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甲基丁香酚对桔小实蝇的生物学效应及其在防控应用中的研究进展*

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摘 要 桔小实蝇 *Bactrocera dorsalis* (Hendel)是一种毁灭性果蔬害虫，具有寄主范围广、繁殖能力强、生命周期长和世代重叠等特性，常常爆发成灾。根据持续控制、安全有效的防治思路，防控成虫是当前防治桔小实蝇的主要策略。甲基丁香酚（Methyl eugenol, ME）是一种天然的苯基丙烷化合物，对桔小实蝇性成熟雄虫有强烈的引诱作用，被广泛应用于监测、诱杀、根除桔小实蝇田间种群。该文综述了 ME 对桔小实蝇的生物学效应，及其在防控应用中的研究进展和存在问题，以期为桔小实蝇的绿色综合防控提供参考。

关键词 桔小实蝇；甲基丁香酚；引诱作用；化学感受；生物代谢物

Progress in research on the biological effects of methyl eugenol on *Bactrocera dorsalis* (Hendel) and its function in biocontrol

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Abstract The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is one of the most destructive global pests of fruits and vegetables. It is a highly polyphagous pest with large host range, long-life span, and high adult fecundity that is capable of causing severe damage to more than 250 commercially valuable tropical and subtropical crops. Because the larval stage lives within host plant tissues, pest control strategies focus mainly on adults. The natural phenylpropanoid, methyl eugenol (ME), is a powerful attractant for adult male *B. dorsalis*, and has been widely used in male annihilation technique (MAT) systems to detect, lure, and eradicate *B. dorsalis* populations worldwide. This paper summarizes research on the application of ME for the prevention and control of *B. dorsalis*. Current problems in the application of this compound are discussed and new insights and references for the integrated pest management of *B. dorsalis* are provided.

Key words *Bactrocera dorsalis*; methyl eugenol; attractive efficacy; chemoreception; biological metabolite

桔小实蝇 *Bactrocera dorsalis*（Hendel）隶属双翅目 Diptera，实蝇科 Tetriphitidae，果实蝇属 *Bactrocera* Macquart，是一种严重危害果蔬业生产的世界性农业害虫（Zheng *et al*., 2013; Liu *et al*., 2016a）。该虫原产于亚洲热带和亚热带地区，现已成为中国、东南亚、印度次大陆和夏威夷群岛一带的危险性果蔬害虫（Stephens *et al*., 2007; Shi *et al*., 2012; Wan *et al*., 2012; De Villiers *et al*., 2016）。桔小实蝇于 1912 年在我国台湾地区首次被发现并记录，于 1934 年入侵海南岛，于 1937 年入侵我国大陆华南地区和西南地区，目前该虫主要分布于我国广东、广西、湖

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南、贵州、福建、海南、云南及四川等省区（Hardy, 1973; Li *et al*., 2011; Yi *et al*., 2016; Wei *et al*., 2017; Liu *et al*., 2019）。2007 年在《中华人民共和国进境植物检疫性有害生物名录》中将该虫属列为检疫性有害生物（朱雁飞等, 2020）。桔小实蝇幼虫为典型的杂食类潜食性害虫，能取食为害香蕉、柑橘、杨桃、番石榴、芒果、苹果及草莓等 46 个科 250 多种特色经济水果（图 1）（李培征等, 2012; Cheng *et al*., 2014）。由于该虫寄主范围广、繁殖力强、扩散能力和适应能力强及危害性大，往往给果蔬业和花卉业造成严重的经济损失（Malacrida *et al*., 2007; Wan *et al*., 2011; Shen *et al*., 2012）。

在桔小实蝇的防治中，化学防治方法对这类钻蛀性害虫的防治效果并不理想，而且大量不合理的农药施用已致使桔小实蝇抗性急剧增加，并导致了严重的食品安全和环境污染等问题（Hsu *et al*., 2004, 2011; 潘志萍等, 2008; Jin *et al*., 2011; Vontas *et al*., 2011; 陈朗杰等, 2015; Zhang *et al*., 2015）。生物防治如利用寄生蜂防控桔小实蝇已取得了良好的成效，但其成本较高且防效滞后（Vargas *et al*., 2007; Luo and Zeng, 2010; 章玉苹等, 2010; Zhao *et al*., 2013; 龙秀珍等, 2014）。害虫行为调控的方法已沿用了几个世纪，其中一种有效的方法是引诱剂的应用，引诱剂能特异性诱杀目标害虫、保护靶标作物免受其为害，同时又保护天敌昆虫资源。国内外主要采用以甲基丁香酚（Methyl eugenol，ME）为核心成分的诱杀剂对桔小实蝇的野生种群动态进行监测与防控（陆永跃等, 2006; Vargas and Prokopy, 2006; Jayanthi *et al*., 2012;Lin *et al*., 2012; Shelly, 2016）。ME 是一种天然的植物源苯基丙烷化合物，目前已至少在 10 个科的植物中发现该化合物（Tan and Nishida, 2012）。该文聚焦 ME 对桔小实蝇的生物学效应、ME 诱杀法防控桔小实蝇的研究进展和存在的问题，旨在为桔小实蝇的绿色持效防控提供科学依据。

图 1　桔小实蝇对寄主植物的为害状

Fig. 1　Damaging symptoms of *Bactrocera dorsalis* to host plants

A. 雌成虫在番石榴上产卵；B. 雌成虫在柑橘上产卵；C. 雌成虫聚集取食；D, E. 芒果为害状。

A. *B. dorsalis* female laying eggs on a guava fruit; B. *B. dorsalis* female laying eggs on an orange fruit; C. *B. dorsalis* adults gathered and fed on the rotten guava fruit; D, E. Symptoms of the mango fruits damaged by *B. dorsalis*.

1　ME 对桔小实蝇的生物学效应研究进展

1.1　ME 引诱桔小实蝇雄虫的活性规律

生理状态和日节律均会影响桔小实蝇雄虫趋向 ME 的行为反应。性成熟程度的不同导致雄虫对 ME 趋性有所差异，羽化 1-5 d 性未成熟雄虫对 ME 趋性很弱，羽化 15 d 性成熟雄虫对 ME 趋性最强，羽化 25-30 d 雄虫对 ME 仍有较强的趋性（Karunaratne and Karunaratne, 2012; Liu *et al*., 2017）。风洞试验和诱捕行为试验表明，在一天中的不同时间点桔小实蝇雄虫对 ME 的趋性程度不同，早上趋性最强，中午次之，晚上最弱，桔小实蝇雄虫对 ME 趋性能力的波动规律与其交配行为日节律刚好相反（Karunaratne and Karunaratne, 2012; Liu *et al*., 2018）。触角电位 EAG 检测也证明了桔小实蝇雄虫对 ME 的最高反应值出现在上午 9:00-10:00（杜迎刚等, 2015）。值得注意的是，虽然 ME 对性成熟的雄虫具有强烈的引诱作用，但作为一种类性外激素（Paraphermones）对雌虫却无明显的引诱活性（Shelly, 1997; 梁光红等, 2003; Satarkar *et al*., 2009）。

1.2　ME 引诱桔小实蝇雄虫的嗅觉分子机制

昆虫主要依靠高度敏感的嗅觉系统来辨别不同的化学信息物质，从而调节其重要的生命活动（Fleischer *et al*., 2017; Choo *et al*., 2018）。桔小实蝇的嗅觉系统是非常复杂和敏感的，对性信息素、寄主植物和非寄主植物挥发物均有特殊的行为反应（Jang *et al*., 1997）。鉴定及功能解析其嗅觉相关蛋白基因的有助于深入理解桔小实蝇嗅觉识别的分子机制。目前已从桔小实蝇成虫触角中成功鉴定了约 31 种气味结合蛋白（Odorant binding protein, OBP）、5 种化学感受蛋白（Chemosensory protein, CSP）、50 种气味受体（Odorant receptor, OR）、1 个非典型气味受体（Odorant receptor coreceptor, Orco）、14 种离子型受体（Ionotropic receptor, IR）、4 种感觉神经元膜蛋白（Sensory neuron membrane protein, SNMP）和多种气味分子降解酶（Odorant degrading enzymes, ODEs）（Zheng *et al*., 2013; Wu *et al*., 2015; Liu *et al*., 2016b）。随着桔小实蝇基因组的绘制成功和研究的深入，越来越多的嗅觉基因将被鉴定出来，为全面解析桔小实蝇的嗅觉识别机制提供了理论基础，同时也为研发高效、专一的行为调控技术提供分子靶点。

解析 ME 引诱桔小实蝇雄虫的分子机制，不仅有助于揭示桔小实蝇嗅觉识别的分子机制，而且也对以 ME 分子结构为模板或 ME 作用的嗅觉蛋白为靶标研发新型引诱剂具有重要的指导意义。研究表明，气味结合蛋白（*BdorOBP2*、*BdorOBP13*、*BdorOBP69a* 和 *BdorOBP83a-2*）、气味受体 *BdorOR88a* 和非典型性气味受体 *BdorOrco* 均参与桔小实蝇雄虫识别 ME 的分子过程（Zheng *et al*., 2012; Wu *et al*., 2016; Liu *et al*., 2017, 2018, 2020, 2022a; Chen *et al*., 2021, 2022; Xu *et al*., 2022）。当 ME 气味分子通过桔小实蝇雄虫触角上的感觉小孔扩散进入触角后，气味结合蛋白（*BdorOBP2*、*BdorOBP13*、*BdorOBP69a* 或 *BdorOBP83a-2*）迅速与 ME 结合，形成复合体通过淋巴液到达气味受体 *BdorOR88a*，然后激活 *BdorOR88a/Orco* 异源二聚体产生动作电位，最终信号传导进入桔小实蝇大脑并产生趋向 ME 的行为反应；激活 *BdorOR88a/Orco* 异源二聚体后，ME 气味分子被气味降解酶 ODEs 降解（图 2）（Liu *et al*., 2018）。

1.3　ME 引诱桔小实蝇雄虫的生理机制

桔小实蝇是一种具有求偶行为的昆虫，求偶炫耀的雄虫通过释放远程性信息化合物吸引雌虫到求偶场（Lekking sites），然后雄虫开始进行一系列的求偶炫耀表现行为，雌虫选择具有最佳求偶行为的雄虫并与之进行交配（张秀歌等, 2017; 陈瑶瑶等, 2020）。性成熟雄虫具有强烈的摄食 ME 的习性，取食 ME 的雄虫的性活力和性能力显著提高，能吸引更多雌虫前来交配，表现出明显的交配优势（Shelly and Nishida, 2004; Zheng *et al*., 2012; Liu *et al*., 2017, 2018）。在研究

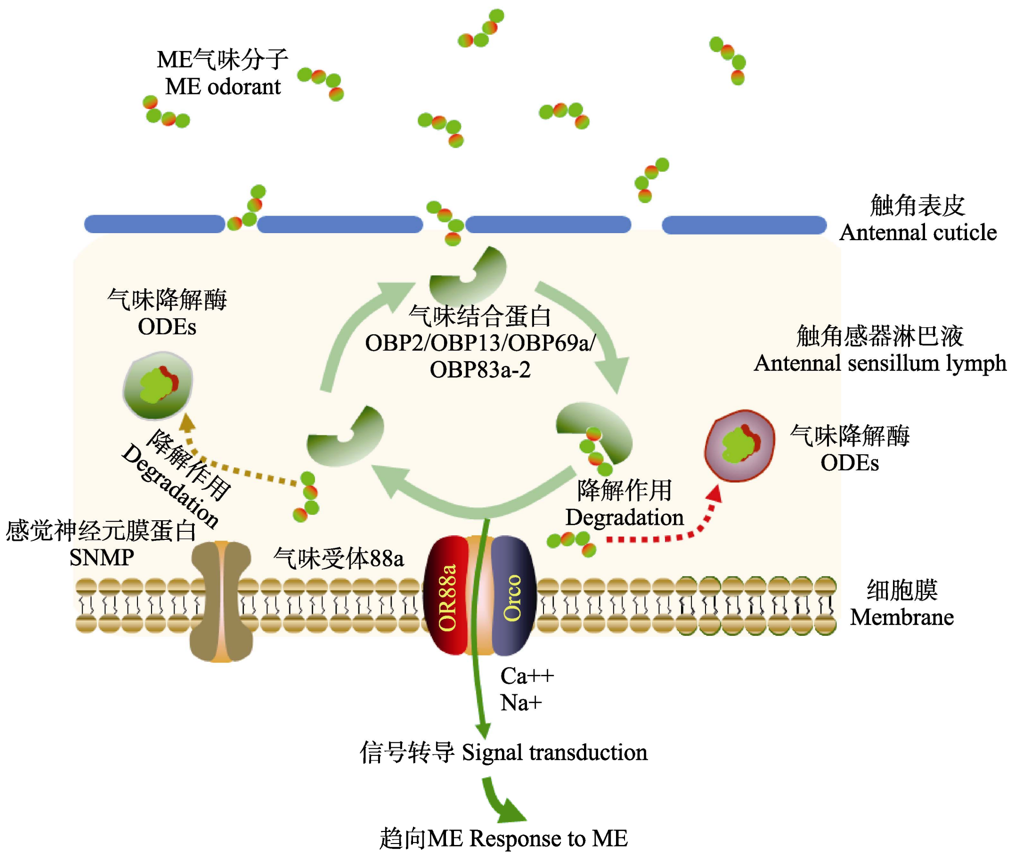

图 2　桔小实蝇雄虫识别 ME 气味分子的嗅觉分子机制

Fig. 2　Molecular mechanism of ME odorant detection process in the antennae of mature *Bactrocera dorsalis* male flies

ME 对桔小实蝇雄虫的引诱作用时发现，ME 对桔小实蝇的引诱作用并不是基于雄虫对营养的需要，但它又与化学过程有区别，ME 是通过类似激素的作用特点引诱桔小实蝇（Shelly, 2001）。进一步研究发现，桔小实蝇雄虫取食 ME 后在中肠将其迅速代谢转化为 2-烯丙基-4,5-甲氧基-芍药醇（2-allyl-4,5-dimethoxyphenol, DMP）和反式松柏醇（*E*-coniferyl alcohol, E-CF）（图 3），然后作为性信息功能化合物通过血淋巴转运并储存于直肠性腺内（Nishida *et al*., 1988; Shelly and Nishida, 2004; Hee and Tan, 2006; Khrimian *et al*., 2006; Orankanok *et al*., 2011）。在傍晚求偶交配时，雄虫利用这些类信息素功能化合物吸引雌虫前来交配，增加雄虫的交配竞争能力（Shelly *et al*., 2010; Obra and Resilva, 2013; Haq *et al*., 2014）。作者课题组近期的研究结果也证实了这一观点，我们发现在求偶前期 DMP 和 E-CF 对桔小实蝇性成熟雄虫有明显的引诱活性，且 DMP 的诱雄活性明显强于 E-CF，表明 DMP 和 E-CF 在桔小实蝇交配前期形成求偶场的过程中起着聚集雄虫的重要作用；而在求偶交配期仅 E-CF 对性成熟雌虫有强烈的引诱活性，且能明显刺激雌虫与雄虫交配，表明 E-CF 在增进桔小实蝇两性生殖交流的过程中起着至关重要的作用（Deng *et al*., 2021; Liu *et al*., 2022b）。

2　ME 对桔小实蝇诱杀防控的研究进展

2.1　影响 ME 诱捕桔小实蝇效率的环境因素

温度、光照强度及寄主植物能显著影响桔小实蝇雄虫对 ME 的趋性。在 18-40 ℃范围内桔小实蝇对 ME 趋性活动活跃，其中以 25-32 ℃最为活跃，500-2 000 lx 光照强度时桔小实蝇对 ME 的趋性反应最为活跃；当温度低于 14 ℃或高于

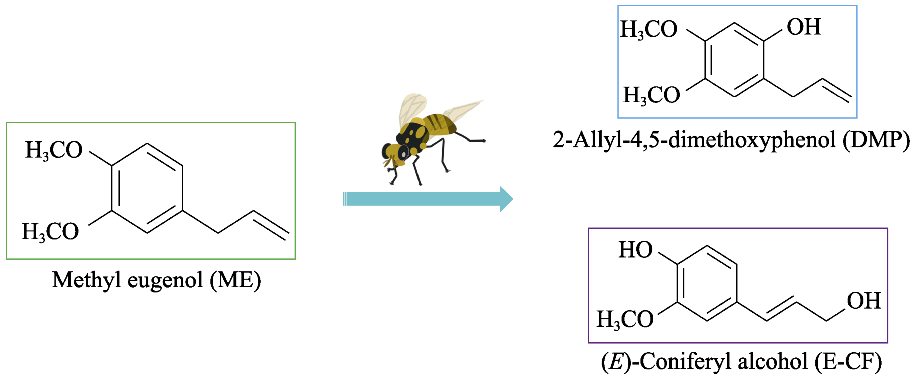

图 3　甲基丁香酚在桔小实蝇雄成虫体内的代谢产物

Fig. 3　Chemical structures of ME and its metabolites (DMP and E-CF) accumulated in the rectal gland of *Bactrocera dorsalis* males

40 ℃、光照强度低于 150 lx 或高于 3 000 lx 时，桔小实蝇对 ME 趋性能力显著下降(李周文婷等, 2010)。此外，桔小实蝇幼虫的取食经历对其雄虫趋向 ME 的能力有显著的影响。*Terminalia catappa* L.为桔小实蝇寄主植物之一，其果实中富含 ME，幼虫取食该寄主果实后显著降低了雄虫对 ME 的趋性（ Manoukis *et al*., 2018 ）。

诱捕器的颜色和种类、诱芯材质、放置位置、ME 使用剂量对诱捕桔小实蝇数量均有影响（ 席涵等, 2019)。透明诱捕器的诱虫数量显著高于黄色、红色、蓝色或绿色诱捕器的诱虫数量，涡旋式诱捕器和纤维板诱芯组合诱杀效果最好，桔小实蝇的诱捕量也随 ME 剂量的增加而增加(蔡波等, 2013; Howarth, 2000)。此外，田间诱集监测位置的选择和 ME 的添加方式对桔小实蝇雄虫的诱捕效果有重要影响，诱集监测点应包括果园内和果园外，选择较大且环境复杂的区域作为监测点可获得更明确的年发生动态规律，采用分期分批、多次添加 ME 的方式监测桔小实蝇雄虫动态，可消除因监测区域内所有诱瓶同一时间添加性引诱剂而造成的浓度突变所引起的成虫出现干扰性高峰，从而确保虫情监测结果的准确性（ 陆永跃等, 2006)（ 图 4)。

在 ME 中添加不同成分的引诱物、化学药剂或填充物，可发挥显著的增效作用。香茅油、甜橙香精和甲基丁香酚按 2.5：47. 5：50 比例混配时引诱效果最好 (吴华等, 2004)。当 ME 与糖酒醋液[糖：酒：醋：水=76：152：53：760(g/L)] 混合后对性成熟雄成虫的引诱效果要显著强于

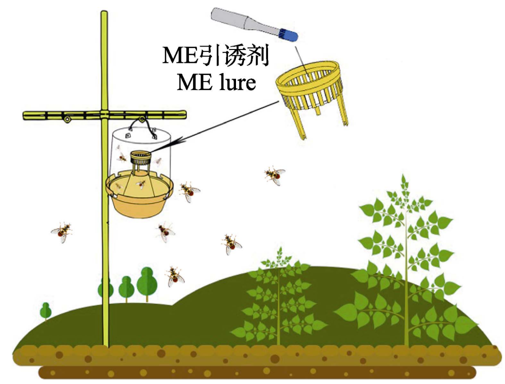

图 4　ME 田间诱捕法防控桔小实蝇（ Pherobio Technilogy Co., Ltd, 2019 ）

Fig. 4　Trapping technology based on ME lure in control of natural *Bactrocera dorsalis*（ Pherobio Technilogy Co., Ltd, 2019 ）

单独使用 ME 的诱杀效果（ 孙文等, 2009)。ME 与水解蛋白混合马拉硫磷置于专用诱捕器对桔小实蝇进行田间诱杀也具有良好效果（ Vargas and Prokopy, 2006)。ME 与多杀菌素、啶虫脒、二溴磷、氟虫腈等化学药剂按一定体积混配，对桔小实蝇诱杀效果显著（ Chuang and Hou, 2008; Chen *et al*., 2019)。此外，将活性炭与引诱剂混合，采用 5-10 孔型诱芯瓶不仅可减少 ME 的挥发浪费，可将其持效期延长近 40 d，同时还增加了诱杀虫量（ 薛超等, 2015)。值得注意的是，田间化学杀虫剂频繁使用会对桔小实蝇种群对 ME 的趋性产生明显的负面影响，低剂量阿维菌素处理后桔小实蝇雄虫对 ME 趋性降低(李周文婷等, 2011)。因此，需要合理协调引诱剂与农药的使用策略和方法，以达到监测结果更准确和防治效

果更好的目的。

2.2 ME 诱杀防控技术的不足之处

虽然 ME 诱杀法被用作一种经济、高效的防治措施，但随着桔小实蝇的猖獗为害，ME 诱杀防治技术也凸显出防控效果下降和生物安全性降低等明显的弊端。首先，ME 仅能诱捕到性成熟的雄虫，但对雌虫和性未成熟的雄虫没有引诱作用（Shelly *et al*., 1997; Satarkar *et al*., 2009; Liu *et al*., 2017, 2018）。其次，并不是所有的性成熟雄虫均对 ME 有明显趋性反应（Zheng *et al*., 2012），经人工汰选后，子代雄虫对 ME 无趋性个体的比例显著增加，但最高比例稳定维持在 28%左右，人为汰选不会导致雄虫对 ME 的趋性完全丧失。然而无趋性雄虫的交配竞争能力与有趋性雄虫没有差异，仍能满足与雌虫多次交配并大量繁殖后代（Shelly, 1997; 郭庆亮等，2010; Liu *et al*., 2017）。此外，ME 对非靶标昆虫也表现出一定的引诱活性（Leblanc *et al*., 2009; Dowell and Robert, 2015）。最后，ME 被发现是一种有毒致癌物质，不适合田间长期使用。因此，长时间、大面积使用 ME 诱杀田间雄虫，必然会改变桔小实蝇田间种群对 ME 有、无趋性雄虫的比例，从而改变其种群结构，导致 ME 灭雄效果变差，进而影响使用 ME 诱杀监测桔小实蝇种群动态数据的准确性。面对当前的防控困局，开发新型、高效、绿色的桔小实蝇防控技术成为亟待解决的科研问题和实际生产问题。

2.3 ME 衍生化合物的合成工艺及引诱效果评价

美国卫生与公众服务部（US Department of Health and Human Services）曾于 1998 和 2002 年发表声明指出 ME 是一种致癌物质（Khrimian *et al*., 2009; Jang *et al*., 2011）。另有研究表明，ME 的代谢产物 1′-羟基代谢物（1′-hydroxy metabolites）对小鼠肝细胞有致死作用，田间长期使用必然会对人类健康造成威胁（Miller *et al*., 1983; Shelly, 1997; Smith *et al*., 2002; Khrimian *et al*., 2009; Jang *et al*., 2011; 张秀歌等，2017）。因此，寻找 ME 的替代物成为国际同行研究的热点和亟需解决的科研难题。通过化学方法在 ME 侧链添加单一氟原子改变其化学结构式能显著降低其毒性，但该物质（(*E*)-1, 2-二甲氧基-4-（3-氟-2-丙烯基）苯，(*E*)-1,2-dimethoxy-4-(3-fluoro-2-propenyl) benzene）对桔小实蝇的田间引诱作用明显降低（Khrimian *et al*., 1994, 2006; Liquido *et al*., 1998）。此外，Khrimian 等（2009）合成新的 ME 氟化衍生物 1,2-二甲氧基-4-氟-5-(2-丙烯基）苯（1,2-dimethoxy-4-fluoro-5-(2-propenyl) benzene），发现该物质对桔小实蝇的毒性降低、体内代谢速度加快，但对桔小实蝇雄虫有引诱效果一般。随后，研究者将 2 个氟元子同时添加到 ME 结构的碳骨架上，合成得到 1-氟-4,5-二甲氧基-2-（3,3-二氟-2-丙烯基）苯（1-fluoro-4,5-dimethoxy-2-(3,3-difluoro-2-propenyl)benzene）和 1-氟-4,5-二甲氧基-2-（3-氟-2-丙烯基）苯（1-fluoro-4,5-dimethoxy-2-(3-fluoro-2-propenyl)benzene）两种新的化合物，室内试验表明这两种化合物对雄虫引诱作用较强，但田间诱杀作用较差，且生产制备工艺复杂、生产成本较高（Jang *et al*., 2011）。此外，ME 氟化衍生物对非靶标昆虫也表现出明显的引诱性，其田间应用的生物安全性仍需进一步研究评估（Dowell and Jang, 2016）。值得说明的是，本课题组通过急性毒性试验和细胞毒力试验，发现 ME 的雄虫代谢产物 DMP 和 E-CF 对 Kunming 小鼠及人源离体培养细胞系等非靶标生物没有明显毒性，且对桔小实蝇成虫有显著的引诱活性，表明 DMP 和 E-CF 具备进一步开发安全、高效、特异的桔小实蝇新型引诱剂的潜力（Deng *et al*., 2021; Liu *et al*., 2022b）。

3 展望

目前已有大量的研究报道了桔小实蝇的监测和防治方法，包括雄虫不育技术（Sterile insect technique, SIT）、雄虫灭绝技术（Male annihilation technique, MAT）、引诱剂诱捕法、化学药剂防治法、迷向干扰法和生物防治法（Vargas *et al*., 2007; Manoukis *et al*., 2019; Hou *et al*., 2020）。但这些防控措施在应用中仍存在不足之处，研究高效行为调控技术将为桔小实蝇的绿色防控提供新的思路，主要包括以下几个方面：首先，性信息素

在实蝇两性生殖通讯交流中起着关键作用，桔小实蝇雌雄成虫均可产生、释放性信息素，但由于其分泌微量性信息素化学结构的复杂性和特异性阻碍了性诱剂的研究进展。因此，应将性信息素组分鉴定和应用技术研发作为未来研究工作的重点，从而建立基于桔小实蝇求偶行为的诱杀防治策略。其次，桔小实蝇雌雄成虫因存在多重交配行为而具有强大的繁殖能力，而雌虫是决定子代虫口密度和寄主危害程度的关键因素（Malacrida *et al*., 2007），研发雌成虫高效引诱剂具有更重要的实践意义和实用价值。蛋白食物饵剂对雌虫有较强的引诱作用，但蛋白本身不具有杀虫作用及极易变性，要发挥蛋白的防治作用必须与其它物质混配使用，如何改善蛋白食物引诱剂配方以提高蛋白食物饵剂的引诱活性和持效期仍需进一步研究和探索。另外，雌虫对某些寄主植物的挥发性物质或次生代谢物有特殊的趋向性，随着化学分析的发展，开发植物源雌虫引诱剂将是未来研究的重点；同时，应深入研究雌虫的嗅觉识别分子机制，基于“反向化学生态学（Reverse chemical ecology）”策略研发雌虫高效行为调控技术。最后，应充分深入研究桔小实蝇的行为学和生态学，研发基于成虫视觉和听觉行为的新型防控技术。

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