

组学在水稻叶蝉和飞虱传病毒研究中的应用现状*

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摘 要 水稻叶蝉和飞虱传病毒在农田生态系统中的影响是复杂多样的。随着技术的快速发展, 组学研究已经成为当今的热点, 利用组学可以探索水稻病毒对介体昆虫(稻飞虱、叶蝉)及寄主植物的影响机制。本文综述了水稻叶蝉和飞虱传病毒基因组的研究进展, 以及近年来利用组学手段和衍生数据探索水稻病毒侵染介体昆虫和寄主植物、对介体昆虫生态适应性的影响等机制, 旨在为进一步理解水稻-病毒-昆虫三者关系以及为水稻病毒病防控策略的制定提供理论依据。

关键词 水稻病毒; 基因组学; 转录组学; 代谢组学; 多组学

Application of omics to research on rice leafhopper and planthopper-borne viruses

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Abstract The effects of rice leafhopper and planthopper-borne viruses in paddy ecosystems are complex. The rapid development of technology has made omics a popular tool for investigating these viruses in planthoppers, leafhoppers and rice plants. We here review progress in research on the rice virus genome, including the mechanisms through which vector insects and rice plants become infected with rice viruses, and ecological adaptations of vector insects, with the aim of furthering understanding of the relationship between rice plants, viruses and vector insects, and providing a theoretical basis for establishing a control strategy for rice viruses.

Key words rice virus; genomics; transcriptomics; metabonomics; multi-omics

自 1975 年桑格等发明了链终止法测序开始, 到目前为止测序技术已经经历了三次迭代更新, 发展到了第四代测序技术 (Rhee and Burns, 2006)。随着测序技术的发展, 基因组、转录组和蛋白质组的研究取得了巨大进步。而代谢组学是继基因组学和蛋白质组学之后发展起来的一门学科, 迅速发展并渗透到多项领域, 比如疾病诊断、医药研制开发、营养食品科学、毒理学及

植物学等与人类健康密切相关的领域 (Wishart, 2019)。不同组学从不同层面反映生物体的信息, 通过生物体转录组、蛋白质组和代谢组较全面的了解生物体生理代谢情况, 可以帮助研究者更加充分完整生物体不同层面的表达信息。

目前为止, 已经发现了 17 种水稻病毒, 其中十余种水稻病毒对我国水稻生产安全造成严重威胁 (Sasaya *et al.*, 2014; 庄新建等, 2020;

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Wu *et al.*, 2022)。2010-2020 年这十年间, 水稻病毒每年造成水稻产量损失约 5 万吨 (开璐等, 2021)。病毒侵染水稻或介体昆虫后, 会改变寄主的生理生化反应 (Bellure *et al.*, 2010; Shapiro *et al.*, 2013; Watts and Kariyat, 2021), 从而影响介体或非介体昆虫的种群数量 (Xu *et al.*, 2014; 王前进, 2017) 及取食行为 (周长伟, 2018) 等。

1 水稻病毒及其基因组

1.1 水稻病毒

从 20 世纪 50 年代开始, 我国就深受水稻病害的困扰 (Wei and Li, 2016)。经过稻飞虱、叶蝉等介体昆虫传播的水稻病毒有十余种 (表 1), 介体昆虫通过刺吸病株汁液获得病毒并在田间传播。水稻被病毒侵染以后会出现稻株矮化、叶

片皱缩以及抽穗不全等现象, 造成产量损失甚至绝收。

1.2 水稻病毒基因组

1991 年, 通过基因克隆得到了 RTBV 的完整序列是目前发现的唯一一个 DNA 水稻病毒 (Hay *et al.*, 1991)。1994 年, RSV 的测序完成标志着第一个 RNA 水稻病毒完整基因组的诞生 (Toriyama *et al.*, 1994); 在同一年内, RDV 也完成了最后一个片段的 (S2) 的测序 (Uyeda *et al.*, 1994), 病毒基因组的测序完成拉开了 RNA 水稻病毒基因组研究的序幕。随后, 利用相同的方法也完成了 RGSV (Toriyama *et al.*, 1998b) 和 RYSV (Huang *et al.*, 2003) 基因组的测序组装 (表 2)。

在传统的实验过程中, 主要是通过分离病毒

表 1 水稻病毒及其传播方式
Table 1 Rice virus and their modes of transmission

水稻病毒 Rice virus	病毒类型 Virus type	传播方式 Modes of transmission	病症 Symptom	参考文献 References
水稻矮缩病毒 Rice dwarf virus, RDV	RNA 病毒	黑尾叶蝉、电光叶蝉 经卵传播, 增殖型	矮缩、分蘖增多、叶片浓 绿、僵直	阮义理等, 1981
水稻瘤矮病毒 Rice gall dwarf virus, RGDV		黑尾叶蝉、电光叶蝉 不经卵传播, 增殖型	病株严重矮缩, 叶背叶鞘 上长出淡黄绿色瘤	Omura <i>et al.</i> , 1980
南方水稻黑条矮缩病毒 Southern rice black-streaked dwarf virus, SRBSDV		白背飞虱 不经卵传播, 增殖型	叶色浓绿、明显矮缩、分 蘖增多、根系不发达	周国辉等, 2010
水稻黑条矮缩病毒 Rice black-streaked dwarf virus, RBSDV		灰飞虱 不经卵传播, 增殖型	浓绿矮缩、叶片僵直、不 抽穗或者穗小	孙枫等, 2013
水稻条纹叶枯病毒 Rice stripe virus, RSV		灰飞虱 经卵传播, 增殖型	褪绿的条纹斑点或斑块, 可分为卷叶型和展叶型	阮义理等, 1983
水稻草状矮化病毒 Rice grassy stunt virus, RGSV		褐飞虱 不经卵传播, 增殖型	矮化、分蘖增多、叶片细 小、淡绿到淡黄或橙黄色	石超南等, 2018
水稻黄矮病毒 Rice yellow shunt virus, RYSV		黑尾叶蝉 不经卵传播, 增殖型	矮化, 花叶黄枯、株型松 散, 根系短小衰朽	Chiu <i>et al.</i> , 1965
水稻条纹花叶病毒 Rice stripe mosaic virus, RSMV		电光叶蝉	抽穗不完全, 籽粒不饱满	Yang <i>et al.</i> , 2017
水稻齿叶病毒 Rice ragged stunt virus, RRSV		褐飞虱 持久性传播	叶片扭曲、锯齿状缺刻	郑璐平等, 2008
水稻东格鲁杆状病毒 Rice tungro bacilliform virus, RTBV	DNA 病毒	二点黑尾叶蝉 半持久性传播	受害植株矮缩和叶片变 色, 生长衰退	吴刚等, 2000

表 2 水稻病毒基因组
Table 2 Rice virus genome

水稻病毒 Rice virus	基因组片段 Number of chromosomes	基因组大小 Genome size	基因组完成过程 Genome completion process
水稻东格鲁杆状病毒 Rice tungro bacilliform virus, RTBV	3 条双链 DNA 组成	8.0 kb	组装完成 (Hay <i>et al.</i> , 1991)
水稻矮缩病毒 Rice dwarf virus, RDV	S1-S12, 12 条双链 RNA 片段组成	24.8 kb	基因组片段 S3 完成测序 (Suzuki <i>et al.</i> , 1990), 基因组片段 S1 完成测序 (Suzuki <i>et al.</i> , 1992), 组装完成 (Uyeda <i>et al.</i> , 1994)
水稻条纹叶枯病毒 Rice stripe virus, RSV	S1-S4, 4 条双链 RNA 组成	17.1 kb	基因组片段 S3 测序完成 (Zhu <i>et al.</i> , 1991), 基因组片段 S4 完成测序 (Zhu <i>et al.</i> , 1992), 基因组片段 S2 完成测序 (Takahashi <i>et al.</i> , 1993), 基因组片段 S1 完成测序, 组装完成 (Toriyama <i>et al.</i> , 1994)
水稻草状矮化病毒 Rice grassy stunt virus, RGSV	S1-S6, 6 条单链 RNA 组成	25.1 kb	基因组片段 S5 和 S6 完成测序 (Toriyama <i>et al.</i> , 1997), 组装完成 (Toriyama <i>et al.</i> , 1998a)
水稻黄矮病毒 Rice yellow shunt virus, RYSV	1 条复义单链 RNA 组成	14.0 kb	组装完成 (Luo <i>et al.</i> , 1998)
水稻齿叶病毒 Rice ragged stunt virus, RRSV	10 条双链 RNA 组成	26.2 kb	基因组片段 S9 完成测序 (Upadhyaya <i>et al.</i> , 1995), 基因组片段 S5 (Li <i>et al.</i> , 1996) 和 S8 (Upadhyaya <i>et al.</i> , 1996) 完成测序, 基因组片段 S7 和 S10 完成测序 (Upadhyaya <i>et al.</i> , 1997), 组装完成 (Upadhyaya <i>et al.</i> , 1998)
水稻黑条矮缩病毒 Rice black-streaked dwarf virus, RBSDV	S1-S10, 10 条双链 RNA 片段组成	29.1 kb	组装完成 (Zhang <i>et al.</i> , 2001)
水稻瘤矮病毒 Rice gall dwarf virus, RGDV	S1-S12, 12 条双链 RNA 片段组成	25.7 kb	基因组片段 S9 完成测序 (Koganezawa <i>et al.</i> , 1990), 基因组片段 S8 和 S10 完成测序 (Noda <i>et al.</i> , 1991), 基因组片段 S11 完成测序 (Moriyasu <i>et al.</i> , 2000), 组装完成 (Moriyasu <i>et al.</i> , 2007)
南方水稻黑条矮缩病毒 Southern rice black-streaked dwarf virus, SRBSDV	S1-S10, 10 条双链 RNA 片段组成	29.1 kb	组装完成 (Yin <i>et al.</i> , 2011)
水稻条纹花叶病毒 Rice stripe mosaic virus, RSMV	1 条复义单链 RNA 组成	12.8 kb	组装完成 (Yang <i>et al.</i> , 2017)
水稻矮化相关布尼亚样病毒 Rice dwarf-associated bunya-like virus, RDaBV	L、M 和 S 片段组成	9 349 nt	组装完成 (Wang <i>et al.</i> , 2022)

株来进行鉴定,但是该方法周期长,对于新病毒的发现产生了一定的局限性。随着技术的进步,利用高通量测序可以快速且高质量的鉴定自然界中水稻病毒(洪健等,2021)或发现新水稻病毒(Wang *et al.*, 2022)。目前该新发现的水稻病毒暂时被命名为水稻矮化相关布尼亚样病毒(Rice dwarf-associated bunya-like virus,

RDaBV),由 L、M 和 S 片段组成, L 片段负责编码保守蛋白, M 片段编码非结构蛋白, S 片段负责编码核衣壳和另一个非结构蛋白。通过系统发育分析发现该病毒与 2021 年国际病毒分类委员会 ICTV 新创建的 *Discoviridae* 家族(https://talk.ictvonline.org/taxonomy/p/taxonomy-history?taxnode_id=202112952)位于同一分支,但是目前该家

族中的病毒宿主均为卵菌门和子囊菌门,这是第一次发现利用褐飞虱 *Nilaparvata lugens*、白背飞虱 *Sogatella furcifera*、灰飞虱 *Laodelphax striatellus* 和电光叶蝉 *Inazuma dorsalis* 这些常规的介体昆虫均不能将该病毒传播到水稻上,说明水稻病毒很有可能有的新的传播介体(Wang *et al.*, 2022),值得进一步的关注。

2 病毒对水稻植株影响的组学研究

随着水稻病毒的基因组的深入研究,关于水稻病毒对水稻影响机制的研究也愈来愈多。水稻感染水稻病毒后,其形态特征会发生变化,其原因是多种多样的。通过分析 RSV 感染后的水稻原生质体蛋白质组数据和叶绿体蛋白质组数据,发现叶绿体中叶绿体相关蛋白含量显著性降低,但原生质体中的叶绿体相关蛋白含量没有显著性差异。通过基因富集发现,RSV 侵染水稻会改变水稻叶绿体相关蛋白运输到叶绿体的过程(Zhao *et al.*, 2019),从而抑制叶绿体内叶绿体相关蛋白的积累,使水稻叶片出现不同程度的褪绿情况(Nemoto *et al.*, 1994)。而水稻感染 RBTV 以后,叶绿素相关基因表达发生变化,从而导致水稻叶片褪绿(Srilatha *et al.*, 2019)。

水稻在被病毒侵染以后会产生不同程度的防御反应,来抵御病毒的侵染(Yang *et al.*, 2014)。通过比较 RBSDV 病株和健康水稻的转录组,发现水稻感染 RBSDV 后与防御相关的基因显著上调(Zhang *et al.*, 2020)。病毒也会对水稻的防御做出反应。通过分析 RSV 病株和健康水稻的转录组数据(Yang *et al.*, 2016)和蛋白质组数据(Tan *et al.*, 2022),发现 RSV 侵染水稻后会促进转录因子 NF-YA 和 B7EPB8 的表达,NF-YA 表达升高会进一步抑制水稻茉莉酸(Jasmonic acid, JA)途径的相关基因表达,从而会抑制水稻防御反应。拟南芥同源蛋白 B7EPB8 可以与 RSV P2 蛋白相互结合,该蛋白可以促进 JA 途径的表达,因此 P2 蛋白可能通过与 JA 途径竞争性结合 B7EPB8,从而抑制水稻对 RSV 的抗性。

在组学快速发展之前,主要利用田间试验来

筛选对水稻病具有抗性的水稻,工作周期长,抗性机制不明确。通过多组学的大数据挖掘可以探究水稻对病毒的抗性机理,为遗传育种提供方向(Reinke *et al.*, 2018)。如利用基因组筛选出与 RBSDV 抗性相关的基因,后期可以通过转基因技术选育抗 RBSDV 的水稻品系(Liu *et al.*, 2021b)。通过田间试验筛选出对 SRBSDV 具有抗性的杂交稻,再通过荧光定量比较抗性水稻中病毒表达量,得到具有较高抗性的杂交稻 Z1、L2186,随后利用多维液质联用技术比较 SRBSDV 胁迫过的高抗水稻 Z1、L2186 的蛋白质组,发现富含甘氨酸的 PR-1 蛋白均上调,但是蛋白上调表现不完全相同,不同水稻对相同水稻病毒的防御机制可能有所差异(Wang *et al.*, 2017)。除此之外,多组学也可以用于转基因水稻的安全性评价。通过对 RSV 具有稳定抗性的转基因水稻品系(KRSV-1)的转录组数据和蛋白质组数据进行分析,确认了该转基因水稻品系营养物质较野生型水稻无明显差异,而且不会因为转基因而积累有毒蛋白质(Xu *et al.*, 2019)。通过气相色谱-质谱分析转基因水稻 T1C-19(Cry1C 水稻)在感染 RDV 后的代谢组数据变化,发现 Cry1C 水稻较亲本非转基因水稻明恢 63 号对 RDV 的反应更加强烈,更多的代谢物发生显著变化,但是 RDV 感染率并未上升,不会造成 RDV 的广泛传播(Chang *et al.*, 2021)。组学数据还可以用于研究防治病毒农药的作用机制。嘧啶霉素是高效、低毒的胞嘧啶核苷类抗病毒农用抗生素(吴元华等, 2005),比较嘧啶霉素处理过的 SRBSDV 病株和未处理过的 SRBSDV 病株的蛋白质组,发现病株体内部分蛋白可以富集到防御反应上,同时荧光定量验证部分抗性基因和保护酶表达量显著提高(Yu *et al.*, 2018)。

3 病毒对介体昆虫影响的组学研究

水稻病毒侵染介体昆虫以后会诱导其启动防御机制。通过转录组研究发现,灰飞虱体内的泛素缀合酶编码基因可以抑制 RSV 在灰飞虱体内积累(Li *et al.*, 2020)。但是水稻病毒突破屏障在介体昆虫体内复制增殖,会抑制昆虫防御机

制的发生。在比较 RSV 灰飞虱和健康灰飞虱的转录组数据,发现了选择性剪接事件参与调节水稻病毒与介体昆虫之间存在复杂关系,约有 31.4%的剪接基因对飞虱肠道感染 RSV 有响应。通过选择性剪接产生 c-Jun 氨基端激酶 (c-Jun N-terminal kinase, JNK) 3 个转录本亚型,这 3 种亚型对 RSV 感染表现出不同的反应,并且至少有两种亚型促进了飞虱中的病毒积累 (Tong *et al.*, 2022)。利用荧光定量 PCR 发现,RSV 在灰飞虱体内脂肪体和血淋巴含量最高。进一步比较了携带 RSV 的灰飞虱与健康灰飞虱脂肪体的蛋白质组数据,共有 156 种差异表达蛋白,其中 mRNA 衰变蛋白 ZFP36L1 丰度增加了 69%,将该基因沉默后发现灰飞虱对 RSV 的抗性显著增加,表明 RSV 可能通过诱导该蛋白的表达促进 RSV 的积累 (Huang *et al.*, 2021)。通过定量蛋白质组学分析取食 RBSDV 病株 3 d 和 5 d 后的灰飞虱线粒体蛋白丰富度呈现下降的趋势,并且逆转录荧光定量 PCR 验证线粒体相关基因的表达水平也呈现下降的趋势,选择性自噬基因转录水平上调, RBSDV 可能通过促进灰飞虱线粒体自噬来提高其在灰飞虱体内的积累 (Liu *et al.*, 2021a)。

介体昆虫感染水稻病毒后,其生态适应性会发生变化。通过分析 5、25 和 36 °C 处理下携带 SRBSDV 的白背飞虱和无毒白背飞虱的代谢组数据,发现白背飞虱感染 SRBSDV 以后体内能量物质海藻糖的积累减少,脂肪酸的积累增加,从而降低白背飞虱的低温耐受性,提高白背飞虱高温耐受性 (Zhang *et al.*, 2018)。通过测定携带 SRBSDV 的白背飞虱雌性成虫、接毒后不携带病毒的雌性成虫和未接毒的雌性成虫的转录组,发现差异基因主要负责初级代谢和免疫,同时发现接毒失败的白背飞虱特异基因表达较健康成虫也呈上调的趋势 (Liu *et al.*, 2022)。灰飞虱感染 RSV 以后,种群数量会下降 (周益军等, 2012)。为了探究 RSV 抑制种群数量的机制,使用同位素标记进行相对和绝对定量方法分析了携带 RSV 和健康雌性灰飞虱之间卵子的蛋白质组学变化,共发现了 147 种差异蛋白,其中约

66.7%的蛋白在携带 RSV 的灰飞虱体内表达增加,并通过荧光定量 PCR 验证相关基因与蛋白的变化趋势一致,其中部分差异蛋白参与灰飞虱的减数分裂 (Liu *et al.*, 2021a) 这些差异蛋白与卵子减数分裂的关系有待后续开展。另外,通过比较 RSV 灰飞虱种群和健康灰飞虱种群的卵巢转录组数据,发现灰飞虱卵黄原蛋白受体参与 RSV 垂直传播给 F1 代的过程 (He *et al.*, 2019)。

4 展望

利用基因组学、转录组学、蛋白质组学、代谢组学等分析水稻病毒对植食性昆虫翅型影响、取食行为变化以及其他生态适应性变化的机制是当前的研究热点之一,其结果有助于了解水稻病毒对植食性昆虫种群数量产生的影响,从而为植物病毒病防控以及在病毒病流行的条件下害虫的管理提供理论依据。目前为止,组学主要应用在分析水稻病毒对水稻产生的影响上,关于水稻病毒侵染介体昆虫后种群适合度机制的研究主要集中在 RSV、RBSDV 和 SRBSDV 等,在其他水稻病毒以及病毒对非介体昆虫影响机制等方面的研究则较少。另外,大多数的研究都是针对单一组学进行分析。然而由于水稻病毒与介体昆虫、非介体和水稻之间的关系是复杂多样的,通过单一组学难以深入理解复杂的相互关系。

随着组学测序技术的不断创新和发展,越来越多组学数据能快速获得,利用多组学数据整合分析现象和探索相关机制,可以补充单一组学中缺失或不可靠的信息。从大量而繁杂的多组学数据中找到内在关联,系统研究探索介体(非介体)昆虫-植物病毒-寄主植物之间的相互作用,对于揭示三者互作关系及其背后更复杂的机制具有重要作用。

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