烟粉虱传播植物病毒特性及机制研究进展

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摘要 烟粉虱是一类小型刺吸式口器昆虫, 目前被认为是一个包含数十个隐存种的隐存种复合群. 近年来随着进出口贸易的增加, 烟粉虱在世界范围内急速扩散. 烟粉虱主要通过传播植物病毒危害植物, 对世界范围内的多种作物、蔬菜以及园林植物等造成巨大危害. 目前可由烟粉虱传播的植物病毒涵盖5个属400多个种, 其中菜豆金黄花叶病毒属为单链DNA病毒且均由烟粉虱以持久循环型方式传播, 其余4个属均为单链RNA病毒并由烟粉虱以半持久型或非持久型方式传播. 明确烟粉虱传播植物病毒的生物学特性, 解析烟粉虱与病毒间的互作机制将为阻断烟粉虱传播植物病毒提供新方法、新思路. 本文分别对烟粉虱传播不同属病毒的特性进行了综述, 并着重讨论了烟粉虱与菜豆金黄花叶病毒属病毒的互作机制. 菜豆金黄花叶病毒属病毒跨越烟粉虱中肠、唾液腺和卵巢屏障的过程需要多种介体蛋白的参与. 烟粉虱不同隐存种传播同一种病毒的能力往往存在差异, 而这种差异性传播往往与病毒穿过不同烟粉虱体内屏障的能力有关. 同时, 烟粉虱免疫系统在抵御病毒侵染过程中发挥重要作用. 此外, 多项研究表明病毒在烟粉虱体内存在复制迹象.

关键词 烟粉虱, 植物病毒, 传播机制, 免疫响应, 复制

烟粉虱 *Bemisia tabaci*, 又称甘薯粉虱, 是一类植食性刺吸式口器昆虫. 虽然体型微小, 体长不足1 mm, 但对世界范围内木薯、棉花、豆类及蔬菜的生产造成严重危害. 烟粉虱目前被广泛认为是由数十个遗传结构差异明显但外部形态无法区分的隐存种(cryptic species)组成的隐存种复合群(cryptic species complex)^[1,2]. 不同隐存种在寄主范围、能否诱发植物生理异常、杀虫剂抗性、入侵能力和传播病毒特异性等方面都具有很大差异. 目前烟粉虱各隐存种的命名还未有明确的结论, 因此本文主要采用De Barro等人^[1]提出的以烟粉虱起源地进行命名的规则. 如起源于中东-小亚细亚地区的烟粉虱命名为Middle East-Asia Minor 1(MEAM1), 也是以前报道中的“B”烟粉虱. 20世纪80年代末,

MEAM1隐存种通过观赏植物的全球贸易, 从中东-小亚细亚地区迅速入侵到至少54个国家和地区. 而起源于地中海的Mediterranean(MED)隐存种(即以前报道中的“Q”烟粉虱)也于21世纪初开始大规模入侵到至少10个国家^[2]. 入侵烟粉虱MEAM1和MED分别于20世纪90年代中叶及2003年在我国被发现^[3,4], 目前在全国30多个省区市均有分布.

烟粉虱可通过直接取食、诱发植物生理异常、分泌蜜露引发煤污病以及传播植物病毒等多种方式危害植物. 其中危害最大的是其可以传播多种植物病毒, 引发病害从而造成植物减产甚至绝收. 例如, 对农业生产造成灾难性破坏的番茄黄曲叶病毒^[5]、木薯花叶病毒^[6]、棉花曲叶病毒^[7,8]以及近几年在我国流行的番

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茄褪绿病毒^[9]均由烟粉虱传播,并且这些病毒病的流行与烟粉虱的爆发息息相关.目前研究发现,经烟粉虱传播的植物病毒包括双生病毒科(*Geminiviridae*)的菜豆金黄花叶病毒属(*Begomovirus*)、长线型病毒科(*Closteroviridae*)的毛形病毒属(*Crinivirus*)、伴生豇豆病毒科(*Secoviridae*)的番茄灼烧病毒属(*Torradovirus*)、马铃薯Y病毒科(*Potyviridae*)的甘薯病毒属(*Ipomovirus*)以及乙型线性病毒科(*Betaflexiviridae*)的麝香石竹潜隐病毒属(*Carlavirus*)^[10](表1).

根据介体昆虫获取病毒的时间、病毒在介体昆虫体内存留的时间以及可被传播的时间可将介体昆虫传播植物病毒的方式分为三类:非持久型(non-persistent transmission)、半持久型(semi-persistent transmission)以及持久型(persistent transmission)^[11].对于非持久型病毒,介体昆虫在带毒植物上取食几分钟甚至几秒钟即可获取并传播病毒,但病毒在介体体内存留时间也仅有几分钟.持久型病毒在介体昆虫体内可以长期甚至终身存留,但其被获取和传播的时间也会较长,需要几小时甚至几天的时间.半持久型病毒则介于两者之间.进一步分析病毒在介体昆虫体内的位置,发现非持久型和半持久型病毒仅存留于昆虫口针或前肠,而持久型病毒在肠道、血淋巴以及唾液腺组织均有分布^[12].在烟粉虱传播的病毒中,菜豆金黄花叶病毒属病毒均以持久型方式传播,而其他病毒多以半持久型方式传播^[10,13~15].

植物病毒病因其难以防治一直被认为是“植物癌

症”,由介体昆虫传播的植物病毒可以通过防治介体昆虫进而防治植物病毒病的发生.因此,了解介体昆虫传毒机制,探究参与病毒传播的关键病毒和介体蛋白有助于开发新的方法来控制病毒病的发生和扩散.卫静等人^[16]、Rosen^[17]以及Czosnek^[18]对烟粉虱传播菜豆金黄花叶病毒属病毒的特性、分子机制以及植物-病毒-烟粉虱三者互作机制等方面进行了综述.但是目前系统性分析烟粉虱与其传播的所有植物病毒的相互作用关系的综述还较少,因此本文将重点概述近几年关于烟粉虱传毒特性的新进展和分子机制.

1 烟粉虱传播双生病毒的特性及其机制

双生病毒是一类具有孪生颗粒形态的单链环状DNA(single stranded DNA, ssDNA)病毒^[19].其基因组由一个(单组分)或两个(双组分)环状DNA链组成,可以编码5~7个蛋白参与病毒的复制、运动、传播以及引发症状^[20].菜豆金黄花叶病毒属是双生病毒科中种类最多(>400种)、危害最大的一个属,由烟粉虱以持久型方式传播^[17,21].烟粉虱取食带毒植物后,病毒随植物汁液进入烟粉虱体内,穿过中肠进入血淋巴.随后一部分病毒会侵染唾液腺,最终随烟粉虱分泌的唾液进入植物^[22];另有一部分病毒可以侵染雌性烟粉虱的卵巢,进而由烟粉虱经卵传播给后代^[23](图1).这里将从水平传播和垂直传播这两方面分别探讨烟粉虱传播双生病毒的特性及机制.此外,我们也对烟粉虱对抗病毒的免疫反应,以及病毒在烟粉虱体内复制的研究进展进行

表1 烟粉虱传播的植物病毒

Table 1 Plant viruses transmitted by whitefly

科名	属名	传播方式	传播媒介 ^{a)}
双生病毒科 <i>Geminiviridae</i>	菜豆金黄花叶病毒属 <i>Begomovirus</i>	持久型	烟粉虱 <i>B. tabaci</i> 蓖麻粉虱 <i>Trialeurodes ricini</i> * 温室白粉虱 <i>T. vaporariorum</i> *
长线型病毒科 <i>Closteroviridae</i>	毛形病毒属 <i>Crinivirus</i>	半持久型	烟粉虱 <i>B. tabaci</i> 温室白粉虱 <i>T. vaporariorum</i> 纹翅粉虱 <i>T. abutiloneus</i> 非洲伯粉虱 <i>B. afer</i> *
伴生豇豆病毒科 <i>Secoviridae</i>	番茄灼烧病毒属 <i>Torradovirus</i>	半持久型	烟粉虱 <i>B. tabaci</i> 温室白粉虱 <i>T. vaporariorum</i> 纹翅粉虱 <i>T. abutiloneus</i>
马铃薯Y病毒科 <i>Potyviridae</i>	甘薯病毒属 <i>Ipomovirus</i>	半持久型	烟粉虱 <i>B. tabaci</i> 温室白粉虱 <i>T. vaporariorum</i> * 螺旋粉虱 <i>Aleurodicus dispersus</i>
乙型线性病毒科 <i>Betaflexiviridae</i>	麝香石竹潜隐病毒属 <i>Carlavirus</i>	非持久型	烟粉虱 <i>B. tabaci</i>

a) *: 关于该种粉虱传播对应病毒目前仅有一例报道

图1 (网络版彩色)双生病毒在烟粉虱体内的循环路径示意图。s, 口针; e, 食道; mg, 中肠; psg, 唾液腺主腺; asg, 唾液腺副腺; hg, 后肠; o, 卵巢

Figure 1 (Color online) The circulative transmission pathway of begomoviruses in whitefly. s, stylet; e, esophagus; mg, midgut; psg, primary salivary gland; asg, accessory salivary gland; hg, hindgut; o, ovary

了总结。此部分提及的病毒均属于菜豆金黄花叶病毒属。

1.1 烟粉虱对双生病毒的传播

1.1.1 双生病毒经烟粉虱在植物间传播

烟粉虱传播双生病毒的过程受到多种因素影响。从病毒角度来说, 双生病毒的外壳蛋白(coat protein, CP)是唯一的结构蛋白, 对病毒在烟粉虱体内的循环十分重要。目前有多篇综述对病毒CP在其传播过程中的作用进行了总结^[18,24]。从烟粉虱角度来说, 一般认为病毒被成功传播需要克服3个屏障: 中肠屏障、血淋巴屏障和唾液腺屏障^[18]。该部分将着重围绕双生病毒穿过烟粉虱体内各屏障的机制展开。此外, 有研究表明烟粉虱共生菌在双生病毒传播过程中也具有一定的作用^[25~28], 但目前由于试验体系限制, 该观点还值得进一步探究, 因此这里暂不讨论。

中肠屏障是病毒侵染烟粉虱的第一道也是至关重要的屏障。研究发现, 温室白粉虱 *Trialeurodes vaporariorum* 不能够传播番茄黄曲叶病毒(tomato yellow leaf curl virus, TYLCV)是因为该病毒无法进入温室白粉虱的中肠细胞^[29]。Pan等人^[30]发现MEAM1粉虱传播烟草曲茎病毒(tobacco curly shoot virus, TbCSV)效率极低, 但将纯化的病毒粒子直接注入烟粉虱血淋巴中, 病毒传播效率显著提高到60%左右。不同烟粉虱隐存种传播同种双生病毒效率的差异与病毒穿过不同隐存种中肠的能力息息相关。中国番木瓜曲叶病毒(papaya leaf curl China virus, PaLCuCNV)可由MEAM1烟粉虱高效传播, 而MED烟粉虱传播效率很低。通过定量比较这两

个隐存种各组织中的病毒量, 研究者发现, MEAM1中肠、血淋巴及头胸中的病毒量均显著高于MED; 而无法穿过中肠, 进而随蜜露一起排出体外的病毒的量则是MED显著高于MEAM1^[31]。木尔坦棉花曲叶病毒(cotton leaf curl Multan virus, CLCuMuV)可由Asia II 1烟粉虱高效传播, 而MEAM1和MED烟粉虱的传播效率较低^[8]。同样, 进一步分析发现, Asia II 1中肠、血淋巴及和唾液腺中的病毒量都显著高于MEAM1和MED, 而MEAM1和MED蜜露中的病毒量则显著高于Asia II 1。

囊泡运输系统在双生病毒跨越烟粉虱中肠屏障过程中具有重要作用。Uchibori等人^[32]最先通过免疫电子显微镜发现, 带毒烟粉虱的中肠上皮细胞中番茄黄曲叶病毒出现在类似囊泡的结构中。随后Pan等人^[33]通过饲喂抑制剂、抗体阻断和RNA干扰等方法证明, 网格蛋白介导的胞吞以及细胞内体网络可以帮助TYLCV跨过烟粉虱中肠。进一步地, 研究人员通过RNA干扰和饲喂抑制剂证明早期内体参与TYLCV在中肠细胞中的运输, 而循环内体、晚期内体、溶酶体和高尔基体均不参与病毒的运输过程, 推测病毒是直接从早期内体运输到细胞基底膜从而进入血淋巴中。此外, 通过沉默参与早期内体管状囊泡结构形成的Snx蛋白, 证明这种管状囊泡结构可能参与了病毒的运输^[34]。Zhao等人^[35]利用分离-泛素酵母双杂交系统筛选到烟粉虱囊泡相关蛋白(VAMP associated protein B, VAPB)可与TYLCV外壳蛋白CP发生互作。病毒侵染可诱导VAPB的表达, 沉默该基因后烟粉虱血淋巴和唾液腺中病毒量显著升高, 推测该蛋白可能作用于中肠细胞的囊泡运输系统, 阻止病毒进入血淋巴。

热激蛋白家族也可能影响了双生病毒在烟粉虱中肠中的存留。Ohnesorge等人^[36]通过酵母双杂交筛选到烟粉虱热激蛋白16(heat shock protein 16, HSP16)与番茄黄曲叶撒丁岛病毒(tomato yellow leaf curl Sardinia virus, TYLCSV)外壳蛋白互作, 但该蛋白在病毒传播中的作用尚不清楚。随后, 其他研究者发现TYLCV和南瓜曲叶病毒(squash leaf curl virus, SLCV)侵染会促进烟粉虱HSP70(heat shock protein 70)的表达。通过免疫捕获PCR、免疫共沉淀以及病毒覆盖蛋白结合法等方法证明TYLCV可以与HSP70发生互作。免疫荧光发现, TYLCV病毒粒子和HSP70在中肠细胞中共定位。给烟粉虱饲喂HSP70的抗体后, 烟粉虱传播TYLCV的效率升高。因此, 研究者推测HSP70与病毒的互作可能促进了病毒的降解^[37]。

此外, 还有一些烟粉虱蛋白被证明可以与病毒的CP互作并参与病毒的传播. Kanakala和Ghanim^[38]发现, 亲环素B(cyclophilin B, CypB)可以结合TYLCV病毒粒子, 并在烟粉虱中肠及唾液腺都存在共定位. 饲喂该CypB蛋白的抗体及抑制剂都有效抑制了病毒的传播, 推测该蛋白在烟粉虱传播TYLCV的过程中起重要作用. 以新德里番茄曲叶病毒(tomato leaf curl New Delhi virus, ToLCNDV)及拉贾斯坦棉花曲叶病毒(cotton leaf curl Rajasthan virus, CLCuV)的外壳蛋白为诱饵筛选烟粉虱的cDNA文库后, 研究者发现中肠蛋白(midgut protein, MGP)^[39]、胶原蛋白(collagen protein)^[40]和类硫氧还蛋白(thioredoxin-like protein, TLP)^[41]均可以与这两种病毒CP发生互作. 其中, MGP和胶原蛋白均与病毒CP在烟粉虱中肠存在共定位, 且饲喂抗体后病毒传毒效率显著下降, 推测这两个蛋白很可能帮助病毒跨越中肠屏障来促进病毒的传播. 而TLP是否参与病毒传播还有待进一步研究.

烟粉虱唾液腺由两个至少含有13个细胞的主腺(primary salivary gland, PSG)和两个仅有4个细胞的副腺(accessory salivary gland, ASG)组成^[42,43]. 已有研究表明, 唾液腺主腺参与双生病毒的传播^[44,45], 而唾液腺副腺则不参与^[43]. Caciagli等人^[45]发现, 外壳蛋白突变的TYLCSV可以进入烟粉虱的中肠、血淋巴和唾液腺中, 但并不能被传播到新的植物上. 推测病毒未能离开唾液腺进入烟粉虱唾液腺中, 从而造成病毒不能被传播. Wei等人^[44]发现MED烟粉虱能够高效传播TYLCV, 但不能传播中国番茄黄曲叶病毒(tomato yellow leaf curl China virus, TYLCCNV). 进一步研究发现, 在MED烟粉虱中肠、血淋巴和唾液腺中均能检测到TYLCCNV, 而唾液腺中则检测不到. 通过持续追踪TYLCV和TYLCCNV在烟粉虱唾液腺主腺中的运动轨迹, 发现TYLCV可以进入并聚集到烟粉虱唾液腺主腺的中间区域, 而TYLCCNV则不能. 因此, 研究者推测病毒进入烟粉虱唾液腺主腺中间区域是病毒能够被传播的必要条件. 进一步地, 研究者将TYLCV和TYLCCNV的部分CP区域进行互换, 发现突变的TYLCV无法高效进入烟粉虱唾液腺主腺中间区域, 其传播效率也极大地降低; 而突变的TYLCCNV则能够高效进入到烟粉虱唾液腺主腺中间区域, 也能够被高效传播. 该研究充分说明, 病毒CP与烟粉虱唾液腺细胞之间的特异性识别决定了病毒传播的特异性, 但具体机制目前尚不明确, 还需要进一步研究.

1.1.2 双生病毒由烟粉虱经卵传播

病毒能否由介体昆虫经卵传播对于病毒的扩散和流行具有重要意义, 因此该问题也得到了昆虫学家和病毒学家的持续关注^[46,47]. 目前, 仅有少数可在介体昆虫体内复制的病毒可以经卵传播给后代^[11]. 双生病毒能否由烟粉虱经卵传播一直受到广泛关注, 但早期来自不同研究团队的实验结果存在较大差异, 因此该问题一直没有定论^[48-51]. Wei等人^[23]发现, TYLCV能否进入MEAM1和MED烟粉虱卵巢与卵巢的成熟度有关, 只有发育成熟的卵巢中才有TYLCV病毒粒子. 相应地, 研究结果表明, 只有发育到一定阶段的高龄烟粉虱才能高效地经卵传播TYLCV, 而初羽化的烟粉虱则无法经卵传播TYLCV. 进一步地, 研究人员发现, TYLCV外壳蛋白可以与烟粉虱卵黄原蛋白(vitellogenin, Vg)互作, 并在后者的帮助下进入烟粉虱卵子中. 沉默烟粉虱Vg后, 病毒进入卵巢的效率降低, 随后经卵传播的频率也显著下降. 该研究还发现, 另一种双生病毒PaLCuCNV的外壳蛋白不能与烟粉虱Vg发生互作, 而该病毒也始终无法由烟粉虱经卵传播. 将TYLCV与PaLCuCNV外壳蛋白的部分区域互换后, 突变的TYLCV无法进入烟粉虱卵巢, 也无法由烟粉虱经卵传播; 而突变的PaLCuCNV则可以高效进入卵巢, 进而被高效经卵传播. 该研究揭示了烟粉虱经卵传播双生病毒的机制, 同时推测早期关于TYLCV经卵传播研究的不同结果可能是因为不同研究中使用的烟粉虱龄期不同. 随后, Guo等人^[52]对TYLCV能否由中国境内7个本地种烟粉虱经卵传播的情况进行了研究. 结果发现, 除Asia II 7外, 在其余6个烟粉虱隐存种(Asia 1、Asia II 6、Asia II 1、Asia II 3、China 1和China 2)的卵中均可检测到病毒. 在一龄若虫中Asia II 3和China 1的带毒率为50%~56%, Asia 1的为2.5%, 其余隐存种均未检测到病毒. 在7个烟粉虱隐存种的F1代成虫中均未检测到TYLCV. 该研究说明, 不同烟粉虱隐存种经卵传播TYLCV的能力存在差异.

1.2 烟粉虱对双生病毒的免疫响应

昆虫的先天性免疫是其对抗病原体侵染的重要防御机制^[53,54]. 通过比较携带双生病毒及不带毒烟粉虱基因表达量的变化, 发现双生病毒侵染后烟粉虱体内一些免疫相关通路基因的表达发生显著的上调或下调. 因此推测双生病毒侵染可能激活了烟粉虱体内某些抗病毒免疫反应. 同时, 其也抑制了一些免疫通路, 从而

利于病毒在烟粉虱体内的存活^[55-57]。目前,关于双生病毒对烟粉虱免疫系统影响的研究多数还仅限于基因转录水平或蛋白量水平的变化,具体机制还需进一步研究。这里对已有一定研究的抗菌肽和自噬途径在烟粉虱抵御双生病毒中的作用进行讨论。

抗菌肽是生物体合成的一类阳离子型活性肽,分子量较小,一般小于10 kD^[58]。在昆虫中抗菌肽主要参与体液免疫,能够抵御细菌、真菌以及病毒等病原物的侵害^[59]。Shatters等人^[60]从烟粉虱的cDNA文库中鉴定到抗菌肽knottin-like基因家族中的4个成员(Btk-1、Btk-2、Btk-3和Btk-4),其中Btk-1和Btk-3的会被番茄斑駁病毒(tomato mottle virus, ToMoV)诱导表达。Btk-3也会被TYLCCNV诱导表达^[55]。Wang等人^[61]鉴定到了一个新的抗菌肽Btdef,属于defensin-like家族。进一步研究发现,在携带TYLCCNV的烟粉虱体内该基因的表达量上调。但沉默Btdef后,TYLCCNV的病毒量及基因表达量都显著下调,推测该基因对病毒并没有直接作用^[62]。

自噬是细胞先天免疫系统的重要组成部分,在寄主抵御病毒侵染中起到重要作用。此外,有些病毒也可以利用该过程促进自身在宿主细胞中的复制^[63]。Luan等人^[55]通过比较不携带和携带TYLCCNV烟粉虱的差异表达基因,发现病毒侵染后烟粉虱体内自噬相关基因的表达均显著上调。免疫印迹检测自噬体特异性蛋白Atg8-II的出现,进一步证明了TYLCCNV侵染诱导了烟粉虱自噬的发生。随后,Wang等人^[64]研究发现,TYLCV侵染也会诱导介体烟粉虱体内自噬的发生。该研究还发现,在烟粉虱持毒期间,烟粉虱体内病毒的量逐渐升高,在48~96 h达到最高点,随后逐渐降低。而烟粉虱体内Atg8-II蛋白也在持毒48~96 h开始大量出现,说明激活的自噬反应可能促进了病毒的降解。进一步研究表明,通过给烟粉虱饲喂自噬激活剂诱导烟粉虱体内自噬的发生后,相比于对照组,烟粉虱体内病毒量显著减少,烟粉虱传播病毒的效率也相应降低;而通过饲喂自噬抑制剂或沉默自噬相关基因的表达后,烟粉虱体内病毒量显著增加,病毒传播效率也相应升高。该研究充分证明了TYLCV侵染激活了介体烟粉虱的自噬反应,而激活的自噬反应促进了TYLCV的降解,说明烟粉虱通过自噬途径来对抗TYLCV的侵染。此外,该研究还发现,TYLCCNV侵染也会激活烟粉虱的自噬反应,而PaLCuCNV则不会,说明对介体烟粉虱自噬反应的激活具有病毒特异性,而其具体机制还有待进一步

研究。

1.3 双生病毒在烟粉虱体内的复制

双生病毒能否在烟粉虱体内复制是一个颇有争议的问题。目前,普遍接受的观点是双生病毒由烟粉虱以持久循环型(persistent-circulative)方式传播,即不能在烟粉虱体内复制^[11]。然而,近30年来不断有研究人员对这个问题进行了深入研究,并认为某些双生病毒,例如TYLCV,可以在烟粉虱体内复制^[64-69]。Mehta等人^[65]将获取埃及分离的TYLCV(TYLCV-Eg)12 h的烟粉虱转移至病毒非寄主植物上,持续监测烟粉虱体内病毒基因组DNA量的变化。研究者发现烟粉虱体内病毒量自12 h后就不断增加直至108 h,随后保持稳定直至180 h。持毒期间烟粉虱体内病毒量的增加被认为最可能是由于病毒的复制造成的。Rubinstein和Czosnek^[66]发现,烟粉虱可以终身携带以色列分离的TYLCV(TYLCV-Is),且一直具备一定的传毒能力。进一步研究发现,带毒后的烟粉虱平均寿命及产卵量都有一定程度的降低,表明TYLCV具有昆虫病原物的特性。烟粉虱获取TYLCV-Is 1 h后转移至人工饲料上,烟粉虱体内病毒量先增加后降低。在人工饲料中加入放射性标记的dCTP,被标记的病毒信号也有先增加后降低的趋势,证明了TYLCV DNA可以在烟粉虱体内合成^[67]。随后,Sinisterra等人^[68]在烟粉虱持毒过程中在其体内检测到了TYLCV的转录增多。Pakkianathan等人^[69]和Wang等人^[64]均发现烟粉虱短时间获取TYLCV后,转移至病毒非寄主植物上,烟粉虱体内的病毒量会先逐渐增加然后降低,说明病毒可以在烟粉虱体内短暂复制。此外,研究发现,TYLCV可以由雌性烟粉虱经卵传播给后代,且至少可以传两代,后代烟粉虱成虫仍可以传播病毒使健康植物发病^[23]。然而,也有研究认为TYLCV不能够在烟粉虱体内复制。Becker等人^[70]和Sánchez-Campos等人^[71]通过实时荧光定量PCR检测持毒期间烟粉虱整虫中病毒DNA量的动态变化,均未发现增多的趋势,因此认为TYLCV很可能无法在烟粉虱体内复制。

除了TYLCV外,还有一些关于其他双生病毒在烟粉虱体内复制情况的研究。Sinisterra等人^[68]发现烟粉虱获取ToMoV后转移至病毒非寄主植物棉花上,病毒的转录很快就检测不到了,推测ToMoV无法在烟粉虱体内复制。Wang等人^[64]发现,在烟粉虱持毒过程中,TYLCCNV的基因组DNA和外壳蛋白的量均先逐渐增加然后减少,而PaLCuCNV的量则持续降低,推测

TYLCCNV可以在烟粉虱体内复制, 而PaLCuCNV则不能。此外, Wang等人^[72]通过酵母单杂系统筛选到数十个与TYLCCNV基因间隔区(intergenic region)互作的烟粉虱蛋白, 并证明了烟粉虱蛋白HES1可以通过结合TYLCCNV基因间隔区来促进病毒的转录, 这也支持了TYLCCNV可能在烟粉虱体内复制。

双生病毒究竟能否在烟粉虱体内复制目前仍无定论, 而判断病毒是否能复制也未有统一的标准。倘若双生病毒可以复制, 那为什么有些研究没有看到复制的现象? 病毒在烟粉虱体内复制的机制又如何? 倘若不能复制, 那么很多研究人员观察到的病毒量的增加是什么原因造成的? 这些问题都亟待进一步的研究。

2 烟粉虱对毛形病毒属病毒的传播

毛形病毒属(*Crinivirus*)属于长线形病毒科, 是一类线性并弯曲的正义单链RNA病毒, 目前该属包含14个种^[73]。该属病毒对甜菜、葫芦、莴苣、甘薯以及番茄等重要经济作物的生产造成巨大影响, 并且常常会与其他病毒复合侵染危害作物^[74]。毛形病毒属病毒其基因组可达约20 kb^[14]。除马铃薯黄脉病毒(potato yellow vein virus, PYVV)为三组分基因组外^[75], 该属的其他病毒均为双组分, 并且每个组分都被单独包被。RNA-1编码的蛋白主要参与病毒的复制, 而RNA-2(和RNA-3)编码的蛋白参与病毒的包装、运动以及传播^[10]。研究发现, 病毒粒子的外壳由4个蛋白组成: 热激蛋白70的同系物(heat shock protein 70 homologue, HSP70h)、59 kDa蛋白(P59)、主要外壳蛋白(major coat protein, CP)和次要外壳蛋白(minor coat protein, CPm)^[76]。该属病毒由烟粉虱、非洲伯粉虱(*B. afer*)、温室白粉虱(*T. vaporariorum*)以及纹翅粉虱(*T. abutiloneus*)中的一种或几种以半持久方式传播。

病毒在介体昆虫体内何处存留以及哪个或哪几个病毒蛋白参与介体昆虫的传播过程一直是研究病毒传播特性的关键问题。Chen等人^[77]通过免疫荧光定位发现, 莴苣侵染性黄化病毒(lettuce infectious yellows virus, LIYV)的病毒粒子会特异性地存留在NW(new World)烟粉虱的前肠前端或食窦。随后, 另一个毛形病毒属病毒莴苣褪绿病毒(lettuce chlorosis virus, LCV)也被发现可以特异性地存留在MEAM1和NW烟粉虱的前肠或食窦^[78]。Stewart等人^[79]发现, 莴苣侵染性黄化病毒LIYV编码的CPm对于介体昆虫传播是必须的。突变LIYV的CPm或将病毒粒子提前与anti-CPm抗体进行孵

育, 均导致存留于烟粉虱前肠或食窦的病毒粒子显著减少, 随后的病毒传播效率也大大降低^[77]。以上结果证明了病毒的CPm决定了其可以停留于烟粉虱前肠或食窦, 从而影响病毒的传播, 而决定CPm存留在烟粉虱体内的关键序列还未确定, 有待进一步的研究。

病毒的传播存在物种特异性。葫芦黄化发育失调病毒(cucurbit yellow stunting disorder virus, CYSDV)和葫芦褪绿黄化病毒(cucurbit chlorotic yellows virus, CCYV)均可以被MEAM1和MED烟粉虱传播^[80,81], 而NW并不能有效传播CYSDV^[82]。甜菜伪黄化病毒(beet pseudo yellows virus, BPYV)和番茄侵染性褪绿病毒(tomato infectious chlorosis virus, TICV)由温室白粉虱传播^[83]。

同一种病毒不同烟粉虱的传播效率也有差异。番茄褪绿病毒(tomato chlorosis virus, ToCV)可由温室白粉虱、纹翅粉虱以及NW、NW2、MEAM1和MED烟粉虱传播^[84,85]。从传播效率来看, 纹翅粉虱和MEAM1烟粉虱均高于NW烟粉虱和温室白粉虱。而从持毒时间来看, 纹翅粉虱可达5 d, MEAM1其次, NW烟粉虱和温室白粉虱最短^[86]。De Marchi等人^[87]研究发现, MEAM1传播ToCV效率高于NW2。Shi等人^[88]对比MEAM1和MED烟粉虱获毒、持毒以及传毒后植物中病毒量, 发现MED传播的植物中, ToCV的量高于MEAM1传播的植物。甘薯褪绿矮化病毒(sweet potato chlorotic stunt virus, SPCSV)常常和通过蚜虫传播的甘薯羽状斑驳病毒(sweet potato feathery mottle virus, SPFMV)复合侵染造成甘薯病毒病(sweet potato virus disease, SPVD), 对甘薯生产造成严重影响^[89]。Sim等人^[90]以被SPCSV和SPFMV复合侵染的番薯作为毒源植物, 发现MEAM1烟粉虱传播SPCSV的效率显著高于纹翅粉虱。随后, Gamarra等人^[91]发现, 非洲伯粉虱也可以传播SPCSV, 并且无论单独接种SPCSV还是和SPFMV复合侵染, 非洲伯粉虱的传毒效率和MEAM1烟粉虱都差别不大。

3 烟粉虱对其他病毒的传播

3.1 甘薯病毒属

甘薯病毒属属于马铃薯Y病毒科, 是一类单组分的单链正义RNA病毒, 病毒粒子弯曲线性^[92]。目前, 仅有木薯褐条病毒(cassava brown streak virus, CBSV)、红瓜斑驳病毒(coccinia mottle virus, CocMoV)、黄瓜黄脉病毒(cucumber vein yellowing virus, CVYV)、南瓜黄

脉病毒(squash vein yellowing virus, SqVYV)、甘薯轻型斑驳病毒(sweet potato mild mottle virus, SPMMV)、番茄轻型斑驳病毒(tomato mild mottle virus, TomM-MoV)以及乌干达木薯褐条病毒(Ugandan cassava brown streak virus, UCBSV)7个种^[93]。

甘薯病毒属的大多数病毒都由烟粉虱以半持久型方式传播,且传播效率大都相对较低,常低于50%^[15]。Maruthi等人^[94]发现,CBSV可由烟粉虱传播,而不能由非洲伯粉虱传播。最近,Njoroge等人^[95]发现,温室白粉虱和螺旋粉虱(*A. dispersus*)也可传播CBSV。SPMMV早在1976年就被发现可由烟粉虱传播^[96],但目前可能还存在有争议^[97,98]。CVYV可以由采集自约旦和以色列的烟粉虱以半持久型方式传播,但具体的烟粉虱隐存种并未明确^[99,100]。SqVYV也被证明可由MEAM1烟粉虱以半持久型方式传播^[101]。

目前,关于哪些病毒蛋白参与甘薯病毒属病毒传播还不清楚。多数马铃薯Y病毒科病毒的传播都依赖于病毒编码的HC-Pro蛋白,而有些甘薯病毒属病毒并不编码该蛋白^[102]。因此,除外壳蛋白外是否有其他病毒蛋白参与病毒传播还有待进一步研究。Ateka等人^[103]通过对几种甘薯病毒属病毒的基因组进行分析,发现CBSV、SqVYV以及CocMoV的外壳蛋白上都有与蚜虫传播病毒相关的DAG(Asp-Ala-Gly)基序,大胆猜测蚜虫也很可能是这些病毒的传播媒介,但蚜虫能否传播还需进一步研究。

3.2 麝香石竹潜隐病毒属

麝香石竹潜隐病毒属属于乙型线性病毒科,也是一类单组分的单链正义RNA病毒。该属目前有53个独立种,仅有豇豆轻斑驳病毒(cowpea mild mottle virus, CPMMV)和甜瓜泛黄相关病毒(melon yellow-associated virus, MYaV)被证明可由烟粉虱传播^[104-107],其他病毒被认为由蚜虫传播^[15]。CPMMV可以侵染花生(*Arachis hypogaea*)、大豆(*Glycine max*)以及菜豆(*Phaseolus vulgaris*)等作物,但对大豆生产造成的损失最为严重^[108]。CPMMV一开始被认为通过烟粉虱以半持久型方式传播^[104],随后更多的证据表明其获取病毒以及传播病毒的时间均只有几分钟且没有潜伏期,因此目前认为该病毒是通过烟粉虱以非持久型的方式传播的^[108,109]。不同烟粉虱隐存种传播CPMMV效率也存在差异。De Marchi等人^[87]发现,MEAM1烟粉虱可以高效传播CPMMV(100%),而NW2传毒效率则相对较低(40%)。

MYaV的传播方式目前还没有被研究。

3.3 番茄灼烧病毒属

番茄灼烧病毒属属于伴生豇豆病毒科,是一类双组分的单链正义RNA病毒,病毒粒子呈球形。番茄灼烧病毒(tomato torrado virus, ToTV)是该属的代表种^[110],除此之外可侵染番茄的番茄灼烧病毒属病毒还有番茄枯萎病毒(tomato marchitez virus, ToMarV)以及3个目前分类地位尚不明确的番茄巧克力病毒(tomato chocolate virus, ToChV)、番茄巧克力斑病毒(tomato chocolate spot virus, ToChSV)和番茄坏死矮化病毒(tomato necrotic dwarf virus, ToNDV)^[111]。

Verbeek等人^[13]发现,MEAM1烟粉虱、温室白粉虱以及纹翅粉虱均可以半持久型方式传播ToTV、ToMarV以及ToChV。进一步地,将介体昆虫解剖为喙、头、胸和腹四部分分别检测病毒,发现仅可以在口针中检测到病毒,说明病毒存留在粉虱的口针上。Verbeek等人^[112]和Wintermantel等人^[113]发现,ToNDV也可以由NW1和MEAM1烟粉虱、温室白粉虱以及纹翅粉虱传播,且纹翅粉虱的传播效率要略高于温室白粉虱,但是否也以半持久型方式传播且停留在介体昆虫的口针上还不清楚。

番茄灼烧病毒属目前认为有6个种,除ToTV和ToMarV外,还有胡萝卜灼烧病毒(carrot torrado virus, CaTV)、莴苣坏死曲叶病毒(lettuce necrotic leaf curl virus, LNL CV)、益母草黄斑病毒(motherwort yellow mottle virus, MYMoV)以及南瓜褪绿叶斑病毒(squash chlorotic leaf spot virus, SCLSV)^[114]。目前研究发现,CaTV可以由桃蚜(*Myzus persicae*)以及肿管双尾蚜(*Cavariella aegopodii*)传播,能否由烟粉虱传播尚不明确^[115]。LNL CV则已被证实不能由烟粉虱传播,而是由莴苣蚜(*Nasonovia ribisnigri*)传播并且有可能停留在蚜虫口针上^[112]。因此该属其他病毒是否有烟粉虱传播还需进一步实验论证。

4 展望

目前,烟粉虱可以传播的植物病毒包括5个属,其中占据主要部分的是菜豆金黄花叶病毒属和毛形病毒属,并且关于这两个属的病毒经烟粉虱传播的特性及机制都研究得相对清楚。但对于甘薯病毒属、麝香石竹潜隐病毒属以及番茄灼烧病毒属的病毒来说,病毒经烟粉虱以何种方式传播等基本问题还亟待研究。经

烟粉虱传播的植物病毒达400多种,同一病毒经由不同烟粉虱隐存种传播的效率常常不同.同时,烟粉虱隐存种至少包含30多种,同一烟粉虱隐存种传播不同病毒的能力也有较大差异.因此,对于某一种或某些病毒的扩散流行来讲,不同地区各烟粉虱隐存种的组成和比例往往起着至关重要的作用.开展此类研究对于病毒病在不同地区的流行预测预警提供了生物学基础,为进一步有效防控病毒病提供了理论基础.

菜豆金黄花叶病毒属病毒是唯一可以在烟粉虱体内循环的一类病毒,其需要跨越多个屏障从而进行水平和垂直传播,寻找影响病毒传播的关键蛋白对于阻断病毒传播路径、实现有效控制病毒传播具有重要意义.目前研究人员已解析了病毒通过网格蛋白介导的胞吞进入烟粉虱中肠细胞,并在细胞内依赖早期内体进行胞内运输的机制^[33,34],但病毒与中肠细胞膜上哪个或哪些受体结合从而进入细胞尚不清楚.唾液腺是病毒经烟粉虱在植物间传播的最后一道屏障,病毒如何进入唾液腺、如何从唾液腺中逃逸以及是否与中肠有相似机制等仍需进一步研究.此外,通过分析带毒及不带毒烟粉虱的差异表达基因和蛋白发现,许多免疫相关通路基因或蛋白相对于不带毒烟粉虱来讲都有一定程度的上调或下调^[55~57].目前仅发现TYLCCV以及

TYLCCNV可以激活自噬,而PaLCuCNV则不能激活自噬^[64].该结果说明,不同病毒激活的免疫途径可能存在差异,是否还有其他免疫通路参与病毒的降解有待进一步研究.同时,病毒侵染还造成部分免疫通路基因下调,这可能是病毒抵抗免疫系统的途径,但具体机制尚不清楚.菜豆金黄花叶病毒属病毒在烟粉虱体内的复制问题仍有争议,仍需更多的证据来证明是否可以复制,同时也需要实验证据来解释已有研究结果出现差异的原因.目前已发现毛形病毒属病毒的CPm蛋白决定了其在烟粉虱体内的存留及后续的传播,而CPm上的关键位点或关键序列还有待研究,与病毒CPm互作从而介导病毒存留的烟粉虱蛋白也亟待发现.

近年来,随着转录组、蛋白质组以及基因组等组学技术日趋成熟,烟粉虱遗传信息逐步揭示,编码蛋白种类及功能也日渐完善.同时酵母双杂交以及免疫沉淀质谱联用等多种技术手段方便了我们寻找与病毒互作的烟粉虱蛋白,甚至是决定病毒传播的关键烟粉虱受体.而更为方便快捷的定向基因编辑技术不仅仅为功能研究提供便利,也使得构造不能传播病毒的烟粉虱成为可能.此外,运用新型生物材料携带dsRNA渗透到害虫体内,对靶基因进行RNAi(RNA interference)沉默,也为阻断烟粉虱传播病毒提供了新的思路.

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Summary for “烟粉虱传播植物病毒特性及机制研究进展”

Mechanisms of plant virus transmission by the whitefly *Bemisia tabaci*

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The whitefly *Bemisia tabaci* is a group of small sap-sucking insects, which is now recognized as a cryptic species complex containing at least 35 species. During the last 30 years, the Middle East Asia Minor 1 (MEAM1) and Mediterranean (MED) species of the complex have invaded many countries worldwide with the import and export trade. With the exception of direct feeding, whiteflies harm plants mainly by transmitting plant viruses, causing huge damage to crops, vegetables and ornamental plants worldwide. Tomato yellow leaf curl viruses, cassava mosaic viruses, cotton leaf curl viruses, and tomato chlorosis virus are all transmitted by *B. tabaci*, and the prevalence of these viral diseases is closely related to the outbreak of these whiteflies. Currently, more than 400 species of plant viruses in five genera, i.e. *Begomovirus*, *Crinivirus*, *Torradovirus*, *Ipomovirus* and *Carlavirus*, are transmitted by whiteflies. Among them, begomoviruses are single-stranded DNA viruses and are exclusively transmitted by whiteflies in a persistent-circulative manner. All the others are single-stranded RNA viruses and are transmitted in a semi-persistent or non-persistent manner. Here, we summarize the interactions between *B. tabaci* and the plant viruses they transmit, particularly recent advances in the understanding of the molecular mechanisms underlying whitefly transmission of plant viruses. There are multiple barriers during the circulative transmission of begomoviruses within the whitefly, including the midgut barrier, hemolymph barrier, salivary gland barrier and transovarial transmission barrier. Passage of viruses through these barriers requires specific interactions between virus and whitefly components. The ability of a virus to cross the barriers within different cryptic species of *B. tabaci* can lead to differential transmission efficiencies. Moreover, the whitefly immune systems, such as the autophagy pathway and anti-microbial peptides, have been proved to play important roles in suppressing virus infection in *B. tabaci*. In addition, some whitefly and endosymbiont proteins have been identified that participate in virus circulation within whitefly, which has greatly improved our understanding of this process. However, whether begomoviruses replicate in their whitefly vector is still controversial, and further investigation is urgently needed. We also reviewed the information on the differential transmission efficiency of whitefly-transmitted RNA viruses by different species of whiteflies. However, except the verified critical role of the minor coat protein of criniviruses in virion retention and transmission, the key factors that affect the transmission of these whitefly-transmitted RNA viruses remain largely unknown. A detailed knowledge of the mechanisms underlying plant virus transmission by its whitefly vector can lead to new strategies to combat virus spread in the field. Recent advances in the sequencing of insect genomes, reverse genetic systems and genome editing technologies, such as the CRISPR/Cas9 system, may help us to further reveal the mechanisms of virus transmission and to design novel strategies that interfere with virus transmission.

whitefly, plant virus, transmission mechanism, immune response, replication

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