田间背景气味对植物源引诱剂的干扰及相应研发策略

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摘要：植物挥发物在害虫的寄主选择过程中发挥着重要作用。植物源引诱剂是一类重要的害虫绿色防控产品，也是目前害虫无害化防治的研究热点。但目前大多数研究还未达到田间可应用的程度。其主要原因是田间引诱效率不理想。已有研究显示田间背景气味可干扰昆虫的嗅觉定向，干扰植物源引诱剂的引诱效率。因此对以往忽略的田间背景气味干扰加以重视，可进一步加快植物源引诱剂的研发进程。本文从气味传播与昆虫嗅觉感知、背景气味干扰嗅觉定向、田间背景气味复杂性和其对引诱剂的干扰等方面进行了综述与探讨，并对引诱剂配方组配过程中如何降低田间背景气味的干扰提出了相应的研发策略，以期促进植物源引诱剂的创新发展。

关　键　词：植物挥发物；植物源引诱剂；嗅觉定向；背景气味；干扰
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Interference of Field Background Odor with Plant Volatile-based Attractants and Coping Strategies

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Abstract: Plant volatiles are the key information for host-plant selection by herbivorous pests. The attractants based on plant volatiles can function as an important technique for pest control, and is one of the research focuses in green control techniques. But most related researches have not reached the stage of field application. The main reason is that the attractive efficiency was unsatisfactory in field. Some research has shown that field background odor could disturb the olfactory orientation of insect and impair the pest attractiveness of plant volatile-based attractants. Therefore, close attention to the previously-ignored interference of field background odor could speed up the development process of plant volatile-based attractants. In this paper, odor transportation, insect olfactory perception, the interference of background odor with insect olfactory orientation, and the complexity of field background odor and its interference with attractants were summarized and discussed, and coping strategies were suggested to reduce the interference of field background odor in the process of attractant development. The review is expected to promote the innovative development of attractants for crop insect pests.
Key words: plant volatiles; attractant; olfactory location; background odor; interference

为了生存繁衍，害虫要取食植物的茎、叶、花、果实、花蜜等。在食物选择过程中，昆虫嗅觉起着主导作用，也就是说害虫可通过植物挥发物进行食物选择[1-3]。而植物挥发物是植物的化学语言，是多种挥发性物质的混合物，具有丰富的多样性[4,5]。目前已从 90 多种植物的挥发物中鉴定出 1700 余种物质，包括脂肪酸衍生物、萜烯类化合物、苯类化合物等[6,7]。植物挥发物的定性、定量组成与植物的种类、品种、生理阶段、器

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官、生长环境以及各种生物、非生物胁迫等密切相关[8,9]。这样植食性昆虫就可根据植物挥发物的定性、定量组成，寻找到喜好的食物。大量研究表明，尽管某种植物挥发物中可包含几十至上百种组分，但其中可被植食性昆虫利用的信息物质通常不到十种，且其组成、相对比例甚至释放量均可对植食性昆虫的食物选择产生较大影响[10-12]。

人们越来越深刻地认识到化学农药对生态环境、食品安全造成的严重威胁，寻求无害化的害虫防控技术成为了大家关注的焦点。植物挥发物对调节植物-害虫间的关系以及害虫种群的消长起着重要作用。利用植物挥发物发展害虫引诱剂和无害化防治技术，已是当前植保领域的研究热点。目前植物源引诱剂已在实蝇类、夜蛾类、蓟马类、甲虫类等害虫的监测与防治中发挥了重要作用[13]。但目前大量相关研究仍止步于室内研究或田间初试阶段。田间试验和应用经验表明，田间背景气味可降低甚至极大降低引诱剂的诱虫效率，阻碍了植物源引诱剂的发展。目前“背景”干扰动物视觉、听觉、嗅觉等感官的信息感知，已被公认[14-17]。特别是听觉方面的研究进行的尤为深入。这种干扰的造成主要包括两方面，背景噪音修改了听觉信息[18,19]、背景噪音影响了接受者对听觉信息的接收[20]。但有关背景气味干扰嗅觉感知的研究还相对匮乏。深入研究昆虫在复杂背景气味中的嗅觉定向，不仅有助于了解自然条件下的化学通讯机制，也有助于研发高效害虫引诱剂，为绿色防控提供重要技术支撑。本文从气味传播与昆虫嗅觉感知、背景气味干扰嗅觉定向、田间背景气味复杂性和其对引诱剂的干扰等方面对已有的研究进行了综述和探讨，并对引诱剂配方组配过程中如何降低田间背景气味的干扰提出了相应的研发策略。

1　气味传播与昆虫嗅觉感知

研究背景气味对昆虫嗅觉定向的干扰，首先要弄清楚气味是如何传播的。气味在大气中的传播有两种方式。即主动的分子扩散和被动的随气流传播。由于分子扩散是气味分子在浓度差异推动下的无规则热运动，其传播速度和传播距离非常有限。因此，气味主要是借助气流以羽流形式进行传播。即从味源释放后，气味被气流吹散形成气羽丝[7,21,22]。气羽丝被无味的空气分隔，以斑块状散布。由于气味传播的这一特性，空间中某一点的气味浓度瞬间变化可达几个数量级[22,23]。气味羽流的结构主要与 2 个因素有关，即味源特征与气流特征。气味羽流的形状、大小等与味源特征密切相关。如一只雌蛾释放性信息素的部位仅有几十个平方微米，而一片盛开的油菜花地，花香释放面积可达上百平方米，它们的羽流结构完全不一样。研究表明，性信息素、单株植物或某一植物器官的挥发物释放后，随气流在空气中形成纤细、蜿蜒曲折的气味羽流，而对于大片田地的气味羽流还缺乏研究[24]。气流方面，羽流结构主要由环境湍流决定。受地表障碍物、地表粗糙度以及空气温、湿度等因素的影响，风在近地表处可形成复杂、无规则的湍流[21]。因此，气味的羽流结构是复杂、随时变化的。气味羽流结构通常以气羽丝的间歇性、间距和大小进行描述。气流湍动程度越高，气羽丝间歇性越强；同时气羽丝的间距、大小可随传播距离增加而增大[7,25,26]。湍流对气羽丝不断地稀释、混合，进而导致气味浓度降低、气味发生改变[10,23,26]。研究显示，气味浓度随传播距离增加而减弱，通常浓度变化与传播距离的平方成反比[21]；由于混入临近灌木挥发物，曼陀罗花香的组成可随传播距离增加而发生变化[27]。

昆虫的嗅觉感知是一个基于嗅觉神经元冲动，在触角叶、前脑等多个层面上的感觉信息整合过程[28]。昆虫嗅觉感器中的气味受体在嗅觉识别过程中发挥关键作用，负责引起嗅觉神经元的电位反应，将化学信号转化为电生理信号，并传递至触角叶和中枢神经系统[29]（图 1）。昆虫具备多个嗅觉受体，可与不同的化合物结合。嗅觉受体的专一性和灵敏性与其化合物结合谱有关；结合谱越宽，激活受体所需的气味浓度就越高[30]。通常性信息素气味受体的结合谱窄、灵敏度高，而其他气味受体的结合谱较宽。多个气味受体对某一气味多个组分的组合编码，保证了昆虫感知的气味数量远超气味受体类型数目[31]。由于湍流的原因，气味在时间和空间上均具有高度的变化，这就要求昆虫的嗅觉在时空也要具有极高的灵敏度、分辨率和快速响应机制。已有研究表明，雄蛾可辨别在空间上分隔 1 mm、时间上分隔 1 ms 的性信息素气羽丝[7]；接触气味后 3 ms 内，果蝇嗅觉神经元即可做出响应，70～85 ms 内可做出行为反应[32,33]。同时昆虫还能通过扇动翅膀、转动触角和身体等，增加与气羽丝的接触[34,35]。这就保证了昆虫能够追寻随风飘散的“化学踪迹”进行高效、精准的嗅觉定向[7,23,36]。研究表明：雄蛾可在几百米远的地方，沿着性信息素气味羽流定位雌蛾[37,38]；棉铃虫 *Helicoverpa zea*、蜜蜂等昆虫的嗅觉可辨别相距仅几毫米的不同味源[39,40]。

2 背景气味干扰嗅觉定向

背景气味是指昆虫嗅觉定向过程中，除目标气味外遇到的其他所有气味[15]。背景气味对昆虫嗅觉定向的影响可分为 3 个方面，即干扰、增强、无作用[15]。增效方面的研究显示：虫害诱导植物挥发物、寄主植物挥发物等背景气味可作为生境信息或补充信息，提高寄生性、捕食性天敌的寄主定位准确率[41-44]，提高求偶雄蛾对雌蛾定位的准确率[45-49]，以及提高聚集信息素的聚集效果[50,51]。但这些不是本文的分析重点，不再详细展开。

背景气味可干扰昆虫种内信息的识别[17]，特别是有关植物挥发物干扰性信息素感知的研究进行的较为深入。通常昆虫性信息素嗅觉受体较为专一，但某些植物挥发物可直接激活或减少它们对性信息素的响应，这可能与嗅觉受体的竞争性结合有关。庚醛、芳樟醇等植物挥发物可显著抑制、延迟小地老虎 *Agrotis ipsilon* 嗅觉神经元和扩大型嗅小球复合体对性信息素脉冲气流的响应，抑制程度与挥发物种类、浓度密切相关。虽然这些背景气味并未显著影响小地老虎雄蛾对雌蛾的定位成功率，但显著延长了小地老虎的起飞时间[52]。对斜纹夜蛾 *Spodoptera litura* 的研究显示，芳樟醇、香叶醇、乙酸香叶酯、(*E*)−4,8−二甲基−1,3,7−壬三烯（DMNT）和乙酸芳樟酯等植物挥发物构成的背景气味，降低、延缓嗅觉神经元对性信息素的响应或影响嗅觉神经元的编码质量及响应重现性，进而明显降低斜纹夜蛾定向性信息素味源的起飞率、移动速度、行为轨迹直线度和定位成功率[53-59]。同时研究显示，背景气味浓度越高，嗅觉神经元感知性信息素的敏感性就越低，对性信息素味源定向行为的干扰程度就越大[60,61]。

背景气味也可影响昆虫对寄主植物的嗅觉定向。在烟芽夜蛾 *Heliothis virescens* 危害的棉花、大豆间，红足侧沟茧蜂 *Microplitis croceipes* 未展现出明显的趋向性。但当以烟芽夜蛾危害的棉花挥发物作为背景气味时，红足侧沟茧蜂明显趋向被害的大豆植株，反之亦然[62]。这一结果表明背景气味可影响寄生蜂的寄主选择，并支持了“嗅觉信息反差”假说。即相对背景气味，嗅觉信号的特异性越大，越容易被感知[63]。由于影响了嗅觉神经兴奋与抑制间的平衡，曼陀罗花香主要成分“苯甲醛”、曼陀罗花香近似气味“芳香灌木挥发物”或苯甲醛类似物“甲苯”、“二甲苯”等构成的背景气味，均可显著抑制烟草天蛾 *Manduca sexta* 嗅觉神经对曼陀罗花香的响应，并显著降低烟草天蛾向曼陀罗花的逆风直线飞行能力[27]。罗勒、薰衣草挥发物构成的背景气味，可分别显著干扰其挥发物主要成分丁子香酚、芳樟醇对西花蓟马 *Frankliniella occidentalis* 的吸引[64]。与嗅觉信息化学结构不相似的背景气味，也可干扰昆虫嗅觉定向。这种干扰有可能是背景气味抑制了昆虫对嗅觉信息的感知，也有可能是具驱避活性的气味引起，又或是背景气味改变了嗅觉信息中关键组分的比例。如 DMNT 可抑制斜纹夜蛾对引诱性化合物(*Z*)−3−己烯醋酸的嗅觉感知[57]；具驱避活性的非寄主挥发物可降低寄主挥发物对油菜花露尾甲 *Meligethes aeneus* 的引诱活性[65]；具驱避活性的 DMNT、(*E*, *E*)−4,8,12−三甲基−1,3,7,11−十三碳四烯（TMTT）可降低九里香、柑橘等寄主挥发物对柑橘木虱 *Diaphorina citri* 的吸引[66]；非驱避性的香菜挥发物可降低番茄挥发物对烟粉虱 *Bemisia tabaci* 的吸引[67]；与无引诱活性的榆树挥发物或(*Z*)−3−己烯醋酸酯混合后，叶甲 *Xanthogaleruca luteola* 危害诱导的榆树挥发物或其关键组分(*E*)−*β*−石竹烯对寄生蜂 *Oomyzus gallerucae* 的引诱活性明显降低[68]。此外有研究显示，果蝇嗅觉系统适应了背景气味后，背景气味仍可干扰果蝇嗅觉定向。这是因为果蝇感知植物挥发物的最低浓度被提高，进而缩短了追踪气味羽流进行嗅觉定位的最远距离[69]。

但上述研究均是在室内可控条件下，通过人工模拟气味进行的。其中的背景气味要么是某种物质，要么来源于某种植物材料，其复杂程度以及气流的湍动程度均要比自然条件下简单，同时气味的浓度也要比田间高。因此这些结果并不能反应田间真实情况。但通过上述研究可以看出，背景气味能够干扰昆虫嗅觉定向。这种干扰要么是由于背景气味与嗅觉信息进行了混合改变了嗅觉信息组成，要么是由于昆虫对背景气味的感知影响了对嗅觉信息的感知，又或两者兼有之。这与背景噪音干扰听觉信息感知相类似。

3 田间复杂背景气味对植物源引诱剂的干扰

田间气味来源是多样的。这些气味包括植物释放的挥发物，昆虫、动物及其排泄物释放的气味以及施肥、打药、工厂、汽车等各种人为活动产生的气味。受种类、品种、生育期、部位以及各种胁迫等的影响，植物挥发物可发生巨大变化[5,70-72]，而且释放后挥发物并不均是稳定存在，有些挥发物可被大气中的臭氧、硝酸根、羟基等快速氧化降解[73,74]。同时，动物、人类产生的某些挥发物也可引起昆虫的嗅觉感知，如苯甲醛、甲苯、氨

类化合物[13,27]。这就导致了影响昆虫嗅觉定向的田间背景气味的组成非常复杂，并且在温度、光照、季节等外部环境的影响下，田间背景气味还随时间发生巨大变化[75,76]。如气温较低的秋冬季或干旱的季节，植物挥发物释放量较低，此时田间背景气味较为简单[77,78]。在光照、温度的作用下，白天植物释放的挥发物较为丰富、释放量也较大[21]。但由于白天气流的湍动程度远大于夜间，因此夜间田间背景气味的浓度较白天高且稳定[79]。田间背景气味是复杂且变化的，可将整片田地的气味环境想象成一个活动的“舞台布景”。处于其中的昆虫，要么稳定地呆在一点，要么循着更喜好的气味，向另一点移动。

田间背景气味的浓度大约在 ppb-ppt 级别[7,80,81]。这些低浓度、种类丰富的背景气味物质，如何影响昆虫的嗅觉定向，目前还不甚了解。但是已有的大量事例证明，田间背景气味可干扰昆虫的嗅觉定向。如生境中植物种类越复杂，寄生蜂的寄生率越低[82]；田间人为大量释放昆虫性信息素或其主要组分，可干扰求偶雄虫对雌虫的定位[83]。同样田间背景气味可以干扰植物源引诱剂对靶标害虫的吸引。如当田间施用粪肥后，蛋白质诱饵对地中海实蝇 *Ceratitis capitata* 的引诱效果明显下降[84]。这是由于动物粪便、蛋白质诱饵均可大量释放对实蝇具有引诱活性的氨。玉米吐丝期可大量释放苯丙素类化合物，而这一时期丁子香酚、肉桂醇、4−甲氧基苯乙醇等物质对北方玉米根萤叶甲 *Diabrotica virgifera virgifera* 的引诱活性最弱[85]。梨成熟期大量释放对苹果蠹蛾 *Cydia pomonella* 具有引诱活性的梨酯，而此时含梨酯的引诱剂对苹果蠹蛾的诱集效果并不理想[86]。目前背景气味干扰已在引诱剂的田间验证试验中被逐步考虑[87-90]。下面通过 3 个植物源引诱剂的研发过程，来说明田间背景气味对引诱剂的干扰。

斑翅果蝇 *Drosophila suzukii* 是欧美浆果产业的重要害虫。2012 年发现酒、醋混合液对斑翅果蝇具良好的引诱效果，其中米醋与梅洛葡萄酒混合液效果最好[91]。在此基础上，通过向基本配方（乙酸、乙醇的混合物）中添加其他嗅觉电生理活性物质，展开了一系列配方研制试验，并最终形成了含乙酸、乙醇、乙偶姻、甲硫醇等 4 种物质的引诱剂产品[92-95]。该引诱剂的诱蝇效果甚至好于酒、醋混合液，并具较强的靶标专一性。但研究起始阶段进展并不顺利，主要原因是室内二项行为选择结果与田间诱捕效果相矛盾[96]，室内研究不能为引诱剂配方研制提供有效信息。如室内研究显示，基本配方添加甲硫醇后，引诱活性无显著变化；添加乳酸乙酯、乙酸−2−甲基丁酯或乙酸乙酯后，具驱避活性[92]。但田间诱捕试验显示，甲硫醇、乳酸乙酯均对基本配方有显著的增效作用；乙酸乙酯、乙酸−2−甲基丁酯对基本配方的引诱活性几乎无影响[93]。作者认为造成这一矛盾的主要原因是相对田间气味环境，室内二项行为测定的气味环境过于简单，而田间复杂的气味环境会影响斑翅果蝇对引诱剂的嗅觉响应。为了在室内制造复杂的气味环境，2018 年作者在生测装置中同时放置了 10 余种的味源，其结果与田间诱捕试验相一致，证明了之前的猜测。

茶小绿叶蝉 *Empoasca onukii* 是我国茶树首要害虫。相较于茶树，茶小绿叶蝉更喜欢桃树和葡萄藤挥发物[97]。基于桃树和葡萄藤挥发物组配出 2 个引诱剂配方，分别为 F−P（桃树）、F−G（葡萄藤）。F−P 中，苯甲醛是关键物质；F−G 中，苯甲酸乙酯是关键物质。这两种物质仅能被茶树少量释放或不释放。室内生测显示，F−P、F−G 对茶小绿叶蝉的引诱活性相似，且均强于茶树挥发物。但与 F−G 不同，F−P 在茶园对茶小绿叶蝉几乎无引诱活性。茶园背景气味测定显示：茶园背景气味中含 10 余种植物挥发物，其中苯甲醛出现最稳定且检出浓度最高，约为 3 ng/L，是其余物质的上百倍[81,98]。进一步研究显示，苯甲醛在茶园空气中的浓度对茶小绿叶蝉具引诱活性，且当 F−P 气味中的苯甲醛浓度小于单独苯甲醛气味的 20 倍时，苯甲醛即可显著干扰 F−P[98]。因此，茶园背景气味中高浓度的苯甲醛与 F−P 中关键组分重叠，是引诱剂 F−P 在田间对茶小绿叶蝉无引诱效果的主要原因。

苹果果蛾 *Argyresthia conjugella* 是挪威、瑞典等国苹果园的主要害虫，其植物源引诱剂的研究从 2006 年开始。当时基于偏好寄主花楸挥发物，组配出含苯乙醇、(*E*)−茴香脑的二元引诱剂配方[99]。但在苹果园中，此引诱剂对苹果果蛾未展现出良好的引诱活性，与室内行为研究结果相矛盾。近十年后，研究者考虑了田间背景气味干扰的因素，重新提出了一个基于花楸挥发物的七元引诱剂配方，包含苯乙醇、(*E*)−茴香脑、p−茴香醛、癸醛、水杨酸甲酯、(*Z*)−3−己烯−2−甲基−丁酸甲酯、(*Z*)−茉莉酮等物质。洁净空气中，该配方对苹果果蛾的引诱活性与原先的二元引诱剂配方相当，但在苹果园中，其诱蛾效果可达二元引诱剂配方的 3 倍多[100]。室内的进一步研究显示，苹果、梨或云杉等植物的挥发物对七元引诱剂有不同程度的干扰。其中，苹果、梨挥发物的干扰程度较大，而云杉挥发物干扰较小。挥发物分析发现，苹果与花楸的混合挥发物、梨与花楸的混合挥发物中，

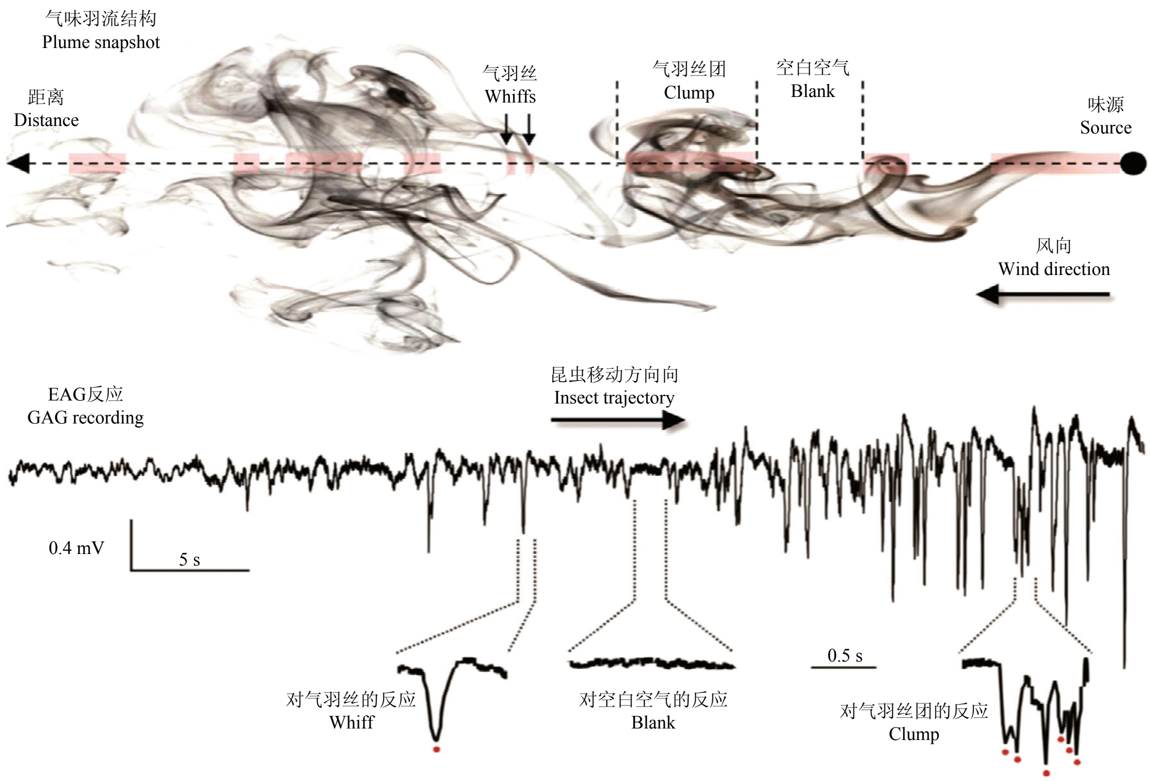
具嗅觉电生理活性的(*Z*)−3−己烯醋酸酯、DMNT 所占比例显著高于云杉与花楸的混合挥发物[101]。这一系列的研究显示，背景气味中具嗅觉电生理活性但非引诱剂组分的物质可干扰引诱剂对靶标害虫的吸引。

4 植物源引诱剂研发过程中田间背景气味干扰的应对策略

综上，田间背景气味能够干扰引诱剂的引诱效果，很大程度上延缓、甚至阻碍了相关研究走向田间应用。如果我们对以往忽略的田间背景气味干扰加以重视，在研发过程中采取相应的应对策略，可进一步加快植物源引诱剂的研发过程，使其在害虫绿色防控中发挥更大的作用。综合上面的研究，我们可在研发过程中通过以下三方面来降低或避免田间背景气味对引诱剂的干扰。即注重在复杂背景气味中进行引诱剂的配方组配、注重对田间背景气味的分析、利用非主栽作物或多种植物挥发物研制引诱剂。

4.1 注重在复杂背景气味中进行引诱剂的配方组配

“成本最优”是配方研制过程中的基本原则，因此在保证引诱活性的前提下，配方组分数会尽可能的少。但在该原则下，室内洁净气味中得到的“最优配方”往往丢失了某些看似不重要的物质。但是它们有可能在抵抗田间背景气味干扰中发挥着重要作用。因此在复杂气味环境中，进行引诱剂的配方研制是十分必要的。对于动态空气中进行的昆虫行为选择测定，可在待测味源的逆风向上方增加一个味源，或直接采集田间空气，作为背景气味[100,102]。如风洞中，在测试味源上方安置一个多孔金属板，金属板后方放置植物材料。植物挥发物随气流经过多孔板后，就在风洞内形成了一个均匀分布的背景气味，同时不影响风洞内测试味源的气味羽流结构[100]。对于静态空气中进行的行为测定，可通过增加味源数量，来增强测试环境的气味复杂性。如斑翅果蝇引诱剂研发成功后，作者建立了一套可同时测定至少 10 个味源的多选择测定装置。该装置内的气味环境远比二项行为选择系统复杂。作者估计，若利用该装置，斑翅果蝇食诱剂的研发时间可由 2 年缩短至 1 周。虽然该装置简单易操作，但适合用于引诱剂基底物质，如乙酸、乙醇、铵盐，已确认的引诱剂配方研制。



注：EAG，昆虫触角电位；红点表示单个电生理反应。

Note: EAG, electroantennogram; Red dots, single detection events.

图 1 气味羽流的模拟结构和昆虫追寻气味羽流进行嗅觉定位的触角电生理反应变化[21]

Fig. 1 Simulation structure of odor plume and variation about electroantennogram response of insect tracking the odor plume[21]

4.2　注重对田间背景气味的分析

注重对田间背景气味的分析可尽早发现田间背景气味中是否存在与引诱剂重要组分相同或相似的物质，提早判断田间背景气味对配方的干扰程度，避免由此产生的无效工作，提高研发效率。由于田间背景气味来源复杂，主栽作物挥发物并不能代表田间背景气味。如前文所述的茶小绿叶蝉引诱剂 F−P，其关键组分苯甲醛，仅能被茶树少量释放，但茶园背景气味中却检测出了高浓度的苯甲醛。因此在引诱剂研制过程中，对田间背景气味进行分析十分必要。但由于组成复杂、浓度低，田间背景气味测定的技术难度较大，无论质子转移反应质谱、光离子化检测器、激光吸收光谱还是生物检测器，都无法同时在灵敏度、物质鉴定上满足要求。2015 年笔者利用热解析气质联用仪建立了一套田间背景气味的测定方法[81]，由于避免了溶剂洗脱对样品的稀释，其灵敏度可达 ppt 级，同时还可通过质谱仪进行准确的物质确认。

4.3　利用非主栽作物或多种植物挥发物研制引诱剂

基于非主栽作物挥发物的引诱剂，因存在主栽作物不能释放的引诱物质，可减少或避免因组分重叠而造成的田间背景气味干扰。但前提是所选择的植物，对靶标害虫的引诱活性要强于主栽作物。在保证引诱活性的同时，尽可能增加引诱剂组分来源的多样性，可更好地减少田间背景气味干扰。这方面最为成功的例子是夜蛾科害虫引诱剂[103,104]。研究起始，挑选了具引诱活性的 18 个科的 33 种植物，包括桉树、相思树、向日葵、棉花、苦苣菜、万寿菊、迷迭香等，从这些植物挥发物中，共筛选出 34 个引诱活性物质。考虑到田间背景气味可能存在的干扰，引诱物质组配过程中遵循了以下 2 条原则。即同时包含多种植物的挥发物，同时包含花香物质和植物叶片释放的物质。该引诱剂在棉花、玉米、花生、大豆、烟草等多种作物田地均对夜蛾科害虫表现出良好的引诱活性，且防治效果显著[105]。

参 考 文 献

[1] 陆宴辉, 张永军, 吴孔明. 植食性昆虫的寄主选择机理及行为调控策略[J]. 生态学报, 2008, 28(10): 5113-5122.

[2] Knolhoff L M, Heckel D G. Behavioral assays for studies of host plant choice and adaptation in herbivorous insects[J]. Annual Review of Entomology, 2014, 59: 263-278.

[3] Meiners T. Chemical ecology and evolution of plant-insect interactions: a multitrophic perspective[J]. Current Opinion in Insect Science, 2015, 8: 22-28.

[4] Šimpraga M, Takabayashi J, Holopainen J K. Language of plants: where is the word?[J]. Journal of Integrative Plant Biology, 2016, 58: 343-349.

[5] 盛子耀, 李为争, 原国辉. 植物气味多样性与昆虫关系的研究进展[J]. 应用昆虫学报, 2019, 56(4): 652-661.

[6] Laothawornkitkul J, Taylor J E, Paul N D, *et al*. Biogenic volatile organic compounds in the earth system[J]. New Phytologist, 2009, 183(1): 27-51.

[7] Beyaert I, Hilker M. Plant odour plumes as mediators of plant-insect interactions[J]. Biological Reviews, 2014, 89(1): 68-81.

[8] Loreto F, Schnitzler J P. Abiotic stresses and induced BVOCs[J]. Trends in Plant Science, 2010, 15(3): 154-166.

[9] Niinemets Ü. Mild versus severe stress and BVOCs: threshold, priming and consequences[J]. Trends in Plant Science, 2010, 15(3): 145-153.

[10] Murlis J, Elkinton J S, Cardé R T. Odor plumes and how insects use them[J]. Annual Review of Entomology, 1992, 37: 505-532.

[11] Bruce T J A, Wadhams L J, Woodcock C M. Insect host location: a volatile situation[J]. Trends in Plant Science, 2005, 10(6): 269-274.

[12] Bruce T J A, Pickett J A. Perception of plant volatile blends by herbivorous insects-finding the right mix[J]. Phytochemistry, 2011, 72(13): 1605-1611.

[13] 蔡晓明, 李兆群, 潘洪生, 等. 植食性害虫食诱剂的研究与应用[J]. 中国生物防治学报, 2018, 34(1): 8-35.

[14] Lürling M, Scheffer M. Info-disruption: pollution and the transfer of chemical information between organisms[J]. Trends in Ecology & Evolution, 2007, 22(7): 374-379.

[15] Schrder R, Hilker M. The relevance of background odor in resource location by insects: a behavioral approach[J]. Bioence, 2008, 58: 308-316.

[16] Barber J R, Crooks K R, Fristrup K M. The costs of chronic noise exposure for terrestrial organisms[J]. Trends in Ecology & Evolution, 2009, 25(3): 188-188.

[17] Conversano J, Tan E J, Wilgenburg E, *et al*. Background odour may impair detection of chemical signals for social recognition[J]. Austrial Entomology, 2014, 53(4): 432-435.

[18] Ord T J, Stamps J A. Alert signals enhance animal communication in 'noisy' environments[J]. Proceedings of National Academy of Science of the United States of America, 2008, 105(48): 18830-18835.

[19] Potvin D A, Parris K M, Mulder R A. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes

(*Zosterops lateralis*)[J]. Proceedings of the Royal Society B, 2011, 278(1717): 2464-2469.

[20] Leonard M L, Horn A G. Ambient noise increases missed detections in nestling birds[J]. Biology Letters, 2012, 8(4): 530-532.

[21] Conchou L, Lucas P, Meslin C, *et al*. Insect odorscapes: from plant volatiles to natural olfactory scenes[J]. Frontiers in Physiology, 2019, 10: 972.

[22] Pannunzi M, Nowotny T. Odor stimuli: not just chemical identity[J]. Frontiers in Physiology, 2019, 10: 1428.

[23] Cardé R T, Willis M A. Navigational strategies used by insects to find distant, wind-borne sources of odor[J]. Journal of Chemical Ecology, 2008, 34(7): 854-866.

[24] Celani A, Villermaux E, Vergassola M. Odor landscapes in turbulent environments[J]. Physical Review, 2014, 4: 041015.

[25] Zimmer R K, Zimmer C A. Dynamic scaling in chemical ecology[J]. Journal of Chemical Ecology, 2008, 34: 822-836.

[26] Riffell J A, Abrell L, Hildebrand J G. Physical processes and real-time chemical measurement of the insect olfactory environment[J]. Journal of Chemical Ecology, 2008, 34: 837-853.

[27] Riffell J A, Shlizerman E, Sanders E, *et al*. Flower discrimination by pollinators in a dynamic chemical environment[J]. Science, 2014, 344(6191): 1515-1518.

[28] Galizia G C, Rössler W. Parallel olfactory systems in insects: anatomy and function[J]. Annual Review of Entomology, 2010, 55: 399-420.

[29] Hansson B S, Stensmyr M C. Evolution of insect olfaction[J]. Neuron, 2011, 72(5): 698-711.

[30] Andersson M N, Löfstedt C, Newcomb R D. Insect olfaction and the evolution of receptor tuning[J]. Frontiers in Ecology and Evolution, 2015, 53(3): 1-13.

[31] de Fouchier A, Walker W B, Montagné N, *et al*. Functional evolution of Lepidoptera olfactory receptors revealed by deorphanization of a moth repertoire[J]. Nature Communications, 2017, 8: 15709-15709.

[32] Bhandawat V, Olsen S R, Gouwens N W, *et al*. Sensory processing in the *Drosophila* antennal lobe increases reliability and separability of ensemble odor representations[J]. Nature Neuroscience, 2007, 10(11): 1474-1482.

[33] Egea-Weiss A, Renner A, Kleineidam C J, *et al*. High precision of spike timing across olfactory receptor neurons allows rapid odor coding in *Drosophila*[J]. Science, 2018, 4: 76-63.

[34] Houot B, Burkland R, Tripathy S, *et al*. Antennal lobe representations are optimized when olfactory stimuli are periodically structured to simulate natural wing beat effects[J]. Frontiers in Cellular Neuroscience, 2014, 8: 159.

[35] Huston S J, Stopfer M, Cassenaer S, *et al*. Neural encoding of odors during active sampling and in turbulent plumes[J]. Neuron, 2015, 88(2): 403-418.

[36] De Bruyne M, Baker T C. Odor detection in insects: volatile codes[J]. Journal of Chemical Ecology, 2008, 34: 882-897.

[37] Cardé R T, Charlton R E. Olfactory sexual communication in Lepidoptera: strategy, sensitivity and selectivity//Lewis T, ed. Insect Communication[M]. London: Academic Press, 1984, 241-265.

[38] Elkinton J S, Schal C, Ono T, *et al*. Pheromone puff trajectory and upwind flight of male gypsy moths in a forest[J]. Physiological Entomology, 1987, 12(4): 399-406.

[39] Baker T C, Fadamiro H Y, Cosse A A. Moth uses fine tuning for odour resolution[J]. Nature, 1998, 393: 530.

[40] Szyszka P, Stierle J S, Biergans S, *et al*. The speed of smell: odor-object segregation within milliseconds[J]. PLoS ONE, 2012, 7: e36096.

[41] Hare J D. Ecological role of volatiles produced by plants in response to damage by herbivorous insects[J]. Annual Review of Entomology, 2011, 56: 161-180.

[42] Heil M. Herbivore-induced plant volatiles: targets, perception and unanswered questions[J]. New Phytologist, 2014, 204: 297-306.

[43] Pierik R, Ballaré C L, Dicke M. Ecology of plant volatiles: taking a plant community perspective[J]. Plant, Cell & Environment, 2014, 37(8): 1845-1853.

[44] Webster B, Cardé R T. Use of habitat odour by host-seeking insects[J]. Biological Reviews, 2017, 92(2): 1241-1249.

[45] Trona F, Anfora G, Balkenius A, *et al*. Neural coding merges sex and habitat chemosensory signals in an insect herbivore[J]. Proceedings of the Royal Society B: Biological Sciences, 2013, 280: 20130267.

[46] Thöming G, Larsson M C, Hansson B S, *et al*. Comparison of plant preference hierarchies of male and female moths and the impact of larval rearing hosts[J]. Ecology Letters, 2013, 94(8): 1744-1752.

[47] Proffit M, Khallaf M A, Carrasco D, *et al*. ‘Do you remember the first time?’ Host plant preference in a moth is modulated by experiences during larval feeding and adult mating[J]. Ecology Letters, 2015, 18(4): 365-374.

[48] Yang Z H, Bengtsson M, Witzgall P. Host plant volatiles synergize response to sex pheromone in codling moth, *Cydia pomonella*[J]. Journal of Chemical

Ecology, 2004, 30: 619-629.

[49] Borrero-Echeverry F, Bengtsson B, Nakamuta K, *et al*. Plant odor and sex pheromone are integral elements of specific mate recognition in an insect herbivore[J]. Evolution, 2018, 72: 2225-2233.

[50] Rochat D, Nagnan-le M P, Esteban-Duran J R, *et al*. Identification of pheromone synergists in the American weevil, *Rhynchophorus palmarum*, and attraction of related *Dynamis borassi* (Coleoptera, Curculionidae)[J]. Journal of Chemical Ecology, 2000, 26: 155-187.

[51] Said I, Renou M, Morin J P, *et al*. Interactions between acetoin, a plant volatile, and pheromone in *Rhynchophorus palmarum*: behavioral and olfactory neuron responses[J]. Journal of Chemical Ecology, 2005, 31: 1789-1805.

[52] Dupuy F, Rouyar A, Deisig N, *et al*. A background of a volatile plant compound alters neural and behavioral responses to the sex pheromone blend in a moth[J]. Frontiers in Physiology, 2017, 8: e00079.

[53] Renou M, Party V, Rouyar A, *et al*. Olfactory signal coding in an odor background[J]. Biosystems, 2015, 136: 35-45.

[54] Rouyar A, Party V, Prešern J, *et al*. A general odorant background affects the coding of pheromone stimulus intermittency in specialist olfactory receptor neurones[J]. PLoS ONE, 2011, 6: e26443.

[55] Party V, Hanot C, Said I, *et al*. Plant Terpenes affect intensity and temporal parameters of pheromone detection in a moth[J]. Chemical Senses, 2009, 34(9): 763-774.

[56] Party V, Hanot C, Büsser D S, *et al*. Changes in odor background affect the locomotory response to pheromone in moths[J]. PLoS ONE, 2013, 8: e52897.

[57] Hatano E A, Saveer A, Borrero-Echeverry F, *et al*. A herbivore-induced plant volatile interferes with host plant and mate location in moths through suppression of olfactory signalling pathways[J]. BMC Biology, 2015, 13: 75.

[58] Rouyar A, Deisig N, Dupuy F, *et al*. Unexpected plant odor responses in a moth pheromone system[J]. Frontiers in Physiology, 2015, 6: 148.

[59] Badeke E, Haverkamp A, Hansson B S, *et al*. A challenge for a male noctuid moth? Discerning the female sex pheromone against the background of plant volatiles[J]. Frontiers in Physiology, 2016, 7: 143.

[60] Elisa B, Alexander H, Hansson B S, *et al*. A challenge for a male noctuid moth? Discerning the female sex pheromone against the background of plant volatiles[J]. Frontiers in Physiology, 2016, 7: e00143.

[61] Maria H, Harald T. Rising background odor concentration reduces sensitivity of ON and OFF olfactory receptor neurons for changes in concentration[J]. Frontiers in Physiology, 2016, 7: e00063.

[62] Morawo T, Fadamiro H. The role of herbivore- and plant-related experiences in intraspecific host preference of a relatively specialized parasitoid[J]. Insect Science, 2019, 26: 341-350.

[63] Wajnberg É, Bernstein C, van Alphen J. Behavioral Ecology of Insect Parasitoids: from Theoretical Approaches to Field Applications[M]. Malden M A: Wiley-Blackwell, 2008.

[64] Koschier E H, Nielsen M C, Spangl B, *et al*. The effect of background plant odours on the behavioural responses of *Frankliniella occidentalis* to attractive or repellent compounds in a Y-tube olfactometer[J]. Entomologia Experimentalis *et* Applicata, 2017, 163: 160-169.

[65] Mauchline A L, Osborne J L, Martin A P, *et al*. The effects of non-host plant essential oil volatiles on the behaviour of the pollen beetle *Meligethes aeneus*[J]. Entomologia Experimentalis *et* Applicata, 2005, 114(3): 181-188.

[66] Fancelli M, Borges M, Laumann R A, *et al*. Attractiveness of host plant volatile extracts to the asian citrus psyllid, *Diaphorina citri*, is reduced by terpenoids from the non-host cashew[J]. Journal of Chemical Ecology, 2018, 44: 397-405.

[67] Togni P H B, Laumann R A, Medeiros M A, *et al*. Odour masking of tomato volatiles by coriander volatiles in host plant selection of *Bemisia tabaci* biotype B[J]. Entomologia Experimentalis *et* Applicata, 2010, 136(2): 164-173.

[68] Büchel K, Austel N, Mayer M, *et al*. Smelling the tree and the forest: elm background odours affect egg parasitoid orientation to herbivore induced terpenoids[J]. BioControl, 2014, 59(1): 29-43.

[69] Martelli C, Carlson J R, Emonet T. Intensity invariant dynamics and odor-specific latencies in olfactory receptor neuron response[J]. Journal of Neuroscience Methods, 2013, 33: 6285-6297.

[70] 娄永根, 程家安. 虫害诱导的植物挥发物:基本特性、生态学功能及释放机制[J]. 生态学报, 2000, 20(6): 1097-1106.

[71] 蔡晓明, 孙晓玲, 董文霞, 等. 虫害诱导植物挥发物(HIPVs): 从诱导到生态功能[J]. 生态学报, 2008, 28(8): 3969-3980.

[72] 孙仲亨, 宋圆圆, 曾任森. 植物挥发物介导的种内与种间关系研究进展[J]. 华南农业大学学报, 2019, 40(5): 166-174.

[73] Atkinson R, Arey J. Gas-phase tropospheric chemistry of biogenic volatile organic compounds: a review[J]. Atmospheric Environment, 2003, 37:

197-219.

[74] Goldstein A H, Galbally I E. Known and unexplored organic constituents in the earth's atmosphere[J]. Environmental Science and Technology, 2007, 41(5): 1514-1521.

[75] Bachy A, Aubinet M, Schoon N, *et al*. Are BVOC exchanges in agricultural ecosystems overestimated? Insights from fluxes measured in a maize field over a whole growing season[J]. Atmospheric Chemistry and Physics, 2016, 16(8): 5343-5356.

[76] Schallhart S, Rantala P, Nemitz E, *et al*. Characterization of total ecosystem-scale biogenic VOC exchange at a Mediterranean oak–hornbeam forest[J]. Atmospheric Chemistry and Physics, 2015, 15(19): 27627-27673.

[77] Fischbach R J, Staudt M, Zimmer I, *et al*. Seasonal pattern of monoterpene synthase activities in leaves of the evergreen tree *Quercus ilex*[J]. Physiologia Plantarum, 2002, 114(3): 354-360.

[78] Staudt M, Joffre R, Rambal S. How growth conditions affect the capacity of *Quercus ilex* leaves to emit monoterpenes[J]. New Phytologist, 2003, 158(1): 61-73.

[79] Staudt M, Byron J, Piquemal K, *et al*. Compartment specific chiral pinene emissions identified in a maritime pine forest[J]. Science of The Total Environment, 2019, 654: 1158-1166.

[80] Wiedenmyer C, Friedfeld S, Baugh W, *et al*. Measurement and analysis of atmospheric concentrations of isoprene and its reaction products in central Texas[J]. Atmospheric Environment, 2011, 35(6): 1001-1013.

[81] Cai X M, Xu X X, Bian L, *et al*. Measurement of volatile plant compounds in field ambient air by thermal desorption–gas chromatography–mass spectrometry[J]. Analytical and Bioanalytical Chemistry, 2015, 407: 9105-9114.

[82] Kruidhof H M, Roberts A L, Magdaraog P, *et al*. Habitat complexity reduces parasitoid foraging efficiency, but does not prevent orientation towards learned host plant odours[J]. Oecologia, 2015, 179: 353-361.

[83] Ando T, Inomata S, Yamamoto M. Lepidopteran sex pheromones[J]. Topics in Current Chemistry, 2004, 239: 51-96.

[84] Michal M. Competitiveness of fertilizers with proteinaceous baits applied in Mediterranean fruit fly, *Ceratitis capitata* Wied (Diptera: Tephritidae) control[J]. Crop Protection, 2009, 28(4): 314-318.

[85] Hammack L. Corn volatiles as attractants for northern and western corn rootworm beetles (Coleoptera: Chrysomelidae: *Diabrotica* spp.)[J]. Journal of Chemical Ecology, 1996, 22(7): 1237-1253.

[86] Casado D, Gemeno C, Avilla J, *et al*. Diurnal variation of walnut tree volatiles and electrophysiological responses in *Cydia pomonella* (Lepidoptera: Tortricidae)[J]. Pest Management Science, 2008, 64(7): 736-747.

[87] Knudsen G K, Bengtsson M, Kobro S, *et al*. Discrepancy in laboratory and field attraction of apple fruit moth *Argyresthia conjugella* to host plant volatiles[J]. Physiological Entomology, 2008, 33: 1-6.

[88] Anfora G, Tasin M, De Cristofaro A, *et al*. Synthetic grape volatiles attract mated *Lobesia botrana* females in laboratory and field bioassays[J]. Journal of Chemical Ecology, 2009, 35: 1054-1062.

[89] Lu P F, Huang L Q, Wang C Z. Identification and field evaluation of pear fruit volatiles attractive to the oriental fruit moth, *Cydia molesta*[J]. Journal of Chemical Ecology, 2012, 38(8): 1003-1016.

[90] Cattaneo A M, Bengtsson J M, Borgonovo G, *et al*. Response of the European grapevine moth *Lobesia botrana* to somatosensory-active volatiles emitted by the non-host plant *Perilla frutescens*[J]. Physiological Entomology, 2014, 39: 229-236.

[91] Landolt P J, Adams T, Davis T S, *et al*. Spotted wing drosophila, *Drosophila suzukii* (diptera: drosophilidae), trapped with combinations of wines and vinegars[J]. Florida Entomologist, 2012, 95(2): 326-332.

[92] Cha D H, Adams T, Rogg H, *et al*. Identification and field evaluation of fermentation volatiles from wine and vinegar that mediate attraction of spotted wing Drosophila, *Drosophila suzukii*[J]. Journal of Chemical Ecology, 2012, 38: 1419-1431.

[93] Cha D H, Adams T, Werle C T, *et al*. A four-component synthetic attractant for *Drosophila suzukii* (Diptera: Drosophilidae) isolated from fermented bait headspace[J]. Pest Management Science, 2014, 70(2): 324-331.

[94] Cha D H, Landolt P J, Adams T B. Effect of chemical ratios of a microbial-based feeding attractant on trap catch of *Drosophila suzukii* (Diptera: Drosophilidae)[J]. Environmental Entomology, 2017, 46(4): 907-915.

[95] Cha D H, Hesler S P, Wallingford A K, *et al*. Comparison of commercial lures and food baits for early detection of fruit infestation risk by *Drosophila suzukii* (Diptera: Drosophilidae)[J]. Journal of Economic Entomology, 2018, 111(2): 645-652.

[96] Cha D H, Loeb G M, Linn C E, *et al*. A multiple-choice bioassay approach for rapid screening of key attractant volatiles[J]. Environmental Entomology, 2018, 47(4): 946-950.

[97] Cai X M, Xu X X, Bian L, *et al*. Attractiveness of host volatiles combined with background visual cues to the tea leafhopper[J]. Entomologia Experimentalis *et* Applicata, 2015, 157: 291-299.

[98] Cai X, Lei B, Xu X X, *et al*. Field background odour should be taken into account when formulating a pest attractant based on plant volatiles[J]. Scientific Reports, 2017, 7: 41818.

[99] Bengtsson M, Jaastad G, Knudsen G, *et al*. Plant volatiles mediate attraction to host and non-host plant in apple fruit moth, *Argyresthia conjugella*[J]. Entomologia Experimentalis *et* Applicata, 2006, 118: 77-85.

[100] Knudsen G K, Tasin M. Spotting the invaders: A monitoring system based on plant volatiles to forecast apple fruit moth attacks in apple orchards[J]. Basic and Applied Ecology, 2015, 16: 354-364.

[101] Knudsen G K, Norli H R, Marco T. The ratio between field attractive and background volatiles encodes host-plant recognition in a specialist moth[J]. Frontiers in Plant Science, 2017, 8: 2206.

[102] Xu X X, Cai X M, Bian L, *et al*. Does background odor in tea gardens mask attractants? Screening and application of attractants for *Empoasca onukii* Matsuda[J]. Journal of Economic Entomology, 2017, 110(6): 2357-2363.

[103] Gregg P C, Socorro A P D, Hawes A J, *et al*. Developing bisexual attract-and-kill for polyphagous insects: ecological rationale versus pragmatics[J]. Journal of Chemical Ecology, 2016, 42: 666-675.

[104] Socorro A P D, Gregg P C, Alter D, *et al*. Development of a synthetic plant volatile-based attracticide for female noctuid moths. I. Potential sources of volatiles attractive to *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)[J]. Australian Journal of Entomology, 2010, 49: 10-20.

[105] 陆宴辉, 赵紫华, 蔡晓明, 等. 我国农业害虫综合防治研究进展[J]. 应用昆虫学报, 2017, 54(3): 349-363.