological communities of GLV was systematacially introduced in the paper. Defense-related genes and secondary metabolites can be induced and generated by GLV in plants defense response. GLV itself and HIPVs and extrafloral nectar induced by GLV can both be spreaded as the warning signals between plants, to attract and repel herbivorous insects, to play the role of synergistic and inhibitive effects with insect pheromones, to attract parasitic wasps and also to affect the growth of pathogenic micro-organisms. Although many natural enemies can be apparently allured by GLV in the laboratory conditions, their parasitic and predatory behaviors are easily influenced by background odors, meteorological conditions, population distribution and quantity of insect pests, and many other factors in the field conditions. It is too complicated and difficult to achieve the ideal biological control efficiency. Before indirect defensive functions of herbivore-induced plant volatiles are used as the regulatory measures with the chemical ecology for phytophagous insect populations in fields, many unknown aspects such as chemical genetics and ecology of insect pests, the interaction mechanism among plants, pest insects and natural enemies, the interactions

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between the control efficiency and different population densities of herbivorous insects in fields, are still needed to do in-depth research in order to determine multiple ecological functions of the key substances of HIPVs and develop application technology in fields.

Key words: Green leaf volatiles; Emission disciplines; Metabolic pathway; Ecological functions; Phytophagous insects; Pararsitic wasps

0 引言

在漫长的协同进化过程中，植物发展了一套完整、积极的防御系统来抵御植食性昆虫的侵害[1]。在这一防御系统中，植物先天具有的组成抗性，以及在遭受植食性昆虫为害后植物所产生的诱导抗性是其中的2个重要方面。植物的诱导抗虫性是指植物在遭受植食性昆虫攻击后所表现出来的一种抗虫特性，包括直接抗性和间接抗性两方面。直接抗性是指植物能直接影响害虫的敏感性及适宜性，主要包括诱导产生的植物次生性化合物和防御蛋白质；间接抗性是指植物通过增强天敌作用而影响害虫适宜性，即植物在受植食性昆虫攻击后释放特异性挥发物引诱植食性昆虫的天敌，从而达到间接防御植食性昆虫的目的[2]。绿叶挥发物(green leaf volatiles, GLV)是虫害诱导植物挥发物(herbivore-induced plant volatiles, HIPVs)和背景气味(background odors)的重要组成部分，绿叶挥发物具有多种生态功能，其自身及其诱导生成的虫害诱导植物挥发物和花外蜜露能够在多个营养级之间传递信号[1,3-6]，更重要的是绿叶挥发物能吸引寄生性和捕食性天敌[7-9]，目前大多数研究是在实验室条件下完成的，绿叶挥发物引诱天敌的效果很明显，虽有一些田间试验成功的报道，但在田间条件下受到诸多因素的影响，很难得到预期结果。绿叶挥发物在植物—害虫—天敌三营养层的化学信息网中具有重要作用，在植物自身防御反应中具有直接防御和间接防御等多种生理生态功能[10-11]，因此，在植物—害虫—天敌三级营养关系的研究中受到越来越多的重视[12]。本研究较系统地介绍了绿叶挥发物的释放规律和代谢途径及其对不同生物群落的生态调控功能，还对绿叶挥发物的田间研究现状和存在问题进行了分析，展望了绿叶挥发物在害虫生态调控中的应用价值和前景，可为后期的深入研究奠定理论基础。

1 绿叶挥发物的释放规律

1.1 绿叶挥发物的概念

GLV普遍存在于植物叶片中，绝大部分植物都可以释放GLV，所以也被称为“普通气味”[13]，即C_6挥发物，主要是指6个碳的醛、醇及其酯类，常见的种类有*n*-hexanal、*n*-hexanol、(*E*)-2-hexenal、(*E*)-2-hexenol、(*Z*)-3-hexenal、(*Z*)-3-hexenol、(*E*)-3-hexenal、(*E*)-3-hexenol和(*Z*)-3-hexenyl acetate等[14-15]。

1.2 绿叶挥发物的释放规律

1.2.1 释放效率 完整健康的植株不释放或只嫩叶释放很少量GLV，但当受到外界胁迫时可在短时间内释放大量GLV。如马铃薯(*Solanum tuberosum*)和蚕豆(*Vicia faba*)受机械损伤5 min内就能释放(*Z*)-3-hexenal、(*E*)-2-hexenal和(*Z*)-3-hexenol等[16]。拟南芥(*Arabidopsis* sp.)遭受虫害后20 s即可释放(*E*)-3-hexenal[17]；茶树[*Camellia sinensis* (L.) O. Kuntze]嫩叶经针扎后能立刻释放(*Z*)-3-hexenal、(*Z*)-3-hexenol、(*Z*)-3-hexenyl acetate、(*E*)-2-hexenal、2-ethyl-1-hexanol和(*Z*)-3-hexenyl butyrate等；被茶丽纹象甲(*Myllocerinus aurolineatus*)、茶尺蠖(*Ectropis oblique*)取食后，也立刻释放(*Z*)-3-hexenal、(*Z*)-3-hexenol、(*Z*)-3-hexenyl acetate和(*E*)-2-hexenal等；被假绿叶蝉(*Empoasca vitis*)取食1 h后可释放(*Z*)-3-hexenyl acetate等[10]，而且释放量远高于健康植株，机械损伤处理的拟南芥叶片5 min内(*Z*)-3-hexenol的释放量是健康叶片释放量的30倍。

1.2.2 释放速率 GLV的释放速率因植物和植食性昆虫种类而异。如茶尺蠖为害茶树28 h后主要GLV的释放量：(*Z*)-3-hexenol约为0.40 μg/h、(*E*)-2-hexenal约为1.04 μg/h、(*Z*)-3-hexenyl acetate约为0.07 μg/h；茶丽纹象甲为害茶树28 h后主要GLV的释放量：(*Z*)-3-hexenal约为0.03 μg/h、(*E*)-2-hexenal约为0.11 μg/h、(*Z*)-3-hexenyl acetate约为0.02 μg/h[17]。而未受害转基因棉花(*Gossypium herbaceum*)的叶和顶心处主要挥发物释放量：*α*-pinene约为0.07 ng/(g·h)、*β*-pinene约为17.67 ng/(g·h)，茎的释放量分别为20.45 ng/(g·h)、12.21 ng/(g·h)[18]。

1.2.3 扩散规律 通常可在植物叶冠上方的气体中检测到GLV[19-20]，仅(*Z*)-3-hexenyl acetate是整株释放的，其他化合物都只在伤叶上才能检出[21]。GLV在空气中容易被O_3、·OH、NO_3氧化，(*Z*)-3-hexenal在空气中的生存周期只有2 h[22]。在风向和风速恒定条件下，气味从气味源出发顺风扩散，气味浓度不断地降低，形成具有气味浓度梯度的气缕结构[23]。对于逆风寻找气味源的昆

虫来说，高于某阈值的浓度范围就是活性空间(active space)[24]，气味活性空间的大小和最大通讯距离随风速而递减。气味信号分子的浓度梯度可调节植物的防御反应，在空气中弥漫着多种挥发物和大气污染物，以及变化不定的生态因素都很容易影响昆虫飞行和寄主定位行为。以往多研究昆虫性信息素在静止或流动空气中的扩散规律，而很少涉及虫害诱导植物挥发物的扩散规律。

1.2.4 昼夜节律 虫害诱导植物挥发物遵循着与明暗循环有关的生理周期，即昼夜节律：挥发物在白天释放量增加，夜间释放量减小，也有的挥发物在夜间达到高峰[25-26]。如烟草夜蛾(*Heliothis virescens*)和棉铃虫(*H. zea*)取食烟草(*Nicotiana tabacum*)[27]、茶尺蠖、茶丽纹象甲和假眼小绿叶蝉取食茶树[10]、斑潜蝇[*Liriomyza huidobrenisis* (Blanchard)]取食利马豆(*Phaseolus lunatus*)[28]和棉铃虫取食棉花诱导释放出的挥发物都具有明显的节律性[29]。

1.2.5 植物挥发物的释放、植食性昆虫和寄生蜂的行为在节律上的一致性 植物挥发物的释放规律、昆虫的取食行为和寄生蜂的行为紧密相联，使植物—害虫—天敌这3个营养级共同形成了明显的昼夜节律[27-30]。如野生牵牛花属(*Petunia*)植物挥发物的释放时间与其传粉蛾触角的感受性和夜间活动习性一致[31]。茶尺蠖、茶丽纹象甲和假眼小绿叶蝉开始为害后，茶树立刻就可释放GLV，而茶树HIPVs其他组分也可在之后的24 h内大量产生，当这3种害虫停止为害15 h后茶树HIPVs大量减少[10]。利马豆受斑潜蝇危害后，挥发物释放高峰滞后于斑潜蝇取食高峰约3 h；寄生蜂主要在晨间羽化，其活动节律恰好与(*Z*)-3-hexenol的挥发高峰相同，与虫害利马豆的挥发物节律具有很好的一致性。植物挥发物的释放节律能够有效帮助寄生蜂找到寄主昆虫。三级营养关系中的节律性也具有双向性：一方面昆虫的取食节律导致了挥发物的释放节律，也决定了寄生蜂的活动规律，同时都符合光照的亮暗周期；另一方面寄生蜂通过经验学习行为，能够在不同时间利用固有的HIPVs信息定位寄主昆虫[28]。

1.2.6 影响因素

影响植物释放挥发物的因子包括植物的种类、生育期、受害部位等，昆虫的种类、发育阶段、种群密度、产卵行为、取食行为和持续时间，病原菌侵染等生物因子；还有光、温度、土壤水肥、二氧化碳、臭氧、外源化学物质等非生物因子[19,32-38]。

2 绿叶挥发物的代谢途径

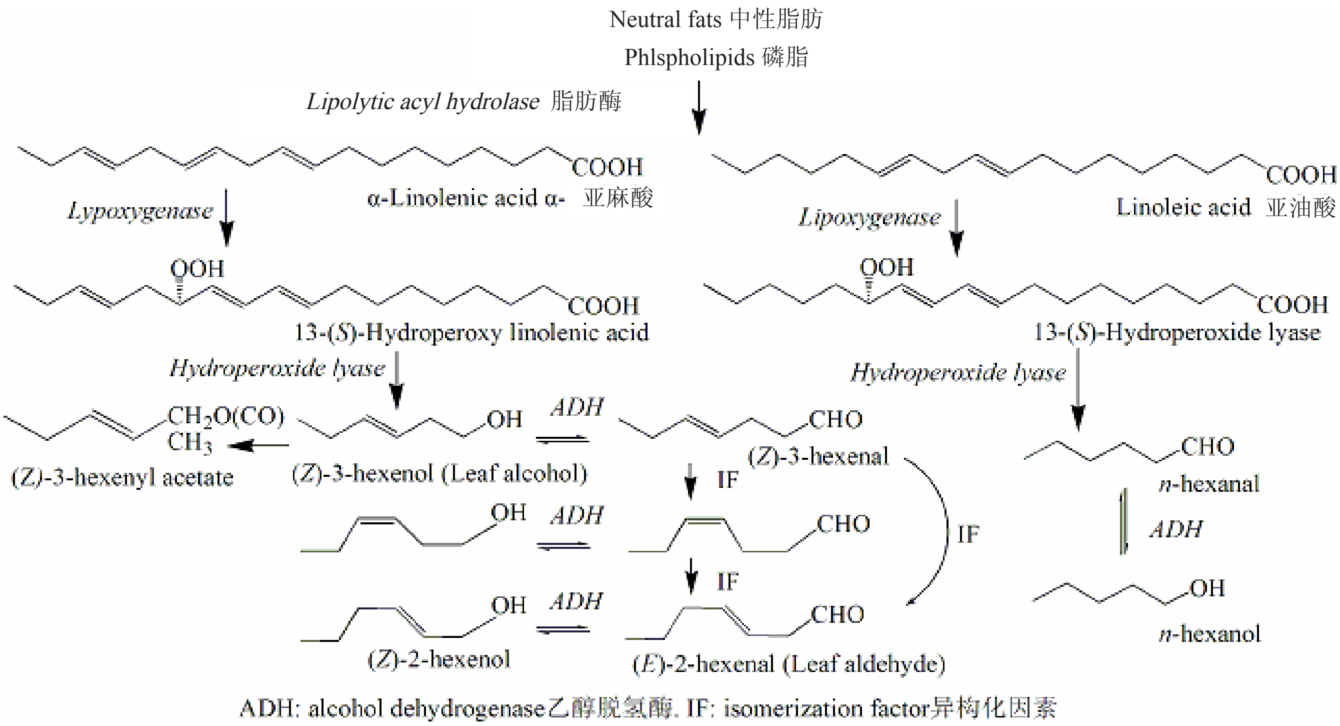
植物细胞受损后释放出的脂肪酸衍生物来自十八烷酸途径的分支，经脂肪酸/脂氧合酶途径合成[39-40]。研究发现诱导GLV释放的基本条件是细胞膜氧化损伤[41-42]，在植物组织遭到破坏后，半乳糖脂快速水解生成大量的α-亚麻酸(α-linolenic acid, ALA)和亚油酸(linoleic acid, LA)，2种脂肪酸在脂氧合酶(lipoxygenase, LOX)和脂氢过氧化物裂解酶(hydroperoxide lyase, HPL)等一系列酶的催化作用下合成。GLV属于组成型挥发物，即存在于植物细胞中，在植物细胞遭受到机械损伤后在受损部位立即释放的物质，主要包括一些积累在植物细胞、组织或器官中的物质，如(*Z*)-3-hexenal和(*E*)-2-hexenal等不是损伤后重新合成的物质，还有脂肪酸衍生物，如(Z)-3-hexenyl acetate是唯一经脂氧合酶途径重新合成，并能系统性释放的绿叶挥发物[26,43]。(*Z*)-3-hexenal是经LOX途径由ALA氧合生成13-氢过氧化亚麻酸(linolenic acid 13-hydroperoxide, 13HPOT)后，在13-氢过氧化脂肪酸裂解酶(13-hydroperoxide lyase, 13HPL)的作用下裂解产生的。*n*-hexanal的起始物源于LA，(*E*)-3-hexenal是由(*Z*)-3-hexenal的酶/非酶异构化作用产生的，C_6醛类可通过醇脱氢酶(alcohol dehydrogenases)的作用进一步转化为C_6醇类，如(*Z*)-3-hexenal转化为(*Z*)-3-hexenol，C_6醇类还可通过脂酰基转移酶(acyltransferase)的作用转化为酯类，如(*Z*)-3-hexenol转化为(*Z*)-3-hexenyl acetate[44](图1)。

3 绿叶挥发物的生态功能

植物挥发物是植物与其他生物交流的复杂的高级“语言”[46]，植物挥发物能直接和间接地影响植食性昆虫及其天敌之间的相互作用关系，这种上行控制作用(bottom-up control)能更有效地调控三级营养层间的信息交流[47]。GLV能诱导植物生成相关防御基因和防御化合物，其自身及其诱导生成的HIPVs和花外蜜露(extrafloral nectar, EFN)能够在植株间传递预警信号、吸引和驱避植食性昆虫、与昆虫信息素的协同与抑制作用、招引寄生蜂，还能影响病原微生物生长。根据近年来研究进展将GLV的生态功能概括为3个方面。

3.1 绿叶挥发物能诱导植物防御

植物之间存在由挥发物介导的损伤信息(MeJA、MeSA、Ethylene)传递，GLV也是一种损伤信息，通过调节植物发送信号和在同种或异种植物间传递信息，能诱导植物表达防御基因和生成防御化合物，使临近的植物处于防御敏感状态(primed state)，释放挥发物、提高植物对天敌的吸引力、降低植物的易感性。所以GLV在植物群落的共同防御中扮演信使角色，承担着化学信号传递的功能[39,48-51]。



注：参见文献[14]、[45]

图1 绿叶挥发物的代谢途径

3.1.1 诱导防御基因和防御化合物 GLV能诱导利马豆、马铃薯、拟南芥、大豆、杨树等植物体内相关防御基因（*LOX*、*AOS*等）的变化和表达[39,52-56]，也能诱导健康植物体内萜类物质在植株系统和受损部位的累积和释放[26,40]。健康杨树和同种损伤植株放在一起后，健康株叶片内的酚类含量和合成速度明显上升；靠近损伤植株后健康糖槭(*Acer saccharum*)体内的酚类和单宁的浓度显著提高[57]。(*E*)-2-hexenal 和 (*Z*)-3-hexenyl acetate处理的植物在受害时能释放更多的萜烯[56]。用MeJA分别与MeSA、cis-hexenal、trans-hexenal和benzothiazole混合后熏蒸杨树，叶片中3种防御蛋白（过氧化物酶、多酚氧化酶和苯丙氨酸解氨酶）的活性明显升高，并且两种混合挥发物的诱导效果高于单独一种挥发物，但不是每一种挥发物诱导效果之和[58]，说明GLV参与诱导了健康植物的防御反应。

3.1.2 诱导HIPVs GLV还能诱导健康植株释放与防御相关的HIPVs，健康植物对这类信号的反应有两种，一是直接启动防御反应，二是武装自身处于防御敏感状态，当受到虫害等胁迫时再立即进行防御[51-56]。如在健康玉米周围喷施(*Z*)-3-henxenol以及Ethylene和(*Z*)-3-henxenol的混合物，玉米能吸收空气中的C_6-醛类和C_6-醇类，将之转化为醋酸盐类后释放出与HIPVs相似的挥发物来吸引天敌[59]。用Ethylene和(*Z*)-3-hexenal的混合物能显著促进己烯醛和(*Z*)-3-henxenol的释放，说明Ethylene在与(*Z*)-3-hexenal在调节合作杨植株间伤害信息产生上具有协同作用，但(*E*)-3-hexenal对合作杨挥发物没有诱导能力，说明合作杨植株能够识别不同构型的C_6-醛[60]，这可能是由于植物细胞质膜上的挥发物的气味结合蛋白或特异受体不同。用(*Z*)-3-hexenyl acetate处理的杨树被舞毒蛾(*Lymantria dispar*)取食为害后，叶片中的JA和ALA的含量显著高于对照[56]。GLV处理的玉米在机械损伤和甜菜夜蛾口腔分泌物涂抹之后，比对照能更快速和持久地合成JA以及相关挥发物，通过诱导临近的健康玉米体内JA含量的增加而发挥诱导防御功能，更重要的是，玉米植株在没有接收到真正的植食性昆虫威胁的信号时，GLV诱导产生的防御准备并不发挥作用[49]，进一步的研究表明，这些GLV通过上调十八烷酸代谢途径(octadecanoids pathway)中的*ZmOPR1/2*，*ZmOPR5*和*ZmOPR8*这3个基因来增加JA的含量[61]。

3.1.3 诱导EFN GLV和虫害等均可诱导植物产生EFN。花外蜜腺指植物具有着生于花外而一般不参与传粉的蜜腺，花外蜜腺能够分泌EFN，在自然界，植物以EFN作为间接防御植食性昆虫的手段之一，EFN与HIPVs具有相似的生态功能，如吸引捕食性昆虫（多为

蚁科Formicidae)聚集在蜜腺附近守卫，所以花外蜜腺也被称为“防御蜜腺”(defense nectaries)[62-63]。如虫害诱导利马豆释放的(*Z*)-3-hexenyl acetate和(*E*)-3-hexenyl acetate等可引起利马豆分泌更多的EFN[63-64]，吸引蚂蚁、寄生蜂、瓢虫和捕食螨等地上害虫的天敌，显著减少了植食性昆虫的数量[63,65-69]，地下害虫(*Agriotes lineatus*)取食棉花能诱导地上组织产生更多的EFN，提高植物对寄生性天敌的吸引[70]。EFN植物上舞毒蛾(*Lymantria dispar*)的被寄生率显著高于非EFN植物[69,71]。

3.2 绿叶挥发物能调控昆虫行为

植食性昆虫及其天敌能够借助植物释放的GLV寻找各自的寄主，完成觅食、交配和产卵等活动，这些行为还能影响植物挥发物的组成和释放，调控昆虫个体行为及对昆虫群落产生影响。

3.2.1 吸引和驱避植食性昆虫 GLV是很多植物所散发的信息化合物的主体，植食性昆虫的取食、交配和产卵等行为大多是在其寄主植物上完成的，所以GLV对许多植食性昆虫具有吸引和驱避的作用(表1)。还有些昆虫能够利用非寄主植物释放的GLV来区分寄主植物与非寄主植物，寄主植物极少释放这些物质，以避免进入非寄主植物的生境，如红脂大小蠹(*Dendroctomus ualens* LeConte)、黑山松大小蠹(*D. ponderosae* Hopkins)、红翅大小蠹(*D. rufipennis*)、云杉八齿小蠹(*Ips typographus* L.)、十二齿小蠹(*I. sexdentatus* Borner)、重齿小蠹(*I. duplicatus* Sahalberg)、纵坑切梢小蠹(*Tomicus piniperda* Linnaeus)、横坑切梢小蠹(*T. minor* Hartig)和松瘤小蠹(*Orthotomicus erosus* Woll)，这些昆虫的触角能感识(*E*)-2-hexenal、(*Z*)-3-hexenol、(*Z*)-3-hexenyl acetate等非寄主植物挥发物，但在行为学测试中却表现为避开这些物质[72-79]，GLV和Aldehyde能阻断至少11种针叶树小蠹虫对寄主植物的趋向性[80]。

3.2.2 对昆虫信息素的协同抑制作用 GLV对昆虫信息素的影响包括两个方面，一是与昆虫信息素协同作用，能增强诱捕效果，通常在寄主植物气味存在时昆虫的交配成功率较高，而有些种类则必须在寄主植物气味的存在下才能成功地交配[96-97]，如多音天蚕

表1 绿叶挥发物调控植食性昆虫行为

植物	植食性昆虫	绿叶挥发物	生态功能	参考文献
茶树 *Camellia sinensis*	茶丽纹象甲 *Myllocerinus aurolineatus*	(Z)-3-hexenyl acetate、(Z)-3-hexenal	吸引成虫	[81]
八棱海棠 *Malus prunifoli*	苹果绵蚜 *Eriosoma lanigerum*	(*E*)-3-hexenol	吸引成虫	[82]
榆树 *Ulmus pumila*	榆紫叶甲 *Ambrostoma quadriimpressum* Motschulsky	(*Z*)-3-hexenol	强烈吸引雌成虫	[83]
复叶槭 *Acer negundo* L.	光肩星天牛 *Anoplophora glabripennis*	(*Z*)-3-hexenyl acetate、(*E*)-2-hexenal、(*Z*)-3-hexenol	吸引成虫	[84]
小麦 *Triticum aestivum*	麦长管蚜 *Macrosiphum avenae*	(*E*)-2-hexenal	吸引有翅和无翅蚜	[85]
	禾谷缢管蚜 *Rhopalosiphum padi*	(*E*)-3-hexenyl acetate	吸引有翅蚜	
		(*E*)-2-hexenol	吸引无翅蚜	
豇豆 *Vigna unguiculata* 菜豆 *Phaseolus vulgaris*	美洲斑潜蝇 *Limyza sativae*	3-hexenol、2-hexenol、2-hexenal、3-hexenyl acetate等	寄主定向的次要组分	[86]
甘蓝 *Brassica oleracea* subsp. *capitata*	小菜蛾 *Plutella xylostella*	(*Z*)-3-hexenyl acetate、(*E*)-2-hexenal、(*Z*)-3-hexenol	吸引雄虫和已交配的雌虫产卵	[87]
马铃薯 *Solanum tuberosum*	马铃薯甲虫 *Leptinotarsa decemlineata* (Say)	(*Z*)-3-hexenyl acetate、(*Z*)-3-hexenol、(*E*)-2-hexenal、(*E*)-2-hexenol	吸引成虫	[88,89]
玉米 *Zea mays*	玉米蚜 *Rhopalosiphum maidis* (Fitch)	(*E*)-2-hexenal、*n*-hexanol、(*Z*)-3-hexenyl acetate	驱避雌虫产卵	[39]

续表1

植物	植食性昆虫	绿叶挥发物	生态功能	参考文献
水稻.*Oryza sativa* (Rathu Heenati, IR64)	白背飞虱 *Sogatella furcifera* (Horváth)	(*E*)-2-hexenal	吸引成虫	[90]
	褐飞虱 *Nilaparvata lugens*	(*E*)-2-hexenal、(*E*)-2-hexenol	驱避成虫	[91]
烟草 *Nicotiana tabacum*、*Nicotiana attenuate*	烟草天蛾 *Heliothis virescens*	(*E*)-2-hexenal	驱避同种雌虫产卵、减少取食、增加的死亡率	[27,92,93,94]
番茄 *Lycopersicon esculentum* Miller、甘蓝 *Brassica oleracea* 和辣椒 *Capsicum annuum* Linn.	B型烟粉虱 *Bemisia tabaci* (Gennadius)	(*Z*)-3-hexenol	驱避成虫	[95]

[*Antheraea polyphemus*(Cramer)]雌蛾的求偶行为是受红橡树(*Quercus* sp.)叶片中的(*E*)-2-hexenal刺激而产生[98]。(*E*)-2-hexenol、(*Z*)-3-hexenol等可明显地增强棉铃虫对性信息素的反应[99]。把(*Z*)-3-hexenyl acetate、(*Z*)-3-hexenol分别与甜菜夜蛾性信息素混合后，能够提高对甜菜夜蛾的田间诱捕效果[100]。(*E*)-2-hexenal可提高墨西哥棉铃象(*Anthonomus grandis*)聚集信息素的诱集效果[101]。有学者详细总结了植物源挥发物对聚集信息素和性信息素的增效作用及其机制[102]。二是抑制昆虫信息素的效果，如(*E*)-2-hexenol、(*Z*)-2-hexenol和(*Z*)-3-hexenol等对云杉八齿小蠹、黑山松大小蠹、红松齿小蠹(*Conophthorus resinosae*)、中穴星坑小蠹(*Pityogenes chalcographus*)等昆虫的信息素具有强烈的干扰或抑制作用，显著减少诱捕数量[73,75,103-107]。

3.2.3 干扰昆虫取食、繁殖和趋光行为 GLV可影响烟蚜等昆虫的取食行为[92,108-109]，而叶片中的GLV本身具有毒性，可干扰昆虫的繁殖行为[110]。GLV还可干扰昆虫的趋光行为，如1龄棉铃虫幼虫取食菜豆(*Pisum sativum*)时释放的(*Z*)-3-hexenyl acetate能降低棉铃虫幼虫对蓝光的趋向率，扰乱了幼虫的趋光行为，从而间接地影响了其他幼虫对食物的定位和取食损害[111-112]。水稻的挥发物和其他一些因素可共同造成稻纵卷叶螟(*Cnaphalocrocis medialis* Guenee)的1龄幼虫趋光性的逆转（即避光性）[113]。还有学者认为植物挥发物对昆虫活动的影响甚至大于光照的影响[114]。

3.2.4 招引寄生蜂 大量文献表明，寄生蜂更倾向于选择植食性昆虫为害的植株（表2）。GLV是植物—天敌的互益素，它能为寄生蜂提供可靠的化学信号，并显著提高寄生蜂对寄主的搜寻能力，帮助寄生蜂能在广大而复杂的生境中找到隐蔽、分散的寄主，从而实现间接防御[27,115-117]。有趣的是植物也会利用“谎报军情”(cry wolf)的策略，即植物在受到轻微损伤时也能释放较多的HIPVs，在植食性昆虫聚集为害之前就把天敌昆虫

表2 绿叶挥发物招引寄生蜂

植物	植食性昆虫	寄生蜂	绿叶挥发物的种类	参考文献
茶树 *Camellia sinensis*	茶尺蠖 *Ectropis obliqua*	单白绵绒茧蜂 *Apanteles* sp.	*n*-hexanal、(*Z*)-3-hexenol、(*E*)-2-hexenal	[119]
		茶尺蠖绒茧蜂 *Apanteles* sp.	(*Z*)-3-hexenyl acetate、(*E*)-2-hexenal	[120]
桑树 *Morus alba*	桑天牛 *Apripona germari*	桑天牛长尾啮小蜂 *Aprostocetus fukutai*	(*Z*)-3-hexenyl acetate	[121]
四季豆 *Phaseolus vulgaris*	三叶草斑潜蝇 *Liriomyza trifolii*	豌豆潜叶姬小蜂 *Diglyphus isaea*	(*Z*)-3-hexenol等	[122]
	温室粉虱 *Trialeurodes vaporariorum*	丽蚜小蜂 *Encarsia Formosa*	(*Z*)-hexen-3-ol、3-octanone和4,8-dimethyl-1,3,7-nonatriene的混合物	[116]
甘蓝 *Brassica oleracea*	菜青虫 *Pieris rapae* 和小菜蛾 *Plutella xylostella*	菜粉蝶盘绒茧蜂 *Cotesia glomerata* 和菜蛾盘绒茧蜂 *C. vestalis*	(*Z*)-3-hexenyl acetate、α-pinene等	[118]
大豆 *Glycine max* (L.) Merr.	棉蚜 *Aphis craccivora* Koch、麦长管蚜 *Macrosiphum avenae* (Fabricius)和大豆蚜 *Aphis glycines* Matsumura	燕麦蚜茧蜂 *Aphidius picipes* Nees和豆柄瘤蚜茧蜂 *Lysiphlebus fabarum* Marshall	(*Z*)-3-hexenol、(*Z*)-hexen-3-yl acetate、(*E*)-2-hexenal和indole的混合物	[123]
		缢管蚜茧蜂 *Aphidius rhopalosiphi* 和缘腹绒茧蜂 *Cotesia marginiventris*	(*Z*)-3-hexenyl acetate、(*Z*)-3-hexenol、(*E*)-2-hexenal	[124]

续表2

植物	植食性昆虫	寄生蜂	绿叶挥发物的种类	参考文献
拟南芥 *Arabidopsis* sp.	粉蝶 Pieridae sp.	菜碟绒茧蜂 *Cotesia glomerata*	(*E*)-2-hexenal、(*Z*)-3-hexenyl acetate	[125]
玉米 *Zea mays*	美洲棉铃虫 *Heliothis zea* (Boddie)	红足侧沟茧蜂 *Microplitis croceipes*	(E)-2-hexenyl acetate、(*Z*)-3-hexenyl acetate、(*E*)-2-hexenol、(*Z*)-3-hexenol、*n*-hexanal、(*E*)-2-hexenal	[126]
烟草 *Nicotiana tabacum*	棉铃虫 *Helicoverpa armigera* (Hübner)	中红侧沟茧蜂 *Micropliti mediator* (Haliday)	*n*-hexanal、(*Z*)-3-hexenyl acetate	[127]
		棉铃虫齿唇姬蜂 *Campoletis chlorideae*	(*E*)-2-hexenol、(*E*)-2-hexenal	[128]

吸引到植株上[118]。

3.3 绿叶挥发物能影响病原微生物生长

绿叶挥发物可启动植物防御体系，影响病原微生物的生长。如花生(*Arachis hypogaea*)释放的(*E*)-2-hexenal能抑制曲霉菌生长[129]。虫害诱导水稻释放的(*E*)-2-hexenal、(*Z*)-3-hexenol、(*E*)-2-hexenol可抑制稻瘟病菌(*Pyricularia grisea* Sacc.)和水稻纹枯病菌(*Rhizoctonia solani* Kuhn.)的生长[6]。此外，根际细菌(plant growth-promoting rhizobacteria)释放挥发物能引发拟南芥(*Arabidopsis thaliana*)系统性防御反应[130-131]。(*E*)-2-hexenal、(*Z*)-3-hexenal和(*Z*)-3-hexenol和Ocimene能提高拟南芥对灰霉病菌(*Botrytis cinerea*)的抵抗能力[125]。锈菌[*Uromyces fabae* (Pers.) Schroet.]能刺激蚕豆释放挥发物，其中Hexenyl acetate等物质能促进植物吸器的生长[132]。

4 田间研究现状

迄今有关在田间成功诱集到天敌的研究报道涵盖了棉花、玉米、蜀黍和苹果等作物[133-136](表3)。人工合成引诱剂中的广谱性HIPVs组分(如MeSA)能吸引多种捕食性昆虫和少数寄生蜂，而一般认为因GLV具有相对较低的扩散性，容易成为高浓度的气团在气流作用下传播[137]，自然界中植物之间有效交流距离不足10 cm，植物吸引天敌的有效距离要大于10 cm[138]，经O_3降解后的GLV和一些萜类对菜蛾盘绒茧蜂(*Cotesia vestalis*)失去引诱作用[139]。所以GLV更可能是寄生蜂用于远距离定位寄主栖境的化学信号，至少能指示寄主可能存在的生境[126]。GLV能吸引广谱性寄生蜂，而对专性寄生蜂则没有作用[140]，即寄生蜂的寄主范围之宽狭可能影响寄生蜂定位行为，专性寄生蜂可能对植物或寄主信息化合物中的某种特异性物质数量变化更敏感，并以此作为高度可信的信息。寄生蜂还能利用除GLV以外的特异性挥发物来定位寄主，GLV和其他物质混合后往往比GLV单一组分对寄生蜂的吸引作用更强，有学者认为GLV与背景气味难以区分，为周围生境中的植物所共有，没有特异性，吸引力弱[141]。这可能是因为GLV是挥发性较低的挥发物，其释放与昆虫取食和其他损伤因素有关，而萜烯类挥发物的释放则更多地与昆虫取食有关，就这一点而言，特异性的萜烯类挥发物对于寄生蜂的精确定位可能更为有利[22,93]。

表3 在田间利用人工合成引诱剂成功引诱天敌昆虫

植物	天敌昆虫	人工合成引诱剂的主要成分	参考文献
棉花 *Gossypium* sp.	瓢虫 *Coccinella septempunctata*	(*Z*)-3-hexenyl acetate	[133,134]
	草间小黑蛛 *Erigonidium graminicolum*	(*Z*)-3-hexenyl acetate等	
	花蝽 *Orius similis*	(*Z*)-3-hexenyl acetate、(*Z*)-3-hexen-1-ol等	
	食蚜蝇 *Paragus quadrifasciatus*	(*Z*)-3-hexen-1-ol等	
	缨小蜂 *Anaphes iole*	(Z)-3-hexenyl acetate等	
玉米 *Zea mays* 蜀黍 *Sorghum bicolor*	大螟盘绒茧蜂 *Cotesia sesamiae*	(*E*)-2-hexenal、(*Z*)-3-hexenol、(*Z*)-3-hexenyl acetate等	[135,142]
苹果 *Malus pumila*	三种草蛉 *Chrysopa nigricornis*、*Chrysopa oculata*、*Chrysoperla plorabunda*	(*Z*)-3-hexenyl acetate、(*Z*)-3-hexen-1-ol等	[136]

笔者认为GLV是背景气味的重要组分。背景气味是指除了资源指示型气味(resource-indicating odor)之外的挥发物，而背景气味中包括了很多背景噪音(background noise)，一般认为背景噪音会影响寄生蜂对寄主信号的感知，干扰其定位行为[143]。GLV是背景气味的主要组分，背景气味不仅暗示着觅食者可能存在的食物源，而且还能使植物、寄主昆虫或捕食者等信

息隐藏在背景气味中,即资源指示型气味可嵌入背景气味之中。背景气味会对资源指示型气味产生的截然不同的效应,可能是由背景气味单一或多种组分引起的,在自然界背景气味与资源指示型气味有3种关系:(1)背景气味与资源指示型气味互无影响,因为昆虫的嗅觉系统不能识别和接收背景气味组分,或者已经完全适应了背景气味,这两种情况下背景气味对资源指示型气味没有影响;(2)背景气味对资源指示型气味的掩盖效应。当寄主植物和非寄主植物的气味混合在一起时,寄蝇(*Drino bohemica*)幼虫对寄主植物的气味即不再有吸引力,又如,在增加了(*E*)-3-hexenol这种组分后,未损伤的马铃薯植株对马铃薯叶甲不再有吸引力[144],这说明(*E*)-3-hexenol可扰乱HIPVs组分的比率;(3)背景气味对资源指示型气味的增强效应。倍半萜类(-)-germacrene能提高未损伤的烟草对烟草夜蛾的吸引力,又如当背景气味中混有甘蔗的气味时,就可提高棕榈象甲(*Rhynchophorus palmarum*)对聚集信息素(资源指示型气味)的响应能力,这种增强效应可能会使昆虫定位寄主的镜像变得更加清晰(Sharpen the view)[117]。对背景气味的研究多集中在前述的植食性昆虫能区分寄主植物与非寄主植物方面,而有关寄生蜂寄主定位方面的研究较少。如松树叶蜂产卵诱导的松树HIPVs组分中含有很高比例的(*E*)-*β*-farnesene,能够吸引一种卵期寄生蜂(*Chrysonotomyia ruforum*)[145],但(*E*)-*β*-farnesene单组分却不吸引该寄生蜂,只有与未被诱导的松树气味混合时才能引起寄生蜂的正趋性,所以,(*E*)-*β*-farnesene的数量变化可作为特定环境中该寄生蜂定位叶蜂的可靠线索[146],由此可知,功能性HIPVs与背景气味的对比线索(contrast cues)在寄生蜂的寄主定位过程也具有重要作用,寄生蜂在背景气味下能做出正确选择。

为此,有学者提出了"嗅觉对比假说"(olfactory contrast hypothesis)来解释寄生蜂如何在复杂环境中辨识和精确地定位寄主[147]。在背景气味复杂组分中,各组分之间也能相互影响,单组分浓度的变化可能积极或消极地影响寄生蜂所感知其他组分,从而提高或降低了信号线索的对比性。一般地,低浓度组分具有低检测性,高浓度组分具有高检测性[115],但一种信息化合物组分与其他组分的对比性效果可能更重要,所以,当资源指示型气味与背景气味具有明显的对比性时,即使是少量的资源指示型气味也仍然具有高检测性,而那些具有高浓度的、但与背景气味对比性不明显的的信息化合物可能很难被寄生蜂检测到。如斑潜蝇的寄主和非寄主植物受伤后几乎都能释放(*Z*)-3-hexenol,而且寄生蜂对该物质表现出最为明显的趋性,说明(*Z*)-3-hexenol对寄生蜂初期定位寄主起到了关键作用[148]。人工合成引诱剂中的GLV起着背景气味的作用,具有提高天敌昆虫搜索效率的作用。所以,向背景气味中适当地添加资源指示型气味可作为提高天敌昆虫引诱力的手段之一。

此外,经历和学习对寄生蜂选择行为的影响已成为人们的共识。引诱寄生蜂的功能性HIPVs须同时具备可检测性和可靠性的特点,这样寄生蜂就能将与寄主有关的资源指示型气味或其对寄主的寄生经历联系起来,从而提高寄生率。另外寄生蜂成虫的行为还与其幼虫期发育所在的寄主有关,幼虫期经历可影响成虫期行为[149],所以推测可能是幼虫的化学经历通过蛹期传递到成虫,并影响成虫对化学物质的反应,这一推论即"Hopkins寄主选择原理"[150]。后来证实,幼虫微栖境的化学信息物质残留在蛹壳内外,成虫羽化后首先即接触这些由幼虫栖境遗留的化学信号,这种短暂的经历对其随后的行为产生影响,即幼虫期的学习实际上是成虫早期的学习(early adult learning)[149]。除此,寄生蜂自身营养、交配状态和卵的发育、植物和寄主昆虫的适合性、与竞争者的关系,这些因素都会影响寄生蜂(特别是没有产卵经历的寄生蜂)的行为。

5 展望

多数研究是在实验室条件下完成的,绿叶挥发物引诱天敌的效果很明显,在田间条件下寄生蜂行为受到背景气味、气象条件、害虫种群分布和数量等众多因素的影响,重演性较差,很难达到理想的生物防治效果。在田间利用HIPVs的间接防御功能对植食性昆虫种群的化学生态调控之前,仍需对植食性昆虫与天敌的化学遗传学、生态学、不同植物—植食性昆虫—天敌三重营养间的互作关系,以及不同植食性昆虫虫口密度对田间防效的影响等诸多方面进行深入研究,以明确HIPVs中关键物质的多重生态功能,并确定HIPVs的田间应用技术。

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（上接第4页）
较好,但该品种为典型的短日照品种,在日照时间渐长的春季结薯不理想。

‘大西洋’品种能很好的满足炸片加工对马铃薯品种的总体要求,如生育期适中,产量及其他经济性状稳定;薯形规则,表皮光滑,芽眼少浅;薯块对光不敏感,皮白色、薯肉白色或淡黄色,还原糖含量低,食味品质中等以上。这与前人对‘大西洋’品质的研究结果基本一致[3,5],并充分说明‘大西洋’品种依然是各地炸片专用马铃薯种植的最佳选择,该品种既适宜北方一季作区种植,又可为南方冬春混作区种植,适用范围较其他品种更加广泛。本试验对不同炸片马铃薯品种的各方面品质进行比较,清晰地展示了不同品种的特性也差异,为炸片马铃薯的种植提供更多的选择依据。

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