

番茄潜叶蛾和植物互作关系的研究进展*

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摘要 植物与植食性昆虫在长期的协同进化过程中形成了复杂的互作关系。为应对昆虫取食压力, 植物逐步演化出多层次抗虫机制; 与此同时, 植食性昆虫也相应地发展出反防御策略, 形成动态的“军备竞赛”式进化格局。广泛分布于环境、植物体内及昆虫组织中的微生物群落, 通过“植物-微生物-昆虫”互动模式深刻影响着进化进程。这些微生物不仅参与调控植物的防御反应, 还显著影响昆虫的环境适应性, 为理解物种间互作关系提供了新的研究视角。番茄潜叶蛾 *Tuta absoluta* 原产于南美洲, 是一种世界性恶性入侵害虫, 对茄科作物生产构成严重威胁。本文概述了番茄潜叶蛾与寄主植物的互作以及农田生态系统中常见微生物影响番茄潜叶蛾害虫种群繁衍、植物生长发育和调控植物对番茄潜叶蛾的防御反应的研究进展, 对于进一步理解植物和害虫的互作关系具有重要意义。

关键词 番茄潜叶蛾; 寄主植物; 微生物; 协同进化

Research advances in the interaction between *Tuta absoluta* and plants

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Abstract Plants and herbivorous insects have developed intricate interaction networks through long-term co-evolutionary processes. To counteract herbivory pressure, plants have evolved multi-layered defense mechanisms, while phytophagous insects have correspondingly developed sophisticated counter-defense strategies, resulting in a dynamic "arms race" evolutionary pattern. Microbial communities ubiquitously distributed in the environment, plant tissues and insect systems, which profoundly influence this co-evolutionary trajectory through tripartite "plant-microbe-insect" interactions. These microbial components not only modulate plant defense responses but also significantly affect the environmental adaptability of insects, providing novel perspectives for understanding interspecies interactions. *Tuta absoluta*, a devastating invasive pest native to South America, poses severe threats to global Solanaceous crop production. In this article, we review the research progress on interactions between *T. absoluta* and host Solanaceous plant, and the impact of common microorganisms (e.g., insect symbiotic bacteria, soil microorganisms, and pathogenic microorganisms) in farmland ecosystems on the reproduction of *T. absoluta* populations, plant growth and development, and the regulation of plant defense responses to the *T. absoluta*. This review has great significance for advancing the understanding of plant-pest interactions.

Key words *Tuta absoluta*; host plants; microorganism; coevolution

番茄潜叶蛾 *Tuta absoluta* 是一种全球入侵性农业害虫, 对农业生产特别是番茄产业构成重大威胁, 可导致 80%-100% 的产量损失 (Zhang *et al.*, 2018; Li *et al.*, 2025)。该害虫寄主范

围广泛, 可危害 11 科 50 种植物, 包括马铃薯、茄子、辣椒等重要经济作物; 其幼虫通过取食叶肉组织形成典型的薄层潜道, 在高密度侵染时还会转移危害宿主果实及幼茎腋芽 (Biondi *et al.*,

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2018)。番茄潜叶蛾具有单季多代繁殖、进化迅速等特性,正逐渐成为全球性常发性害虫。由于对番茄作物的毁灭性影响,该害虫被形象地称为“番茄埃博拉病毒”(Zhang *et al.*, 2018)。番茄潜叶蛾于 1917 年在南美洲秘鲁首次报道,自 2006 年在西班牙东部首次观察到以来,番茄潜叶蛾已经入侵了欧洲、非洲和亚洲的 110 多个国家(Desneux *et al.*, 2010, 2011, 2022; Biondi *et al.*, 2018; Mansour *et al.*, 2018; Han *et al.*, 2019)。我国于 2017 年在新疆伊犁首次发现其危害,随后该害虫迅速扩散至全国 20 余个省(直辖市、自治区)(张桂芬等, 2020, 2025)。我国是茄科作物种植大国,也是世界上番茄第三大种植国和加工番茄制品第一大出口国。同时马铃薯作为全球第四大粮食作物,也在我国农业生产中占据重要地位(Xian *et al.*, 2017)。一旦番茄潜叶蛾暴发成灾,可能对我国番茄和马铃薯产业造成毁灭性打击。鉴于其严重危害性,农业农村部于 2023 年将其列入“一类农作物病虫害名录”,实施专项防控管理。

植物与昆虫相互作用,形成了复杂的生态网络。植食性昆虫依赖植物资源完成其生活史,同时通过自然选择压力驱动植物防御系统的适应性进化。植物通过识别昆虫相关分子模式,激活局部或系统的防御反应;而昆虫则通过适应进化反防御机制维持其取食优势,形成动态平衡的“军备竞赛”式协同进化(Schuman and Baldwin, 2016; Erb and Reymond, 2019)。同时,微生物广泛存在于环境及植物和昆虫体内,在昆虫与植物的攻防互作中发挥了不可忽视的作用,并且一定程度上促进了植物-昆虫攻防方式的多样性(Schmidt and Engel, 2021)。本文概述了番茄潜叶蛾和寄主植物的互作关系,重点揭示了微生物群落在该互作过程中的关键调控作用,为深入解析植物-害虫互作关系提供了新的理论视角,同时为未来开发基于微生物组的害虫绿色防控策略奠定了重要基础。

1 番茄潜叶蛾的寄主植物选择

番茄潜叶蛾是一种多食性害虫,其寄主范围

广泛,主要危害茄科植物,对番茄、马铃薯、茄子、烟草等重要经济作物的生产构成严重威胁(Mohamed *et al.*, 2015; Abbes *et al.*, 2016; Vivekanandhan *et al.*, 2024)。此外,该害虫还危害豆科、苋科、旋花科和锦葵科等非茄科植物,并通过野生寄主(如龙葵)维持种群延续,因此,其具有多食性行为和对各种农作物与杂草物种的适应性(Abbes *et al.*, 2016; Bawin *et al.*, 2016)。

然而,在如此广泛的寄主范围内,番茄潜叶蛾尤其嗜食番茄,这一特性与其极强的生态适应性和寄主适应性密切相关(Biondi *et al.*, 2018)。当前,番茄品种均无法对该害虫实现完全抵抗,但不同品种的感抗水平存在显著差异(Aslan and Birgücü, 2022)。例如,野生番茄 *Solanum galapagense* 对番茄潜叶蛾表现出高度抗性,而 *Solanum pimpinellifolium* 较其他野生品种则更加易感(Rakha *et al.*, 2017)。在栽培品种中,FBT1 比 Kanon F1 和 Cobra 26 F1 更易感虫,发育速度也更快(Sawadogo *et al.*, 2022)。不同番茄品种对番茄潜叶蛾表现出感抗性差异,可能与番茄潜叶蛾对品种挥发性有机化合物和次生代谢产物的选择性识别机制密切相关(Barbehenn *et al.*, 2011)。研究表明,植食性昆虫能够感受寄主的次生代谢产物和挥发性物质等化学信号来定位适宜寄主植物进行取食和产卵活动(Clavijo McCormick *et al.*, 2012; Beyaert and Hilker, 2014)。例如,番茄潜叶蛾显著偏好释放高浓度萜烯的番茄植株(Caparrós Megido *et al.*, 2014),这与该虫嗅觉受体对特定挥发性有机化合物的特异性识别有关。在产卵选择性方面,番茄潜叶蛾雌虫不仅表现出对适宜寄主的明显偏好,在选定的寄主上还会优先选择叶尖区域产卵(Proffitt *et al.*, 2011; Cherif *et al.*, 2013)。进一步研究发现,这一产卵位点选择行为主要受到植物释放的特定挥发性有机化合物的调控,其中 δ -榄香烯等关键信号分子起着决定性作用(Anastasakis *et al.*, 2015)。昆虫在复杂的生态环境中寻找适宜的寄主是其生存繁衍的关键策略,寄主植物释放的化学信号通过调控害虫的产卵偏好、取食选

择、生存适应等关键生命活动,直接影响昆虫种群的适合度。因此,了解介导昆虫寄生定位的化学物质及其作用机制,不仅有助于阐明植物-害虫协同进化关系,更能为开发基于化学生态学的害虫绿色防控技术提供理论支撑。

2 植物对番茄潜叶蛾的防御机制

植物不仅为植食性昆虫提供营养资源和繁殖场所,更在长期协同进化过程中形成了复杂的防御体系 (Schuman and Baldwin, 2016)。番茄潜叶蛾与植物互作中,植物通过多层次的防御机制来抵御其侵害。从防御策略来看,植物抗性机制通常被划分为组成型防御和诱导型防御。

2.1 组成型防御

植物通过组成型防御构建了物理-化学双层防御屏障。在物理防御层面,植物表面的蜡质层、茸毛、刺状结构形成机械屏障,直接阻碍昆虫取食 (Awmack and Leather, 2002)。其中,表皮毛是植物表皮细胞向外凸起的特化毛状结构,有些植物的表皮毛具备合成和分泌代谢物能力,称为腺毛,又被称为植物的“代谢工厂” (Huchelmann *et al.*, 2017)。据报道,番茄中最早鉴定调控表皮毛发育的两个基因是 *Hairless* 和 *odorless-2*, 当 *odorless-2* 基因发生突变后,会使 I 型和 VI 型腺毛的形态发生扭曲和畸形 (I 型腺毛主要合成酰基糖; VI 型腺毛是萜烯类化合物的主要合成场所), 同时显著降低了倍半萜的含量, 最终导致番茄对烟草天蛾 *Manduca sexta* 的抗虫性减弱 (Kang *et al.*, 2010)。MYB 类转录因子 SIMX1 对番茄腺毛和非腺毛的密度及其对甜菜夜蛾 *Spodoptera exigua* 的抗性进行正调控 (Ewas *et al.*, 2016, 2017)。除此之外,毛状体在植物防御许多害虫方面起着至关重要的作用 (Belete, 2018)。番茄品种对番茄潜叶蛾的结构型抗性主要与植株毛状体的类型、密度,以及它们所产生和储存的防御性化学物质相关 (Fernandes *et al.*, 2012; Sohrabi *et al.*, 2016, 2017)。

在化学防御层面,植物体内所富含的防御相

关的黄酮、萜类、生物碱等次生代谢产物在番茄直接抵御害虫中同样发挥了重要作用 (Awmack and Leather, 2002)。抗性番茄品种因其部分挥发物丧失而对番茄潜叶蛾的吸引能力减弱 (Proffit *et al.*, 2011)。同时,番茄品种间姜油烯、酰基糖和 2-三苯甲酮等代谢物质的含量差异会显著影响番茄潜叶蛾的适合度 (Maluf *et al.*, 2010; Ghaderi *et al.*, 2017)。例如,番茄中酰基糖含量与抗虫性呈正相关,酰基糖含量较高的番茄品种对番茄潜叶蛾、甜菜夜蛾和谷实夜蛾 *Helicoverpa zea* (Juvik *et al.*, 1994; de Resende *et al.*, 2006) 表现出更强的抗性。酚胺是一种广泛存在于各种植物中的次生代谢物,番茄潜叶蛾危害显著诱导番茄体内酚胺化合物的积累 (Roumani *et al.*, 2022), 这些化合物可能在植物防御中起重要作用。此外,番茄中含有的绿原酸和咖啡酸具有抗虫功能,可有效抑制斜纹夜蛾 *Spodoptera litura* 幼虫的发育 (Kundu *et al.*, 2018)。未来针对商业化高抗番茄潜叶蛾品种的选育与开发,可基于“腺毛密度-抗虫物质含量”与抗虫性的正相关机制,优先选择高密度腺毛且抗虫物质丰富的番茄品系作为亲本杂交。选育过程中需同步评估抗性对番茄产量、品质的潜在影响,通过性状平衡筛选兼顾抗虫性与生产实用性的品系,从而实现番茄品种更高的经济价值。

2.2 诱导型防御

植物诱导型防御是植物应对虫害的动态响应机制。当受到昆虫取食后,植物能够快速激活受损部位的防御响应,这一过程主要依赖于外源合成的植物激素产生诱导型抗性 (Belete, 2018)。植物对植食性昆虫的诱导型防御涉及合成多种特异性次生代谢产物以及抗营养酶和蛋白,其中咀嚼式口器昆虫诱导的植物防御反应主要由茉莉酸途径调控 (Erb *et al.*, 2012; Grinberg-Yaari *et al.*, 2015; Erb and Reymond, 2019)。研究表明,番茄植株一旦遭到番茄潜叶蛾侵害,便会激活由茉莉酸 (Jasmonic acid, JA) 途径介导的抗性机制 (Strapasson *et al.*, 2014; De Backer *et al.*, 2015; Silva *et al.*, 2017)。此外,时序

分析揭示了这一防御过程的动态特征,在番茄潜叶蛾为害初期叶片中茉莉酸含量下降,随后从 12 h 开始持续升高 (Chen *et al.*, 2021), 这种激素水平的时序变化可能精准对应着防御反应的启动过程。值得注意的是,品种间抗性差异同样显著,高抗性的番茄品种会通过增加毛状体密度并启动 JA 途径等方式,有效抵御番茄潜叶蛾的取食 (D'Esposito *et al.*, 2021)。

茉莉酸 (JA) 信号通路作为植物响应昆虫侵害的核心调控枢纽,不仅能够直接调控抗性物质的合成,同时能够诱导植食性昆虫植物挥发物 (Herbivore-induced plant volatiles, HIPVs) 的合成与释放。虫害诱导挥发物 (HIPVs) 主要通过 3 种途径实现对昆虫的防御: (1) 通过虫害诱导挥发物直接干扰害虫产卵和取食行为的方式减少害虫的进一步危害 (Turlings and Erb, 2018)。研究表明,当番茄植株遭受番茄潜叶蛾幼虫取食时,会特异性释放包括 (Z)-3-己烯-1-醇、水杨酸甲酯和吲哚等在内的多种植物挥发物,这些化合物可以趋避成虫,影响其产卵选择 (Anastasaki *et al.*, 2018)。值得注意的是,番茄潜叶蛾成虫的产卵行为本身也能诱导番茄植株释放 (Z)-3-己烯-1-醇,这属于植物对机械损伤的典型防御反应 (Milonas *et al.*, 2019)。因为健康植株中 (Z)-3-己烯-1-醇的浓度通常维持在较低水平 (Proffit *et al.*, 2011), 而植株受到不同因素的损伤后其浓度显著增加 (Buttery *et al.*, 1987)。当番茄植株受到番茄潜叶蛾产卵刺激时,其顶空挥发物中的多种倍半萜类物质 (如 δ -榄香烯) 含量会显著上升 (Anastasaki *et al.*, 2015)。(2) 通过释放虫害诱导挥发物吸引寄生性或捕食性天敌来防控害虫 (Heil and Silva Bueno, 2007)。研究表明,在番茄潜叶蛾-番茄-寄生蜂 *Dolichogenidea gelechiidivoris* 三者互作系统中,番茄潜叶蛾幼虫的取食行为会激活番茄的防御响应,显著诱导释放更多的 α -蒎烯、 β -月桂烯、 α -水芹烯、 β -水芹烯、(E)- β -罗勒烯、(E)- β -石竹烯、 α -葑烯等挥发物用以吸引寄生蜂 (Ayelo *et al.*, 2022)。此外,在番茄潜叶蛾-番茄-短管赤眼蜂 *Trichogramma pretiosum* 三者

的研究中,外源施用茉莉酸甲酯于番茄植株时可明显增加寄生蜂的觅食行为和寄生率 (Weber *et al.*, 2023)。(3) 植物可通过虫害诱导挥发物预警相邻植株激活其防御反应 (Heil, 2014)。外施苯丙氨酸不仅可以显著地诱导番茄释放苯丙烷衍生的挥发物苯甲醛、苯乙醛和苯乙醇,增强其对番茄潜叶蛾的抗性,还提高了邻近未处理植物的抵抗力 (Kumar *et al.*, 2024)。由此可见,植物挥发物在植物-昆虫-天敌等的多营养级互作过程中发挥着关键的纽带作用。

此外,番茄潜叶蛾的取食行为还会促使植株分泌更多的防御性抗虫物质。研究表明,番茄潜叶蛾幼虫取食数小时后,植株在取食部位及远端器官中会诱导产生防御性酶,如多酚氧化酶 (Polyphenol oxidase, PPO) 和过氧化物酶 (Peroxidase, POD) 等 (Coqueret *et al.*, 2017)。这种诱导型防御为培育新型番茄品系提供了良机: (1) 释放更高量的特定挥发性物质以增强对害虫天敌的吸引力; (2) 可诱导产生更强烈的酶类防御反应。

2.3 植物对番茄潜叶蛾防御的协同与权衡

植物防御反应交叉关联和抗性的时空分布模式可能影响寄主植物上的各类害虫及有益物种的发育 (Stout *et al.*, 2006; Mouttet *et al.*, 2011)。研究发现,粉虱危害番茄后导致番茄潜叶蛾幼虫适应性下降,却促进了白粉病发生 (Mouttet *et al.*, 2013), 这可能源于 JA/SA 通路的交互作用 (Thaler *et al.*, 1999)。因此,调控番茄对番茄潜叶蛾的抗性可能会影响其微观和宏观生物群落,从而对产量引发难以预测的波动,仍需谨慎权衡其潜在生态影响。

尽管诱导型防御和组成型防御在机制和特点上有所不同,但它们在实际的植物防御过程中往往相互补充,共同作用以提高植物的整体防御能力。研究发现,不同防御成分之间的协同效应增强了植物对昆虫的防御 (Belete, 2018)。例如,番茄中的生物碱、酚类与蛋白酶抑制剂的协同作用显著抑制昆虫取食和消化 (War *et al.*, 2012)。在烟草中,胰蛋白酶抑制剂和尼古丁的

表达共同增强了对甜菜夜蛾的防御反应 (Steppuhn and Baldwin, 2007)。此外,一些研究表明,植物在组成型防御和诱导型防御之间存在一种资源分配上的权衡。组成型防御水平高的番茄品种 Castlemart 和 JA 过表达基因型 35S::prosys 表现出低水平的诱导型防御,而组成型防御水平低的番茄品种 MoneyMaker 则表现出高水平的诱导型防御 (Zhang *et al.*, 2020)。不同番茄品种在防御机制上表现出显著的功能权衡,可能是由于遗传背景、生理特性和进化策略的不同所导致的。同时,植物抗性和易感性品种的转录组学和代谢组学分析表明植物存在不同的资源分配策略:抗性品种倾向于将资源优先分配给组成防御机制,而易感品种则主要依赖诱导性反应 (Broekgaarden *et al.*, 2007; War *et al.*, 2012)。这种策略反映了在即时保护与代谢经济性之间的进化平衡。

3 番茄潜叶蛾对植物防御的适应性机制

在植物与植食性昆虫的长期协同进化中,双方的防御与反防御策略形成了动态平衡的军备竞赛。寄主植物防御性状的多样性和昆虫所在生态环境的复杂性直接驱动了植食性昆虫反防御策略的多样化 (Winde and Wittstock, 2011; Alba *et al.*, 2015; Kant *et al.*, 2015)。植物通过组成型防御和由昆虫相关分子模式 (Herbivore-associated molecular patterns, HAMPs) 激活的植物细胞免疫 (AMPs-triggered immunity, PTI) 构成基础防御系统。这一免疫反应过程中会促使植物体内活性氧 (Reactive oxygen species, ROS) 爆发,强化细胞壁,并诱导防御相关基因表达,能够有效抵御多数植食性昆虫的侵害。然而,部分昆虫可通过分泌唾液效应蛋白来抑制或干扰植物 PTI 反应,或通过行为上的改变,避开植物的防御反应,从而适应寄主植物 (Musser *et al.*, 2005; Dong *et al.*, 2023)。

昆虫唾液蛋白是触发植物防御反应的关键因子,其作用机制主要包括 3 种 (Erb and Reymond, 2019): (1) 昆虫利用唾液蛋白适

应植物细胞壁。细胞壁是植物组成型防御的关键组成部分,其不仅通过增强植物组织机械强度形成物理屏障,还能干扰昆虫消化过程,从而有效降低昆虫的取食能力。据报道,棉铃虫 *Helicoverpa armigera* 取食棉花叶片后,唾液腺中的 β -1,4-内切葡聚糖酶活性显著增强,有效降解植物细胞壁中的纤维素,帮助棉铃虫适应棉花细胞壁的物理屏障功能 (Zheng *et al.*, 2022)。抗性品种 (BR221) 番茄通过细胞壁修饰机制抵御番茄潜叶蛾侵害,这些反应可能对应着害虫唾液蛋白的降解作用 (D'Esposito *et al.*, 2021)。(2) 昆虫利用唾液蛋白酶降解植物防御性次生代谢物。谷实夜蛾 *Helicoverpa zea* 幼虫通过唾液中的葡萄糖氧化酶 (Glucose oxidase, GOX) 有效降低烟草叶片中防御性化合物烟碱 (Nicotine) 的积累 (Musser *et al.*, 2002)。在甜菜夜蛾 *Spodoptera exigua*、烟青虫 *Helicoverpa assulta* 和棉铃虫的唾液中均发现 GOX,可抑制多种作物中 JA 的合成 (Weech *et al.*, 2008; Yang *et al.*, 2017)。(3) 昆虫唾液中的效应蛋白可以通过抑制植物防御反应,从而为害虫创造有利的取食环境,促进其生长发育。研究表明,烟粉虱 *Bemisia tabaci* 唾液蛋白 Bt56 作为一种效应子,在取食时进入烟草后与转录因子 NTH202 互作,通过诱导水杨酸 (Salicylic acid, SA) 积累以拮抗茉莉酸 (JA) 信号通路,从而抑制植物的抗虫防御反应 (Xu *et al.*, 2019)。最近,研究人员发现番茄潜叶蛾的口腔分泌物效应子基因 REPAT38 能快速调控植物的防御反应:其在取食 0.5 h 可诱导植物气孔关闭,取食 1 h 后抑制茉莉酸、乙烯 (Ethylene, ET) 和脱落酸 (Absciscic acid, ABA) 的合成。此外,7 个植物激素响应基因 (Allene oxide cyclase [AOC]、MYC2、1-Aminocyclopropane-1-carboxylate synthase 1 A [ACS1A]、PAL、Pathogenesis related gene [PR1]、Ethylene insensitive3-like2 [EIL2] 和 Serine/threonine-protein kinase 2E [SRK2E]) 在不同时间点受到抑制,从而削弱番茄对昆虫的防御能力,有利于昆虫适应植物 (Wang *et al.*, 2024b)。此外,昆虫唾液中含有影响植物挥发物释放的分子,从而可能改变植物吸引天敌的生态功能

(Delphia *et al.*, 2006)。由此可见, 唾液蛋白介导的昆虫-植物相互作用是植物防御和昆虫适应之间的一种动态竞争模式。

4 微生物在害虫-植物互作中的作用

4.1 微生物对植物生长和防御的调控作用

植物根系与微生物群落形成复杂的共生网络, 显著影响植物的生长发育和抗虫能力。根际微生物组通过多种机制促进植物生长 (Davison, 1988)。研究发现, 印度梨形孢 *Serendipita indica* 是耐旱根际真菌, 可以在干旱胁迫下提高番茄植物的水分吸收能力以及氮、钙、钾和磷等必需营养素的吸收。这是通过扩展根系、积累高水平的脯氨酸以及调节叶片温度以促进气孔关闭来实现这一点 (Boorboori and Zhang, 2022)。因此, 尽管受到干旱胁迫, 番茄植物仍能更好地生长。丛枝菌根真菌 (Arbuscular mycorrhizal fungi, AMF) *Rhizophagus intraradices* 和 *Funneliformis mosseae* 可减少食根线虫 *Nacobbus aberrans* 进入番茄根部 (Marro *et al.*, 2018)。恶臭假单胞菌 *Pseudomonas putida* 可以促进番茄幼苗的生长, 还能抑制土壤传播的植物病原体孢子萌发 (Lee *et al.*, 2005)。当植食性昆虫侵害番茄时, 根际微生物可提升番茄抗虫性。

植物受到非生物或生物胁迫时, 通过采取“Cry for help”策略, 从环境中招募有益的微生物, 来增强自身的防御能力 (Liu and Brettell, 2019)。当葡萄植株接种了从葡萄藤内生境中分离的 *Enterobacter ludwigii* EnVs6 菌株后, 其一系列代谢特征发生变化, 防御物质香草酸 (Vanillic acid) 浓度显著增加, 而儿茶素 (Catechin)、七叶苷 (Esculin)、熊果苷 (Arbutin)、鞣花酸 (Astringi)、白藜芦醇 (Pallidol)、蛇葡萄素 (Ampelopsin)、D-四角苷 (D-quadrangularin) 和异厚朴酚 (Isohopeaphenol) 的浓度则有所下降, 表明植物防御途径的激活 (López-Fernández *et al.*, 2016)。从根际土壤中分离的窄食单胞菌 *Stenotrophomonas* sp. T6-4 诱导 JA 依赖的防御反应, 增强了番茄对斜纹夜蛾的抗性 (Ling *et al.*,

2022)。这些发现揭示了植物-微生物互作在作物抗逆育种中的巨大潜力, 为开发基于微生物组的农业应用提供了理论依据。

4.2 微生物对番茄潜叶蛾的影响

微生物不仅会影响寄主植物的生长发育和防御反应, 对害虫的行为、生长发育、繁殖等方面也发挥重要作用。番茄的共生真菌棘孢木霉菌 *Trichoderma asperellum* M2RT4 能够通过减少产卵、幼虫蛀道、化蛹以及成虫羽化的数量, 抑制番茄潜叶蛾的生长 (Agbessenou *et al.*, 2020)。此外, 摩西球囊霉菌 *Funneliformis mosseae* 和恶臭假单胞菌 *Pseudomonas putida* 是植物重要的根际微生物, 能够抑制番茄潜叶蛾的生长, 幼虫期和蛹期均延长 (Zhao *et al.*, 2024)。丛枝菌根真菌与番茄根系形成共生关系, 影响害虫的繁殖能力。番茄接种丛枝菌根真菌后, 导致番茄潜叶蛾的发育时间显著延长, 繁殖潜力显著降低 (Shafiei *et al.*, 2024)。

昆虫体内共生菌则通过营养互补和代谢调控影响其适应性。昆虫与共生菌之间的共生关系有可能影响其宿主的生物学和生态学 (Kontsedalov *et al.*, 2008)。沃尔巴克氏细菌 *Wolbachia* 是包括番茄潜叶蛾在内的许多昆虫体内广泛存在的内生菌。例如, 经过长期共生, 在果蝇自然种群中的沃尔巴克氏菌在 20 年内从寄生变为更加互惠共生 (Weeks *et al.*, 2007)。斑幕潜叶蛾 *Phyllonorycter blancardella* 体内的沃尔巴克氏菌通过操纵寄主植物激素, 在原本衰老发黄的叶片上创造具有光合活性的绿色斑块, 从而间接影响幼虫的营养供给 (Kaiser *et al.*, 2010), 这一表型使得幼虫能够在生命周期中营养受限的阶段完成发育。与茶长卷蛾 *Homona magnanima* 相关的沃尔巴克氏体菌株 wHm-c 不仅缩短了幼虫发育时间并增加了蛹重, 这对宿主生存和繁殖具有积极意义 (Arai *et al.*, 2019)。同样, 灰茶尺蠖 *Ectropis grisescens* 沃尔巴克氏体菌株 wGri 也能增强宿主的繁殖力 (Zhang *et al.*, 2021)。在番茄潜叶蛾成虫和幼虫阶段均检测到沃尔巴克氏细菌 (Mehrkhou *et al.*, 2021), 但与已被深入研究的生殖操纵现象的昆虫相比

(Duploux and Hornett, 2018), 该共生菌对番茄潜叶蛾的适合度及其分子机制仍有待阐明。

肠道共生菌可以通过提供营养物质来帮助昆虫适应宿主。粘质沙雷氏菌 *Serratia marcescens* FLGB16 通过分泌几丁质酶促进小菜蛾 *Plutella xylostella* 幼虫的生长发育 (Indiragandhi et al., 2008)。肠道微生物组还能正反馈东方菜粉蝶 *Pieris canidia* 的生长, 导致存活率升高以及体重增加 (Wang et al., 2020)。肠道微生物组普遍具有调控宿主代谢的关键功能, 同时, 肠道微生物群可以通过启动免疫反应增强宿主的免疫能力。转录组学揭示了海灰翅夜蛾 *Spodoptera littoralis* 幼虫肠道中的孟氏肠球菌 *Enterococcus mundtii* 通过上调耐受碱性胁迫免疫反应通路, 形成生物膜和双组分信号系统及抵抗 ROS 的免疫反应通路, 以协同适应宿主的双重胁迫。尽管这些共生菌依赖宿主获取氨基酸和脂肪酸, 但各种代谢途径之间的差异调节表明幼虫后肠中孟氏肠球菌的赖氨酸合成途径富集 (Mazumdar et al., 2021)。此外, 肠道共生菌参与了昆虫对杀虫剂的抗性。其中, 肠球菌属 *Enterococcus* 在杀虫剂降解方面已被广泛报道。番茄潜叶蛾肠道细菌孟氏肠球菌可以降解氯虫苯甲酰胺, 从而提高番茄潜叶蛾对氯虫苯甲酰胺的抗性 (Chen et al., 2024)。斜纹夜蛾肠道中的 *Enterococcus mundtii* M2A1 和 *Enterococcus casseliflavus* M2B1 的富集能够增强灭多威的代谢, 从而提高昆虫对杀虫剂的抗性 (Hu et al., 2022)。小菜蛾和家蚕 *Bombyx mori* 肠道中的肠球菌属增强了宿主的杀虫剂抗性 (Xia et al., 2018; Chen et al., 2020)。因此, 抗杀虫剂昆虫品系的肠道微生物组可作为具有农药降解功能微生物的重要筛选来源。

4.3 微生物对植物与害虫互作的影响

物种间的共生关系可以赋予个体利用新资源或抵御胁迫的能力, 是生物多样性的重要体现 (Flórez et al., 2015)。土壤微生物组在植物生长发育中起着重要作用, 对植物生理和生态功能的调节也具有重要意义 (Bender et al., 2016;

Rasool et al., 2025)。当遭受植食性昆虫持续取食胁迫时, 植物能够招募与防御相关的微生物, 进而激活一系列复杂的防御机制。而在温室防护、滴灌施肥与害虫综合管理等优化管理的现代农业条件下, 微生物接种剂可以提高植物对番茄潜叶蛾的抗性 (Minchev et al., 2024)。更为复杂的是, 昆虫唾液腺和肠道共生微生物也参与这一互作过程。唾液微生物通过昆虫的取食行为随唾液分泌转染至寄主植物组织, 干扰植物对昆虫防御反应, 调控昆虫生长 (Yamasaki et al., 2021; Zhao et al., 2023)。番茄潜叶蛾取食过程中, 其唾液携带的蒙氏肠球菌 *Enterococcus mundtii* 能显著改变番茄的生理状态, 接种该菌株后, 植株 POD 活性和可溶性糖含量下降, 同时可溶性蛋白、丙二醛含量提高, 这些变化直接影响了植物的防御能力 (曾娜等, 2025)。在草地贪夜蛾 *Spodoptera frugiperda* 中, 通过抗生素处理减少野外采集的幼虫体内的微生物数量后, 植物对幼虫取食及其口腔分泌物的防御反应增强。同时, 从野外采集的幼虫口腔分泌物中分离出的细菌, 如泛菌属 *Pantoea*、拉恩菌属 *Rahnella* 和肠杆菌属 *Enterobacter*, 能够抑制番茄中过氧化物酶和蛋白酶抑制剂的活性 (Acevedo et al., 2017)。

肠道菌群则通过增强解毒代谢来提高昆虫对植物次生代谢物的耐受性, 使其存活率增加 (Ge et al., 2021; Xia et al., 2023)。小菜蛾的阴沟肠杆菌 *Enterobacter cloacae*、阿氏肠杆菌 *Enterobacter asburiae* 和麦芽香肉杆菌 *Carnobacterium maltaromaticum* 是肠道中的优势菌群, 参与了植物细胞壁分解、植物酚类物质解毒和氨基酸合成, 这些肠道共生菌与自身的基因组相辅相成, 使小菜蛾更好的利用植物资源 (Xia et al., 2017)。此外, 取食不同寄主植物的番茄潜叶蛾幼虫肠道细菌组成存在显著差异。以番茄为食的番茄潜叶蛾肠道优势菌为阴沟肠杆菌; 而以马铃薯为食的优势菌是鸡肠球菌 *Enterococcus gallinarum*。进一步研究发现, 取食马铃薯的番茄潜叶蛾肠道细菌鸡葡萄球菌 *Staphylococcus gallinarum* 有助于提高番茄潜叶蛾对马铃薯的适应性, 这可能与 *Staphylococcus gallinarum* 可以

促进解毒代谢酶的合成, 降解植物防御物质有关 (Shang *et al.*, 2024)。总之, 这种由微生物构成的调控网络, 不仅反映了植食性昆虫对寄主的高度适应, 也为开发新型防控策略提供了多重分子靶点。

5 小结与展望

番茄潜叶蛾作为我国重要的入侵害虫, 其地理分布持续扩张, 且在不同生态区的危害程度存在显著差异 (Wang *et al.*, 2024a)。昆虫与植物之间存在着多层次的相互作用关系, 这种关系在生态学和进化学上都具有重要意义 (Biere and Tack, 2013)。其中, 微生物组在害虫适应性进化与寄主植物抗性形成中具有关键作用, 这为发展新型防控策略提供了重要思路。与昆虫相关的微生物是新型化合物和酶的重要来源, 这些化合物和酶在医学、工业、生物修复和农业领域具有潜在的生物技术应用价值。同时, 昆虫肠道微生物群中含有能够促进植物生长的细菌 (Plant growth-promoting bacteria, PGPB), 这些细菌能够促进植物生长并提高产量, 同时调控植物抗虫能力。深入解析植物-昆虫-微生物互作网络, 将推动建立更精准的生态防控体系, 进一步服务于农业害虫防治和生态保护, 为实现农业可持续发展提供新途径。因此, 对于未来防治番茄潜叶蛾提出如下展望: (1) 加强杀虫微生物菌剂的研发力度。昆虫病原真菌 (如绿僵菌 *Metarhizium anisopliae*), 细菌 (如苏云金芽孢杆菌 *Bacillus thuringiensis*) 等菌剂对番茄潜叶蛾的成虫和幼虫均具有显著的灭杀效果。微生物制剂是化学农药的理想可持续替代品, 有助于构建环境友好和经济可行的害虫防治策略。要充分发挥昆虫病原体在可持续农业综合防治中的作用, 持续开展研究创新势在必行。(2) 基于植物次生代谢物的番茄潜叶蛾生物源农药开发。在番茄抗性相关次生代谢物中, 黄酮类对番茄潜叶蛾的毒杀效果显著高于生物碱类。然而, 番茄潜叶蛾的取食能特异性抑制苯丙氨酸途径, 从而减少番茄中黄酮类的合成与积累。据此推测, 番茄潜叶蛾可能对黄酮类物质的解毒能力较弱, 并进化出此种反防御

机制以减轻其毒害。目前, 关键起效的具体黄酮化合物尚未明确。鉴定该高活性单体, 不仅有助于新型生物农药的研发, 也将为揭示番茄潜叶蛾调控寄主次生代谢的特殊效应机制提供关键目标化合物。

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