烟粉虱−双生病毒−寄主植物互作机制的研究进展

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摘要：烟粉虱*Bemisia tabaci*与其传播的双生病毒以及寄主植物之间构成了农业生态系统中精密且复杂的三者互作网络，这种互作关系远超出了传统的病原−媒介互作范畴，演化为一场涉及基因表达重塑、代谢网络调控及神经行为操纵的进化博弈。双生病毒依赖烟粉虱进行持久非增殖型传播，借助烟粉虱体内蛋白及内共生菌突破传播屏障，在长期的协同进化中获得了通过效应因子劫持植物茉莉酸信号通路及次生代谢途径的能力，从而间接调控烟粉虱的取食与偏向行为。最新的研究发现病毒能够直接侵入烟粉虱的神经与免疫系统，通过诱导脑部神经退行性病变、破坏嗅觉受体表达以及重塑胞内免疫稳态，实现对媒介行为的精准操纵。基于病毒通过直接与间接途径调控烟粉虱行为的双重机制研究，该文系统梳理烟粉虱−双生病毒−寄主植物三者间的互作模型，即病毒对烟粉虱的“推−拉”策略，总结基于此策略的病毒传播机制，并探讨病毒与烟粉虱的互利共生如何影响二者在全世界范围内的广泛传播与流行。

关键词：烟粉虱；双生病毒；寄主植物；病毒传播；“推−拉”策略

Research progress on the interaction mechanisms among tobacco whitefly *Bemisia tabaci*, geminiviruses, and host plants

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Abstract: Tobacco whitefly *Bemisia tabaci*, the geminiviruses it transmits, and host plants constitute a sophisticated and complex tripartite interaction network in agricultural ecosystems. This interplay extends far beyond the traditional pathogen-vector relationship and has evolved into an evolutionary arms race involving gene expression remodeling, metabolic network regulation, and neurobehavioral manipulation. Geminiviruses rely on *B. tabaci* for persistent circulative transmission and overcome transmission barriers with the aid of proteins and endosymbiotic bacteria in the insect. During long-term coevolution, geminiviruses have acquired the ability to hijack plant jasmonic acid signaling pathways and secondary metabolic pathways through effectors, thereby indirectly regulating the feeding and preference behaviors of *B. tabaci*. Recent studies have further revealed that viruses can directly invade the neural and immune systems of *B. tabaci*, including neurodegeneration in the brain, disrupting olfactory receptor expression, and remodeling intracellular immune homeostasis to achieve precise manipulation of vector behavior. Based on the dual mechanisms by which the viruses regulate *B. tabaci* behaviour through direct and indirect pathways, this review systematically summarizes the tripartite interaction

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model among *B. tabaci*, geminiviruses, and host plants, namely the viral 'push-pull' strategy towards *B. tabaci*, summarizes the viral transmission mechanisms based on this strategy, and discusses how mutualism between geminiviruses and *B. tabaci* influences their widespread transmission and prevalence across the globe.

Key words: *Bemisia tabaci*; geminivirus; host plants; virus transmission; "push-pull" strategy

烟粉虱 *Bemisia tabaci* 是全球范围内最具破坏性的刺吸式害虫之一，其不仅通过直接刺吸植物韧皮部汁液导致作物生长受阻、叶片黄化及分泌蜜露诱发煤污病，而且可作为超级媒介传播超过400种植物病毒，绝大多数病毒为双生病毒科 *Geminiviridae* 菜豆金色花叶病毒属 *Begomovirus* 病毒（De Barro et al.，2011；Gilbertson et al.，2015；Ghosh & Ghanim，2021；胡明鑫等，2023），其中番茄黄化曲叶病毒（tomato yellow leaf curl virus，TYLCV）、木尔坦棉花曲叶病毒（cotton leaf curl Multan virus，CLCuMuV）和非洲木薯花叶病毒（African cassava mosaic virus，ACMV）等严重威胁着番茄、棉花、木薯等重要经济作物和粮食作物的生产安全，每年在全球造成的农业经济损失高达数十亿美元（Navas-Castillo et al.，2011；Scholthof et al.，2011；Sattar et al.，2013；Yan et al.，2021）。

在早期的植物病理学认知中，媒介昆虫多被视为病毒传播过程中被动的媒介载体（Ng & Falk，2006；Blanc et al.，2014）。然而，随着"媒介操纵假说"的提出与不断验证，这一观点发生了根本性转变。该假说认为，植物病毒在进化压力的驱动下，获得了一种能够显著改变寄主植物表型（间接操纵）或直接重塑媒介昆虫生理行为（直接操纵）的能力，以最大化其获取和传播病毒的效率（Mauck et al.，2012；Luan et al.，2013；Liang et al.，2025）。如TYLCV侵染导致的番茄叶片黄化表型及挥发物组分变化可吸引烟粉虱取食完成获毒（Fang et al.，2013；Johnston & Martini，2020）；同时当烟粉虱获毒后其对带毒植株的趋性发生改变（Fang et al.，2013）；另外，中国番茄黄化曲叶病毒（tomato yellow leaf curl China virus，TYLCCNV）和TYLCV能够改变烟粉虱的取食行为，从而增加对病毒的获取效率（Moreno-Delafuente et al.，2013；He et al.，2015）。但早年受限于技术手段，这些研究基本局限在生态学层面，缺乏更深入的分子机制解析（Zhao et al.，2022）。

近年来，随着技术手段的成熟和研究的逐步深入，国内学者对烟粉虱–双生病毒–寄主植物这一复杂互作网络进行了解析，构建了从宏观生态到微观分子的多层次理论体系。从病毒在媒介体内的循环路径解析（Wang et al.，2016），到发现病毒诱导媒介昆虫的神经退行性病变（Wang SF et al.，2020），再到病毒利用植物挥发物和昆虫受体进行的"推–拉"操纵（Liang et al.，2025），这些研究不仅极大地丰富了协同进化理论，也为开发基于阻断互作链条的新型防控技术提供了关键靶点。本文将围绕这些核心进展，对烟粉虱–双生病毒–寄主植物互作的分子机制进行系统性综述。

1 烟粉虱传播双生病毒的生物学基础

双生病毒是一类单链环状DNA病毒，普遍由媒介烟粉虱以持久非增殖型方式传播（Hanley-Bowdoin et al.，2013；Rosen et al.，2015）。这种传播模式意味着病毒粒子必须在昆虫体内经历一段复杂的跨膜运输、循环和潜伏过程，才能具备再次侵染植物的能力，这一过程涉及病毒对昆虫体内多重生物屏障的突破以及与昆虫蛋白的特异性互作（Hogenhout et al.，2008；Ghanim，2014；Czosnek et al.，2017）。

1.1 病毒在媒介体内的循环路径与关键屏障

当烟粉虱取食感病植物韧皮部汁液时，病毒粒子首先进入烟粉虱的口针，然后随植物汁液进入烟粉虱的消化道，中肠是病毒进入昆虫体腔的第一道关键屏障（Hogenhout et al.，2008）。研究表明，双生病毒主要通过受体介导的网格蛋白依赖性内吞作用进入中肠上皮细胞（Wytinck et al.，2017）。在中肠细胞内，病毒粒子被包裹在早期内体中，随后通过囊泡运输跨越基底膜释放进入血淋巴（Xia et al.，2018）。进入血淋巴的病毒粒子随血流循环到达唾液腺，病毒必须特异性地识别唾液腺周围基底膜上的受体，进入主唾液腺细胞，并最终汇入唾液管（Wei et al.，2014）。当带毒烟粉虱再次取食健康植物并分泌唾液时，病毒随唾液被注入植物韧皮部，从而完成传播循环（Rosen et al.，2015）。任何一道屏障的阻滞都将导致传播失败，目前已挖掘出相当数量的帮助病毒循环与跨越屏障的重要蛋白（表1），涵盖了病毒在媒介体内循环的各个屏障（Morin et al.，1999；Kliot & Ghanim，2013；Mittapelly & Rajarapu，2020）。

表1 烟粉虱体内帮助双生病毒循环与跨越屏障的重要蛋白

Table 1 Key proteins involved in geminivirus circulation and barrier crossing in *B.tabaci*

蛋白名称 Protein name	定位与互作阶段 Localization & interaction stage	核心功能 Core function	参考文献 Reference
BtCubam复合体 BtCUBN complex	中肠 Midgut	识别双生病毒衣壳蛋白，协助穿过中肠屏障 Recognizes the viral coat protein (CP) and facilitates viral pasage across the midgut barrier	Zhao et al., 2020a
胶原蛋白 Collagen	中肠 Midgut	提供初始黏附锚点，辅助病毒颗粒在中肠表面停留 Provides an initial attachment site that facilitates retention of viral particles on the midgut surface	Rana et al., 2019
分选连接蛋白12 Sorting nexin 12	中肠 Midgut	生成管状囊泡网络，帮助病毒躲避溶酶体降解 Generates tubular vesicle network that facilitate viral escape from lysosomal degradation	Xia et al., 2018
囊泡相关膜蛋白2 Vesicle-associated membrane protein 2	中肠 Midgut	可能参与囊泡到早期内体膜融合的过程，以促进病毒的运输 May participate in vesicle−early endosome membrane fusion, thereby promoting viral transport	Fan et al., 2021
Vta1蛋白 Twenty associated 1	中肠及血淋巴 Midgut and haemolymph	不同隐种序列存在差异且影响隐种传毒效率，其中高亲和力突变促进病毒正向转运 Sequence variation among cryptic species affects virus transmission efficiency, and high-affinity variants promote viral translocation	Chi et al., 2021
中肠蛋白 Midgut protein	中肠 Midgut	与病毒CP特异性结合，帮助病毒穿过中肠屏障 Specifically binds the viral coat protein and facilitates viral passage across the midgut barrier	Rana et al., 2016
卵黄原蛋白 Vitellogenin	中肠及卵巢 Midgut and ovaries	携带病毒通过中肠及卵巢屏障，帮助病毒垂直传播 Transports viruses across the midgut and ovarian barriers, facilitating vertical transmission	Wei et al., 2017
磷脂酰乙醇胺结合蛋白4 Phosphatidylethanolamine-binding protein 4	中肠及唾液腺 Midgut and salivary glands	被病毒调控激活细胞凋亡与自噬途径，维持宿主免疫平衡 Activated by viruses to regulate apoptosis and autophagy pathways, thereby maintaining host immune homeostasis	Wang et al., 2022
亲环素B Cyclophilin B	中肠、卵巢和唾液腺 Midgut, ovaries and salivary glands	将病毒引导到各种膜结合囊泡中，帮助病毒避免或抵抗昆虫免疫反应 Directs viruses into membrane-bound vesicles, facilitating evasion of insect immune responses	Kanakala & Ghanim, 2016
Tid蛋白 Tumorous imaginal discs	中肠及唾液腺 Midgut and salivary gland	竞争性结合病毒CP以显著压制病毒过量积累，维持烟粉虱体内免疫平衡 Competitively binds the viral CP, suppressing excessive viral accumulation and maintaining immune homeostasis in whitelies	Zhao et al., 2020b
细菌伴侣蛋白 GroEL	血淋巴 Haemolymph	与病毒颗粒结合形成复合物，保护病毒免受血淋巴中蛋白酶等酶的降解 Forms complexes with viral particles, protecting them from degradation by proteases and other enzymes in the haemolymph	Morin et al., 1999; 2000; Kliot & Ghanim, 2014; Kupper et al., 2014

双生病毒的衣壳蛋白（coat protein，CP）是跨越屏障的核心分子因子。CP不仅负责包裹和保护病毒的ssDNA基因组，更充当了“分子钥匙”的角色（Fondong，2013）。CP表面特定的氨基酸模体决定了病毒能否被烟粉虱中肠和唾液腺上的特异性受体识别（Briddon et al.，1990；Höhnle et al.，2001；Caciagli et al.，2009；Pan et al.，2020）。虽然具体的昆虫受体蛋白如类钙黏蛋白、糖蛋白等尚未被完全鉴定，但定点突变试验证实，CP序列中微小的变异（如保守位点的氨基酸置换）足以改变病毒的传播效率，甚至导致病毒丧失被特定烟粉虱隐种传播的能力（Rana et al.，2016；Gautam et al.，2022；Jiménez et al.，2024）。

1.2 双生病毒与烟粉虱共生菌的协作

植物病毒的流行深刻依赖于病毒、媒介昆虫、内

共生菌与植物免疫系统的多重营养级网络(Sugio et al.,2015;Wu et al.,2022;Hussain et al.,2025)。研究表明,烟粉虱携带的复杂内共生菌群落是病毒成功实现持久传播的重要因素(Gottlieb et al.,2010;Andreason et al.,2020;Kaur et al.,2022)。作为专性原生共生菌,*Portiera*严格定殖于含菌细胞内并经卵巢垂直传播。由于长期协同进化导致基因组极度退化,*Portiera*仅保留了合成必需氨基酸及类胡萝卜素的核心通路。体外试验结果表明,*Portiera*分泌的分子伴侣GroEL并不直接与双生病毒的CP发生物理结合(Rana et al.,2012;Santos-Garcia et al.,2012;Sloan & Moran,2012)。因此,*Portiera*对病毒传播的贡献是基础性的:它从代谢底层弥补了烟粉虱纯韧皮部汁液饮食的严重营养缺陷,维系了烟粉虱的存活、发育与高密度繁衍,为病毒流行提供了不可或缺的媒介基数(Baumann,2005;Douglas,2015;Chen et al.,2016)。

相比之下,次生共生菌则直接参与了病毒粒子在烟粉虱血淋巴中的物理庇护与免疫逃逸(Czosnek & Ghanim,2012;Kliot et al.,2014;Wang et al.,2016)。次生共生菌*Hamiltonella*和*Arsenophonus*能够大量分泌GroEL,该蛋白能与特定双生病毒的CP发生高亲和力结合,防止病毒被烟粉虱血细胞吞噬或被血淋巴中的水解酶降解,保证病毒能够跨越中肠与唾液腺屏障(Morin et al.,2000;Kliot & Ghanim,2013;Kupper et al.,2014)。另一类次生共生菌立克次氏体如*Rickettsia*具有强烈的组织侵袭性,可散布于中肠及全身血淋巴,它通过主动下调宿主如Toll样受体(Toll like receptors,TLR)和免疫缺陷(immune deficiency,Imd)信号通路等天然免疫核心通路相关基因的表达,制造系统性的免疫抑制环境,显著提升了烟粉虱获取、保留和传播病毒的效率(Gottlieb et al.,2006;Kliot et al.,2019;Lei et al.,2021)。

2 病毒与寄主植物防御与代谢的重塑

双生病毒侵染植物后,并非仅仅进行复制和增殖,病毒通过表达特定的毒力因子能够系统性地重塑植物的防御信号网络和次生代谢途径,将带毒植物转变为吸引且有利于烟粉虱生存的场所(Zhang et al.,2012;Li et al.,2014;Zhao et al.,2019;李明骏等,2023)。

2.1 病毒效应蛋白与茉莉酸信号通路的博弈

植物为抵御刺吸式害虫侵害,进化出了一套复杂的防御系统,其中茉莉酸(jasmonic acid,JA)信号通路起着主导作用(Walling et al.,2000;Zarate et al.,2007;Howe & Jander,2008)。JA通路的激活会诱导植物合成一系列抗虫次生代谢产物(如萜烯类、生物碱)和防御蛋白(如蛋白酶抑制剂),从而抑制害虫的取食和发育(Wu & Baldwin,2010;Mithöfer & Boland,2012;War et al.,2012)。然而,双生病毒进化出了以βC1为代表的强效效应子来破坏这一防线(Yang et al.,2008;Gnanasekaran et al.,2019;Wang et al.,2023)。浙江大学研究团队在*The Plant Cell*发表的经典研究指出,双生病毒卫星DNA编码的βC1蛋白能够作为致病因子,直接靶向植物JA信号通路的核心转录因子MYC2,干扰MYC2的同源二聚化或异源二聚化过程,阻断了JA信号的向下传导。最新研究发现,斯里兰卡木薯花叶病毒(Sri Lankan cassava mosaic virus,SLCMV)的复制相关蛋白AC1也能靶向MYC2,促进其降解或抑制其功能,从而降低植物对烟粉虱的抗性,进一步表现为在感染了双生病毒的植株上,烟粉虱表现出更高的存活率、更快的发育速率和更强的繁殖能力(Li et al.,2014;Li et al.,2019;Wang et al.,2026)。

对于缺乏卫星分子的双生病毒(如TYLCV),研究人员发现C2蛋白通过一种完全不同于βC1的机制来抑制植物的JA防御网络(Lozano-Durán et al.,2011;Rosas-Díaz et al.,2016;Guerrero et al.,2020)。C2蛋白被证实能够直接与植物的泛素分子发生互作,进而广泛干预宿主的泛素–蛋白酶体降解途径。JA信号的传递依赖于一种阻遏蛋白茉莉酸ZIM结构域蛋白(jasmonate ZIM-domain proteins,JAZ)。JAZ必须被泛素化并在26S蛋白酶体中被降解,才能释放出包括MYC2在内的转录因子以启动抗虫基因的表达。TYLCV的C2蛋白通过干扰泛素化过程,极大地延缓或阻断了JAZ1的降解(Wu & Ye,2020;Lobaina et al.,2022;Rosas-Diaz et al.,2023)。

双生病毒编码的C4蛋白也是一种受到广泛关注且具有高度多功能性的病毒效应子(Rosas-Diaz et al.,2018;Medina-Puche et al.,2021;Mei et al.,2023)。作为一种传统的病原毒力因子,C4蛋白最为熟知的功能是作为RNA沉默抑制子,能够通过结合小干扰RNA或干扰RNA诱导的沉默复合体来对抗植物的转录后基因沉默机制(Chellappan et al.,2005;Vanitharani et al.,2005;Bisaro,2006)。然而,伴随多组学互作网络的揭示,C4蛋白展现出了远超RNA沉默抑制子的功能。在模式植物拟南芥和自

然宿主番茄中的研究表明，C4蛋白能够广泛地与植物细胞膜上的类受体激酶（receptor-like kinase，RLK）发生物理互作（Li et al.，2018；Li et al.，2020；Ferreira et al.，2021）。RLK家族是植物感知外界环境变化和病原体攻击的第一道防线（Monaghan & Zipfel，2012）。研究明确鉴定出C4蛋白能够与免疫感知的核心蛋白鞭毛蛋白受体2（flagellin-sensing 2，FLS2）、负责激素信号的油菜素内酯受体（brassinosteroid-insensitive1，BRI1）以及调控茎尖分生组织干细胞命运的CLV1蛋白发生互作。通过与这些关键膜受体的结合，C4蛋白不仅钝化了植物对双生病毒的感知能力，还深度干预了植物正常的生长发育调控网络，尤其是生长素和赤霉素的信号传导网络（Li et al.，2018；Garnelo Gómez et al.，2019；Li et al.，2022）。这种对内源激素的深度干预直接导致了感染植物出现典型的双生病毒病理症状，包括叶片向上或向下的严重卷曲、脉间黄化、植株矮缩以及细胞分裂与扩张异常（Mandadi & Scholthof，2013）。从生态学角度推测，叶片的严重卷曲不仅改变了植物的向光性与微气候环境，还可能为隐藏在其内部取食和产卵的烟粉虱提供绝佳的物理庇护所，使其免受天敌的侵害以及恶劣气象条件的干扰（Gerling et al.，2001）。

2.2　基于挥发物谱系病毒–植物–媒介三方博弈

除了抑制直接防御，病毒还通过改变植物的挥发性有机化合物谱系来进行间接的化学操纵（Eigenbrode et al.，2002；Mauck et al.，2010；Luan et al.，2013）。2025年研究发现，TYLCV侵染番茄植株后，通过转录调控机制特异性上调植物体内两个关键单萜合成酶基因*TPS3*和*TPS7*的表达，导致感病植株向环境中释放高浓度的*β*-月桂烯。行为学与神经电生理研究结果证实，高浓度*β*-月桂烯能够与环境中的非带毒烟粉虱触角上的特异性嗅觉受体BtMEDOR6高亲和力结合，促使大量非带毒烟粉虱趋向感病植株，这种由植物气味介导的“拉”效应确保了烟粉虱早期能快速定位病毒源，完成获毒（Liang et al.，2025）。

在植物、植物病毒及媒介昆虫的微观生态网络中，挥发物不仅是病毒跨界招募媒介的诱饵，也是昆虫远程改变寄主微环境的工具，更是植物实现群体预警与防御资源重塑的核心信号分子。作为病毒载体的烟粉虱同样展现出利用挥发物进行寄主微环境改造的能力。当非带毒烟粉虱在番茄韧皮部取食时，会激发宿主释放包含（*Z*）-3-己烯醇、*α*-蒎烯等17种化合物的特定诱导性挥发物谱系。这一化学混合物在特征上高度模仿植物受病原菌攻击的求救信号，当被邻近健康植株感知后，会诱发接收植株内部激素通路的系统性误判，接收植株强烈上调主要用于对抗病原菌的水杨酸依赖型防御通路，而作为拮抗代价，真正用于抵御昆虫取食的JA防御通路被显著抑制。这种跨植株的远程防御解除机制，导致邻近的健康番茄对烟粉虱的易感性大幅增加，不仅使得烟粉虱雌虫产卵量显著提升，后代若虫的发育速率也显著加快（Walling，2008；Zhang et al.，2019）。

在长期的协同进化中，植物同样演化出了严格权衡的抗病毒优先策略。当番茄遭到已携带病毒的烟粉虱取食时，其挥发物释放发生特异性改变，在侵染后第2天*β*-石竹烯的释放量急剧上升（Herms & Mattson，1992；Wu & Baldwin，2010）。最新研究表明，作为早期气传预警信号，*β*-石竹烯被邻近的番茄植株接收后，迅速启动其内部的免疫架构，直接触发编码依赖RNA的RNA聚合酶的*Ty-1*以及*PR-1b*等核心抗病毒基因的提前转录暴发，启动该防御的植株在承受更多昆虫取食的同时，能够极显著压制组织内的病毒积累，从而确保了番茄产量。此外，为弥补直接防御下降的劣势，暴露于*β*-石竹烯信号的植株在遇袭时会放大*β*-石竹烯、水杨酸甲酯和*β*-月桂烯的释放，以此精准招募丽蚜小蜂*Encarsia formosa*等天敌昆虫进行定向清理，从种群密度上控制媒介，切断了病毒的二次传播（Zhang et al.，2026）。

烟粉虱–双生病毒–寄主植物三方在漫长演化中缔造了环环相扣的挥发物博弈网络：病毒上调宿主单萜合成并动态调节媒介嗅觉受体实现推拉传播，媒介通过诱导特定植物气味跨植株解除邻近植株防御以迅速扩张，植物则通过精准识别带毒媒介释放倍半萜预警，在群体层面执行抗病毒优先策略并协同天敌招募，最终成功实现了对病毒–媒介互利共生体系的反击。

2.3　媒介传毒效率与互利共生强度的正相关性

双生病毒在长期的进化过程中展现出了高度选择性，病毒通过精细操纵宿主植物的代谢与防御系统，精准调控植物整体营养表型，帮助能够高效传毒的特定昆虫媒介获得生存优势（Jiu et al.，2007；Moreno-Delafuente et al.，2013；Mauck et al.，2018）。研究发现TYLCV、CLCuMuV及SLCMV在侵染烟草植物后，能够引发截然不同的植物表型和防御状态重塑，高效传毒的媒介（如针对TYLCV的MEAM1和MED隐种烟粉虱）在感染TYLCV的植

株上表现出显著高于对照组的适合度；然而，对于TYLCV传毒效率极低的媒介（如Asia II1烟粉虱），其在感病植株和健康植株上的表现完全相似，并未获得任何优势。同样地，CLCuMuV和SLCMV的侵染显著增强了其高效媒介Asia II1的存活率和生殖力，而对低效媒介MEAM1和MED隐种烟粉虱的适合度则没有促进作用（Luan et al.，2014；He et al.，2025）。这种由植物介导的、与传毒效率高度相关的特异性互惠共生机制，不仅优化了病毒自身的传播效率，也决定了昆虫种群的动态变迁方向。

3 病毒对烟粉虱行为与生理的直接调控

当病毒粒子成功跨越屏障进入烟粉虱体内后，它不再是通过植物间接发挥作用，而是直接作为一种内源性因子，对媒介昆虫的神经系统、免疫系统及基因表达网络进行深度重塑，这种直接操纵是实现病毒高效传播的关键一环（Wang SF et al.，2020；Wang XR et al.，2020）。

3.1 神经退行性病变是化“病”为“利”的致病行为

长期以来，人们认为植物病毒感染对昆虫载体通常是无害的。然而，中国科学院动物研究所孙玉诚团队2020年发表的研究颠覆了这一认知，提出了“致病行为”促进传播的新机制（Wang SF et al.，2020）。该研究发现，TYLCV病毒粒子进入烟粉虱头部神经节后，会被昆虫的免疫受体识别，进而激活核苷酸结合和寡聚化结构域样受体4（nucleotide-binding and oligomerization domain-like receptors 4，NLR4）和Spaetzle 1&2等免疫信号通路。这种免疫反应的过度激活会诱导天冬氨酸特异性的半胱氨酸蛋白水解酶（cysteinyl aspartate-specific proteinase，Caspase）家族的BtCaspase1和BtCaspase3b的级联表达和活化。Caspase作为细胞凋亡的核心执行蛋白，其活化导致烟粉虱脑部神经元发生不可逆的细胞凋亡，即神经退行性病变。这种神经病变直接导致了烟粉虱的认知功能障碍，具体表现为视觉和嗅觉辨识能力的下降。在正常情况下，烟粉虱倾向于定居在气味诱人（如释放β-月桂烯）的感病植株上。然而，发生神经退行性病变的带毒烟粉虱丧失了这种对感病植物的特异性偏好，其寄主选择变得随机化。这种随机性的增加导致带毒个体更容易离开原本已经拥挤且被感染的植株，向周围健康的植株扩散。

3.2 免疫稳态的精细调节

既然病毒会导致神经退行性病变，那么烟粉虱为何不会因此死亡？Wang et al.（2022）的研究指出，病毒利用了烟粉虱体内的磷脂酰乙醇胺结合蛋白4（phosphatidylethanolamine-binding protein 4，PEBP4）作为分子开关。PEBP4一方面参与调控Caspase介导的细胞凋亡，另一方面又能激活细胞自噬通路。病毒通过劫持PEBP4，在诱导适度神经凋亡以改变昆虫行为的同时，通过增强自噬作用来清除过多的细胞损伤，从而在凋亡与自噬之间建立了一种微妙平衡机制。这种机制确保了烟粉虱虽然携带病毒且行为异常，但仍能维持足够的寿命来完成病毒的传播任务（Wang et al.，2022）。

3.3 嗅觉受体的直接抑制

Liang et al.（2025）的研究进一步将病毒的直接操纵机制解析到了受体蛋白的分子水平。该研究首先通过配体-受体结合试验，鉴定了烟粉虱触角中特异性识别β-月桂烯的嗅觉受体——BtMEDOR6，进一步研究发现TYLCV进入烟粉虱体内后，会通过某种转录后调控机制，特异性地抑制*BtMEDOR6*基因表达。此外，蛋白结构模拟和定点突变分析显示，BtMEDOR6受体中的Y204位点是其识别β-月桂烯的关键氨基酸残基。病毒导致的受体表达下调，直接在分子水平上关闭了烟粉虱感知外界β-月桂烯信号的通道。这一发现解释了为何带毒烟粉虱不再被感病植株吸引，由于失去了对“拉”信号（β-月桂烯）的感知能力，带毒烟粉虱不再滞留于原寄主，这种生理上的趋性丧失在行为上转化为一种向外迁飞的动力，即“推”效应。

4 病毒基于“推-拉”策略介导的互作整合模型

“推-拉”策略代表了病毒在长期协同进化中形成的一种高度精密的时空操纵机制，该机制通过整合植物代谢与媒介嗅觉/神经调控，实现了病毒获取与传播效率的双重最大化。

在“拉”的阶段，主要针对非带毒媒介。双生病毒侵染番茄后，通过调控番茄单萜合成酶基因的转录表达，诱导植物叶片向环境释放高浓度的挥发性气味（如β-月桂烯、新植二烯等）。这种化学信号作为强效的嗅觉引诱剂，能够被环境中搜寻寄主的非带毒烟粉虱触角上高表达的特异性受体精准识别，从而产生强烈的正趋向性，将分散的媒介种群高效招募并聚集到病毒源植物上进行取食，极大提升了媒介昆虫获毒效率（Shi et al.，2019；Nebapure et al.，

2022；Liang et al.，2025）。

而在“推”的阶段，一旦烟粉虱摄入病毒，病毒便立即启动对媒介的直接操纵程序。一方面，病毒通过转录后调控机制显著抑制媒介体内气味受体的表达，直接在分子水平上关闭了媒介对趋性物质的感知通道，消除了其对原感病寄主的嗅觉偏好（Liang et al.，2025）；另一方面，病毒CP在进入媒介脑部后，通过激活NLR4-Spaetzle-Caspase免疫信号通路，诱导神经元发生Caspase依赖性的细胞凋亡，导致媒介出现广谱性的视觉与嗅觉认知缺陷。这种“去偏好化”和神经病变的协同作用，实际上产生了一种生态学上的斥力，促使带毒媒介不再留恋已经感染的植株，而是表现出更高的活跃度，主动向周围健康的植株扩散，从而确保了病毒能够突破空间限制，在植物种群间实现高效的传播与流行（Wang SF et al.，2020）。

5 总结与展望

烟粉虱及其传播的双生病毒均是全球农业生产的重大威胁，烟粉虱–双生病毒–寄主植物三者互作系统的研究已经从现象描述深入到分子、神经及生态进化的核心层面，取得了显著进展。在烟粉虱传播双生病毒的生物学基础方面，揭示了双生病毒利用烟粉虱体内原生蛋白及内共生菌跨越媒介体内屏障的分子机制；在基于植物的间接操纵方面，解析了双生病毒通过效应因子蛋白靶向植物转录因子以瓦解JA防御的核心防御途径，破译了基于植物挥发物的化学操纵体系，阐明了二者基于植物表型的互利共生进化策略；在对媒介昆虫的直接操纵方面，确定双生病毒可以直接激活烟粉虱的神经免疫系统，抑制烟粉虱嗅觉受体基因的表达，以达到加速病毒传播的目的。

然而，烟粉虱–双生病毒–寄主植物三者互作机制的研究仍然面临诸多未知。首先，双生病毒表现出的媒介特异性与协同适应的分子基础仍未可知，某些双生病毒只能由特定隐种高效传播，病毒、烟粉虱和植物三者之间究竟有哪些关键的受体–配体在起作用尚未明确。其次，病毒侵染后，如何系统性地改变植物的生理、防御和营养成分，使其变得更利于烟粉虱取食，如抑制JA途径，削弱植物抗虫性；增加游离氨基酸，为烟粉虱提供营养，其核心效应蛋白及作用通路仍有大量空白。最后，虽然已确定病毒可以直接影响烟粉虱的行为及生理，但病毒侵染对烟粉虱的整体生命周期的影响及背后的调控机制，仍然存在较多值得深入挖掘的内容。

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