



李义婷, 李艳, 尹军良. 植物环状RNA的生物学功能及其研究进展[J]. 中国农业大学学报, 2025, 30(03):60-70.

LI Yiting, LI Yan, YIN Junliang. Biological functions of plant circular RNA and its research progress[J]. *Journal of China Agricultural University*, 2025, 30(03):60-70.

DOI: 10.11841/j.issn.1007-4333.2025.03.06

植物环状RNA的生物学功能及其研究进展

李义婷 李艳 尹军良*

(长江大学 农学院/农业农村部长江中游作物绿色高效生产重点实验室(部省共建), 湖北 荆州 434025)

摘要 为深入了解植物环状RNA(circular RNA, circRNA)在植物生长发育过程、胁迫响应中的生物学功能,以“环状RNA”“生物学功能”“biological function”“stress response”为关键词,在中国知网、Web of Science和SPIS Academic Resources Online等数据库检索,获取92篇相关文献,归纳总结了植物circRNA的分类与形成方式、鉴定工具以及生物学功能等。结果表明:植物circRNA分为外显子circRNA、内含子circRNA和外显子-内含子circRNA;circRNA有套索驱动环化、外显子侧翼内含子反向互补配对环化、RNA结合蛋白(RNA-binding protein, RBP)促进外显子环化以及内含子依靠5'和3'端的基序反向拼接驱动环化4种形成方式;目前已发现circRNA具有多种生物功能,包括作为海绵体调控miRNA表达;参与调控植物生长发育、响应生物和非生物逆境胁迫;参与蛋白翻译以及与蛋白互作调控相关通路。

关键词 植物 circRNA; 生物学功能; miRNA 海绵; 非编码RNA

中图分类号 Q752

文章编号 1007-4333(2025)03-0060-11

文献标志码 A

Biological functions of plant circular RNA and its research progress

LI Yiting, LI Yan, YIN Junliang*

(College of Agriculture/Key Laboratory of Sustainable Crop Production in the Middle Reaches of the Yangtze River (Co-construction by Ministry and Province), Ministry of Agriculture and Rural Affairs, Yangtze University, Jingzhou 434025, China)

Abstract In order to gain an insight understanding of the biological functions of plant circular RNA (circRNA) in plant growth and development process and stress response, literature searching was conducted based in CNKI, Web of Science, and SPIS Academic Resources Online by taking "circular RNA", "biological function", "biological function", and "stress response" as keywords. A total of 92 relevant publications were retrieved. The classification and formation mechanisms of plant circRNA, the identification tools, and their biological functions were summarized. The results show that plant circRNA can be classified into exonic circRNA, intronic circRNA, and exon-intron circRNA. The formation mechanisms of circRNA include four main types: Lariat-driven circularization, exon-flanking intron reverse complementary pairing-driven circularization, RNA-binding protein-mediated exon circularization, and intron circularization driven by reverse splicing at the 5' and 3' ends. circRNA are found to play multiple biological functions, including acting as miRNA sponges to regulate miRNA expression; participating in the regulation of plant growth and development, and responses to abiotic and biotic stress, and involving in protein translation and in pathways related to protein-protein interactions.

Keywords plant circRNA; biological function; miRNA sponges; non-coding RNA

收稿日期: 2024-09-12

基金项目: 国家自然科学基金(32272500)

第一作者: 李义婷(ORCID:0009-0001-7414-5750), 博士研究生, E-mail: 202071655@yangtzeu.edu.cn

通讯作者: 尹军良(ORCID:0000-0002-3375-8622), 教授, 主要从事植物抗病性及其利用的研究, E-mail: yinjunliang@yangtzeu.edu.cn

植物体内含有多种类型的非编码RNA,其中包括转运RNA(tRNA)、核糖体RNA(rRNA)、微小RNA(miRNA)、小干扰RNA(siRNA)、反式作用siRNA(tasiRNA)、小核RNA(snRNA)、小核仁RNA(snoRNA)、长链非编码RNA(lncRNA)和环状RNA(circular RNA, circRNA)等^[1-3]。circRNA是近年来加入非编码RNA家族的新成员,是一类经过反向剪接后,由3'端下游供体和5'端上游受体共价结合形成的单链非编码RNA分子,广泛存在于多种生物体中,具有不易降解、细胞或组织特异性等特征^[4]。系统总结circRNA在植物中的作用机制,有助于揭示其在植物抗病响应、生长发育调控和环境适应等过程中的生物学功能,为提高作物的抗逆性和产量提供理论依据和应用指导。

20世纪70年代, Sanger等^[5]首次在植物病毒中发现了闭合的circRNA分子,并在真核细胞中验证了circRNA的存在。Kristensen等^[6]研究表明, circRNA具有结构稳定、种类丰富、序列保守、在细胞和组织中特异性表达等特性,并具备多种生物学功能,可作为miRNA海绵体调控miRNA表达、*cis*调控亲本基因表达、与蛋白互作调控相关通路、参与蛋白翻译等方面发挥重要作用。高通量测序结果显示, circRNA广泛存在于植物中,且在植物正常生长发育过程、应答生物和非生物逆境胁迫中差异性表达^[7]。目前,全面探讨植物circRNA生物学功能的研究鲜见报道。本研究在中国知网、Web of Science和SPIS Academic Resources Online等网站检索,获取相关文献,归纳总结植物circRNA的分类及形成方式;概述植物circRNA已知的生物学功能及其作用机制,对目前植物circRNA研究中存在的问题进行了讨论,并对后续研究做了展望,旨在深入了解circRNA在植物生长发育过程、胁迫响应中的生物学功能,以期能为植物circRNA的功能研究和应用提供参考。

1 文献来源

在中国知网、Web of Science和SPIS Academic Resources Online等数据库,以“环状RNA”“生物学功能”“biological function”“stress response”等关键词检索相关文献92篇。

2 circRNA的分类与形成方式

2.1 circRNA的分类

circRNA是一类由信使RNA前体(precursor message RNA, pre-mRNA)通过反向剪切形成的长度主要在200~600 nt的共价闭环状非编码RNA分子^[8]。目前已发现的circRNA根据其基因组来源区域不同,可分为三类:1)外显子circRNA(exonic circRNA, ecircRNA),这类circRNA主要源自编码基因,由一个或多个外显子形成环状结构,主要分布在细胞质中,大部分此类circRNA不能编码蛋白质^[9];2)内含子circRNA(intronic circRNA, ciRNA),仅由内含子组成的circRNA,一般由2个或多个内含子形成环状结构,仅分布在细胞核内^[10];3)外显子-内含子circRNA(exon-intron circRNA, EIciRNA),由外显子和内含子组合形成的环状结构,主要定位于细胞核中^[11]。

2.2 circRNA的形成方式

circRNA的生物合成方式与线性RNA的经典剪切方式不同^[12-18]。目前已经发现了4种circRNA的主要生物合成机制:套索驱动环化、外显子侧翼内含子反向互补配对环化、RNA结合蛋白(RNA-binding protein, RBP)促进外显子环化以及内含子依靠5'和3'端的基序反向拼接驱动环化^[12](图1)。1)套索驱动环化:由外显子跳跃产生,形成包含外显子和内含子的套索结构,随后该前体进行自剪接,内含子被剪切掉,最终形成环状结构^[13-14];2)外显子侧翼内含子反向互补配对环化:外显子侧翼内含子序列反向互补配对,使内含子和外显子连接,形成环状结构^[15];3)RBP结合外显子侧翼的内含子序列,促使两端内含子靠近,进而驱动外显子环化^[16];4)内含子依靠5'和3'端的剪切信号(AG-GU)反向拼接驱动环化,内含子的5'和3'端通过AG-GU基序反向拼接,形成环状结构,经剪切后形成成熟的circRNA^[17-18]。

3 植物circRNA鉴定工具

目前,已发布的circRNA预测软件有10余种(表1)。根据不同的算法,可将预测软件分为2种:一种是针对内含子驱动模式下的反向可变剪切接头序列而设计,包括CIRCexplorer^[19]、find_circ^[20]和CIRI^[21]等;另一种是通过基因组注释信息推测得到

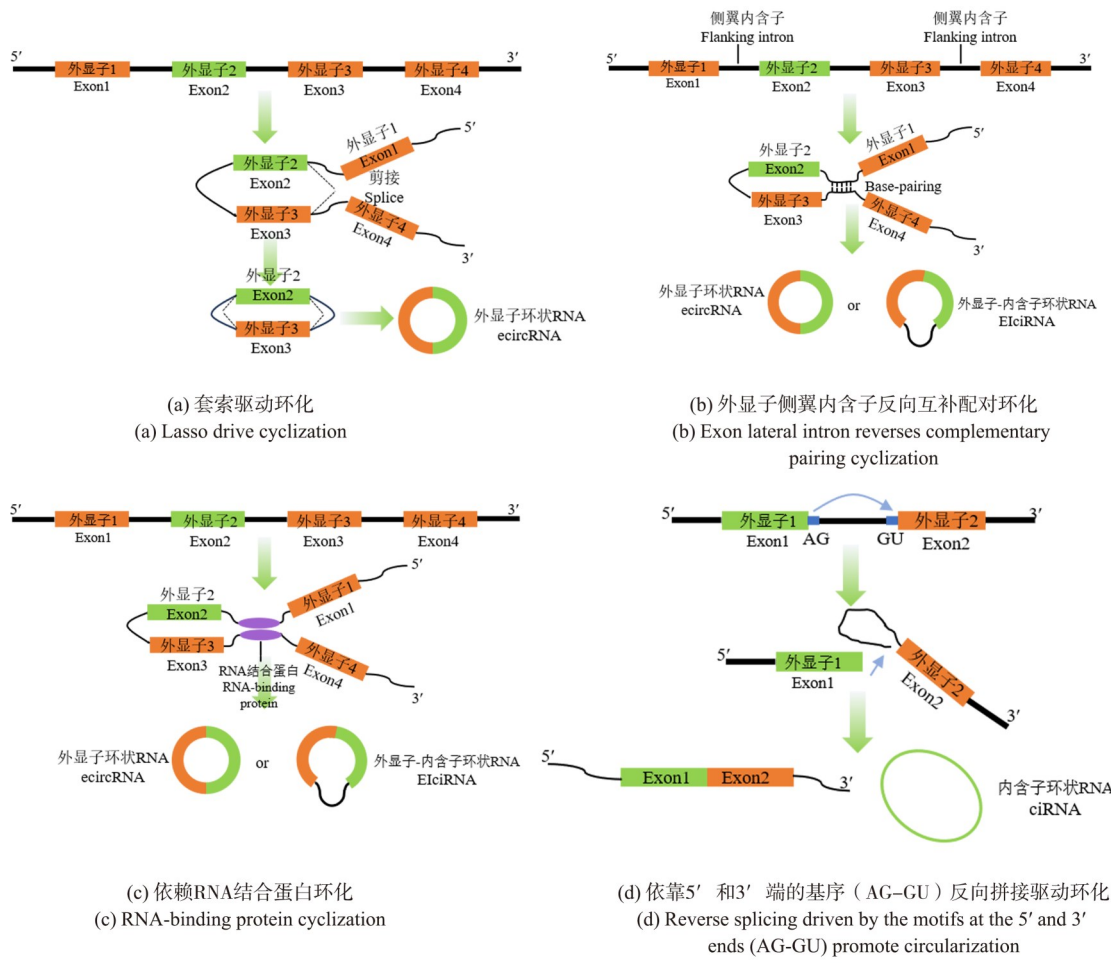


图1 CircRNA形成方式

Fig. 1 Mode of circRNAs formation

反向可变剪切接头序列,然后与注释的外显子序列进行匹配,预测得到新 circRNA 的软件,如 KNIFE^[22]等。以上软件均是以动物和人类 circRNA 为研究对象开发的,对于植物 circRNA 并不完全适用。Chen 等^[23]于 2016 年开发的 pcircRNA_finder 是专门为预测植物 circRNA 而设计的软件,结合了多种算法来检测反向剪接读数,相比而言是更全面、更灵敏以及更精确的植物 circRNA 预测软件,但该软件缺点在于仅能预测外显子 circRNA。随后,Zhang 等^[24]和 Yin 等^[25]分别在 2020 和 2021 年开发了用于鉴定植物 circRNA 的软件 CircPlant 和 PCirc。由于这些生物信息学鉴定工具在识别 circRNA 时表现的精确度和灵敏度不同,在实际应用中,常同时使用多款软件进行预测分析,相互交叉验证,可提高植物 circRNA 鉴定的效率和精度。

4 植物 circRNA 的生物学功能

4.1 发挥海绵功能吸附 miRNA

动物 circRNA 含有大量的 miRNA 结合位点,可通过海绵体作用竞争性吸附 miRNA 分子,进而间接调控 miRNA 下游靶基因的表达^[30-32]。与动物 circRNA 相比,仅发现少数的植物 circRNA 中含有 miRNA 结合位点,且单个 circRNA 中含有多个 miRNA 结合位点的现象更为少见;虽然如此,这些植物 circRNA 也可作为 miRNA 海绵,通过吸附 miRNA 来调控靶基因表达^[33-34]。Kulcheski 等^[35]研究表明,拟南芥中大概有 5% 的 circRNA 具有作为 miRNA 海绵的潜在能力;但 Chen 等^[36]报道的比例更低,只有 0.67%。在水稻 1 356 个外显子 circRNAs 中,有 235 个 circRNAs 被预测含有 miRNA 结合位点,其中 31 个 circRNAs 具有 2 个及

表 1 部分常用 circRNA 预测软件
Table 1 The commonly used software for circRNA prediction

软件名 Software name	网址 Uniform resource locator	开发者 Developer	文献 Reference
CIRCfinder	https://github.com/YangLab/CIRCfinder	Zhang 等	[10]
CIRI-full	https://sourceforge.net/projects/ciri-full/	Zheng 等	[26]
MapSplice	http://www.netlab.uky.edu/p/bioinfo/MapSplice	Wang 等	[27]
circRNA_finder	https://github.com/orzechoj/circRNA_finder.git	Westholm 等	[20]
KNIFE	https://github.com/lindaszabo/KNIFE	Szabo 等	[22]
CircDBG	https://github.com/lxwgcool/CircDBG	Li 等	[28]
find_circ	https://github.com/marvin-jens/find_circ	Memczak 等	[29]
CircExplorer2	https://github.com/YangLab/CIRCexplorer2	Zhang 等	[19]
CIRI2	https://sourceforge.net/projects/ciri/files/CIRI2	Gao 等	[21]
PcircRNA_finder	https://github.com/bioinplant/PcircRNA_finder/	Chen 等	[23]
CircPlant	http://bis.zju.edu.cn/circplant	Zhang 等	[24]
PCirc	https://github.com/Lilab-SNNU/Pcirc	Yin 等	[25]

2 个以上的 miRNA 结合位点^[37]。同时, circRNA *Os08Circ16564* 被预测为 *miR172* 的目标海绵, 但过表达 *Os08Circ16564* 的水稻转基因植株中 *OsmiR172* 表达水平与野生型没有显著差异, 表明其可能不是 *miR172* 的真正海绵^[37-38]。在枸橘早花突变体中, 发现了 176 个差异表达的 circRNAs, 其中 29 个 circRNAs 可作为 16 个 miRNA 的潜在靶标^[39]。玉米的 2 804 个 circRNA 中有 15 个含有 miRNA 结合位点^[36]。Hong 等^[40]研究表明, 番茄中的 *circRNA45* 和 *circRNA47* 可能作为 *miR477-3P* 的海绵, 来调控靶标抗病基因 *SpRLK1/2* 的表达, 从而参与到番茄对晚疫病的抗性免疫中, 并起到正调节作用。另外, 通过鉴定和比较野生型以及乙烯信号转录因子 (ethylene-responsive transcription factors, LeERF1) 转基因番茄果实中的 circRNA, 发现 61 个 circRNA 可能具有吸附 miRNA 的作用, 其中一些 miRNA 已被证实参与了乙烯信号转导途径^[41]。

4.2 调控植物生长发育

circRNA 广泛存在于植物体内, 在生长发育过程中发挥着重要作用 (图 2(a))。circRNA 可以与植物激素信号通路相关基因相互作用, 调节激素信号传导的过程, 从而影响植物的生长和发育^[42-43]。已有研究发现, circRNA 在番茄开花期发挥着重要作

用^[44], circRNA 主要参与调节番茄花期生长发育过程中的生物大分子合成和代谢, 包括氨基酸合成代谢、磷酸戊糖途径、花生四烯酸代谢以及脂肪酸代谢等重要生物过程^[45]。Wang 等^[41]研究结果表明, 番茄果实中 39 个 circRNAs 的 102 个靶标 mRNA 在乙烯合成和信号转导通路中均发挥作用。circRNA 在番茄果实成熟过程中参与调控色素积累, 过表达与色素合成相关的 circRNA (*PSY1-circ1* 和 *PSD-circ1*) 可导致番茄红素和 β -胡萝卜素积累显著减少, 番茄果实呈黄色, 叶片、花瓣和萼片呈白色^[46]。在大豆中, circRNA *Gm03circRNA1785* 的靶标是 *gma-miR167c*, 而 *gma-miR167c* 的靶标中包括 *GmARF6* 和 *GmARF8*, 这 2 个基因均已被证实在大豆结瘤和侧根发育中发挥作用; 通过 qRT-PCR 验证, 也进一步证实了上述 circRNA、miRNA 和靶基因之间的相互作用; 同时也揭示了 *Gm03circRNA1785* 通过 circRNA、miRNA 和 mRNA 调控网络参与大豆结瘤和侧根发育的作用机制^[47]。Cheng 等^[48]研究发现了 1 个转录自拟南芥 *At5g37720* 基因位点的特异性 laciRNA, 过表达该环状 RNA 会导致拟南芥延迟开花、叶片卷曲和簇状叶。 *Os06circ02797 Δ 1* 突变体水稻幼苗比野生型 (WT) 幼苗更绿、更高; 通过对叶绿素含量进行定量分析, 发现 *Os06circ02797 Δ 1* 植株的叶绿素 a 和 b 含量均显著升高; 说明该

circRNA的生物学功能与水稻光合作用相关^[49]。

4.3 响应非生物逆境胁迫

Zuo等^[50]研究表明,在非生物逆境胁迫下,circRNA会受诱导并发生差异表达(图2(b))。在冷胁迫下,甜椒果实中有36个circRNA差异表达。干旱胁迫下,梨中有33个circRNA差异表达,功能分析发现这些circRNA参与多种与脱水反应相关的生物学过程^[51];同时,小麦幼苗在脱水胁迫下有62个差异表达的circRNA,表明这些circRNA可能在小麦响应水分胁迫中发挥着重要作用^[52]。在磷酸盐胁迫下,水稻中有27个外显子circRNA差异表达^[35];在盐胁迫下,水稻中有93个circRNA差异表达^[53]。在寒冷胁迫下,番茄中有138个circRNA受诱导而上调表达,25个circRNA受诱导而下调表达,总计有163个番茄circRNA响应冷胁迫^[54]。在对葡萄进行不同时间段的低温胁迫处理后,共检测到475个差异表达的circRNA^[55]。后续通过在拟南芥中过表达来自葡萄的CircATS1(*Vv-CircATS*),发现*Vv-CircATS1*通过上调*miR156*和*miR396*的表达来增强拟南芥的耐寒性,且*miR156*和*miR396*已被证明对植物的耐寒性具有正向调节作用^[56]。同时,Gao等^[57]研究发现,*Vv-CircSIZ1*通过吸附*VvmiR3631*,减轻*VvmiR3631*对*VvVHAc1*的抑制作用,从而提高葡萄的耐盐性。茶树中的CSS-circFAB1在寒冷胁迫下被显著诱导,通过FISH和基因沉默试验发现,CSS-circFAB1可参与到茶树的耐寒性过程^[58]。在拟南芥中发现大量与热胁迫应答相关的circRNA,数量达1583个,并且circRNA的长度、外显子环化数量、可变剪接事件在热胁迫下都有所增加^[59]。在热胁迫条件下,杨树中的circ_0003418上调会促进*PtoXBAT32.5*的表达水平,导致乙烯和丙二醛含量上升,引发膜脂过氧化,并通过泛素介导的蛋白质修饰途径对杨树的耐热性产生负向调节作用^[60]。在大豆中,通过高通量测序共鉴定到1275个与干旱相关的circRNA,其中,在干旱胁迫6h时,差异表达的circRNA有145个,12h时差异表达的有61个circRNA^[61];在冷处理4h时,大豆中出现41个显著差异表达的circRNA,8h时,共有35个显著差异表达的circRNA^[62]。在黄瓜中共鉴定出2787个circRNA,其中根中有1934个、叶中有44个在盐胁迫下表达差异,对这些circRNA的亲本基因和靶标

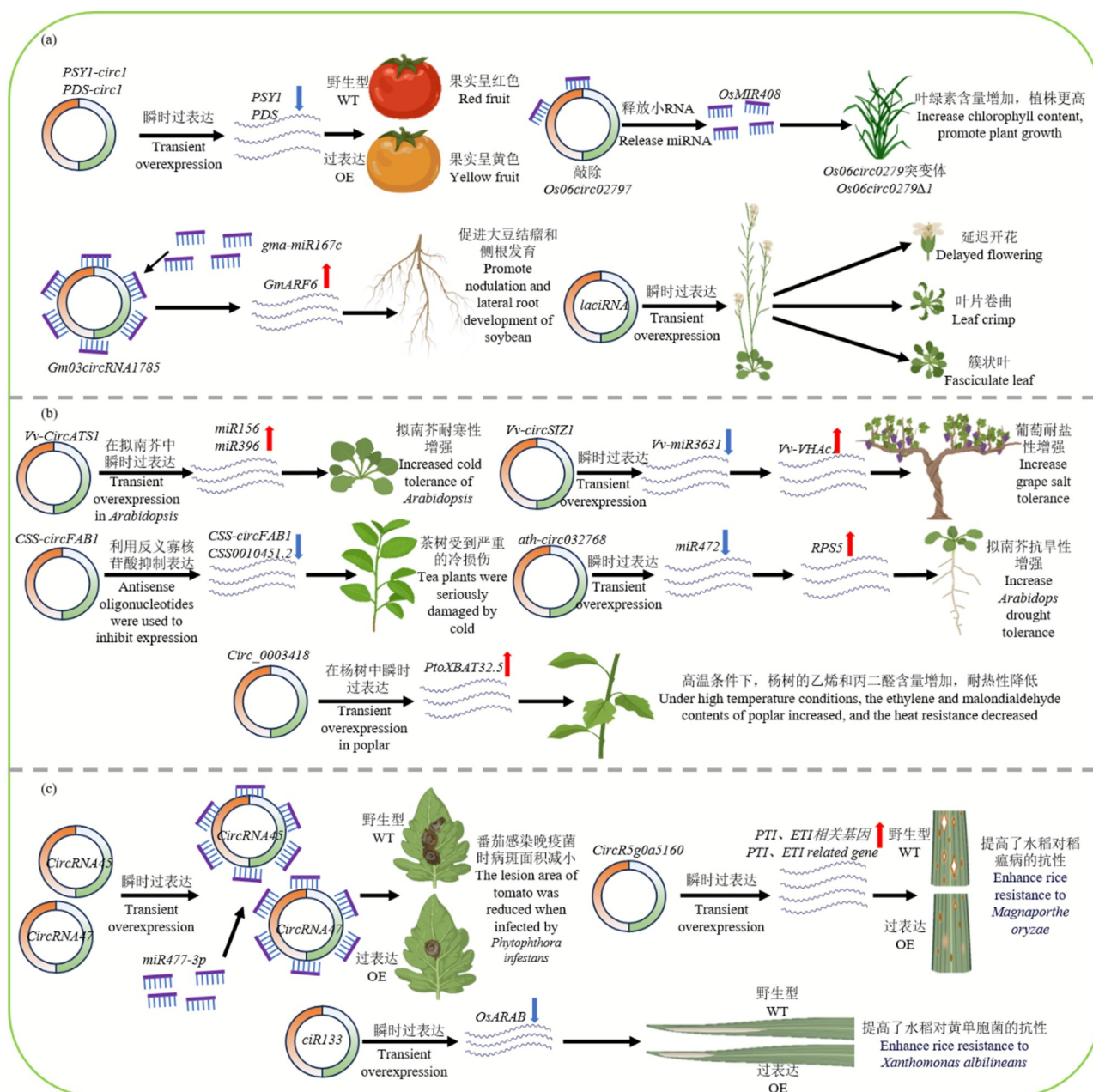
mRNA进行功能注释和富集分析后,发现circRNA可能通过介导转录、信号转录、细胞周期、代谢适应和离子稳态等相关途径在黄瓜响应盐胁迫中发挥作用^[63]。在拟南芥中过表达毛竹circRNA *PecircCDPK*可以提高拟南芥的抗旱性^[64]。

4.4 响应生物逆境胁迫

circRNA在生物胁迫中也发挥着重要作用(图2(c))。通过对猕猴桃circRNA鉴定发现,circRNA对细菌性溃疡病原菌入侵具有特异性响应^[65]。通过基因差异表达分析,Zhou等^[66]在马铃薯中检测到429个在肉毒杆菌巴西亚种(*Pectobacterium carotovorum* subsp. *brasiliense*)感染中显著差异表达的circRNA。此外,受到黄萎病菌感染的棉花中有280个差异表达的circRNA^[67],玉米花叶病毒(Maize mosaic virus, MMV)侵染玉米后发现155个上调和5个下调circRNA^[68];在番茄叶片中,感染黄化曲叶病毒(Yellow leaf curl virus, YLCV)后有32个circRNA特异表达,同时其表达量较对照有所下降^[69]。Yin等^[70]通过对接种禾谷镰孢菌的小麦穗部样品进行测序,共发现2091个差异性表达的circRNA。在水稻中,通过比较circRNA测序结果和转基因方法证明circRNAs参与了水稻-稻瘟病菌的相互作用,并通过试验进一步证实circR5g05160能提高水稻对稻瘟病菌(*Magnaporthe oryzae*)的免疫^[71]。在水稻上过表达*ciR133*可以抑制*OsARAB*的表达,从而抑制黄单胞菌的侵染^[72]。在桃中,circRNA可通过与miRNA、有丝分裂原激活蛋白激酶(mitogen-activated protein kinase, MAPK)靶基因形成互作调控网络,介导桃的MAPK通路,并在桃响应桃蚜胁迫过程中发挥关键作用^[73]。综上,相关研究已证实circRNA在植物抵抗生物胁迫过程中发挥重要作用,但具体的分子作用机制尚不完全清楚,需进一步试验验证。

4.5 调控蛋白翻译

目前,已有研究表明,部分circRNA具有翻译能力^[74-75]。真核生物中,经典的mRNA翻译依赖于40S核糖体亚基和5'端帽子结合发生翻译过程^[76]。由于circRNA分子是一种环状闭合结构,无法与核糖体亚基结合^[77],因此circRNA可能依赖其他蛋白翻译途径。已有研究表明,circRNA翻译的启动主要有两种途径,第一种途径是通过内部核糖体结合位点(Internal ribosome entry site, IRES)序列插入到起始密码子AUG



(a) circRNA在番茄果实的着色和成熟、水稻叶绿素含量积累、大豆结瘤和侧根发育以及拟南芥叶片发育与开花中的作用; (b) circRNA在低温、高温、盐以及干旱胁迫下的作用; (c) circRNA在晚疫病、稻瘟病及黄单胞菌侵染下的作用

(a) The role of circRNA in the coloring and ripening of tomato fruits, the accumulation of chlorophyll content in rice, the nodule formation and lateral root development in soybean, and the leaf development and flowering in *Arabidopsis*; (b) The function of circRNA under cold, heat, salt, and drought stress; (c) The influence of circRNA during infection by *Phytophthora infestans*, *Magnaporthe oryzae*, and *Xanthomonas albilineans*

图中数据结果来源于文献[40]、[46]、[47]、[48]、[49]、[56]、[57]、[58]、[60]、[61]、[71]、[72]。

The data shown in this figure are from the study by [40], [46], [47], [48], [49], [56], [57], [58], [60], [61], [71], [72].

图2 植物 circRNA 已知生物学功能

Fig. 2 The known biological functions of plant circRNA

的上游,促进起始因子或核糖体与可翻译的 circRNA 结合,从而启动翻译^[78-79];通过体内及体外翻译试验证实,IRES序列的存在能够有效驱动 circRNA 翻译^[80-81]。第二种途径是可以通过 N⁶-甲基腺苷(m⁶A)途径翻译

蛋白^[82];Zhou等^[83]发现 eIF4G2可参与 m⁶A 修饰所调控的 circRNA 翻译过程,m⁶A 修饰对 circRNA 的翻译具有直接影响。m⁶A 是真核生物体内 RNA 腺嘌呤碱基的一种重要甲基化修饰方式,参与 RNA 剪接、翻

译等多个过程,在体内主要通过含有YTH结构域的蛋白家族成员来识别并调节RNA二级结构的稳定性以及调控RNA与蛋白的互作^[84]。目前,对拟南芥中m⁶A修饰的研究发现,其修饰位点通常位于mRNA的起始和终止密码子附近^[85-86]。但是关于其他植物m⁶A修饰的相关研究报道还比较缺乏。尽管目前尚未有关于植物环状RNA(circRNA)翻译成蛋白质的相关报道,但已有一些研究对植物中circRNA编码蛋白的潜力进行了预测和分析。Sun等^[87]利用CircCode研究了NCBI中的核糖体图谱数据库发现,在拟南芥中有1 569个具有翻译能力的circRNA;在玉米中预测到229个具有高编码潜力circRNA^[88]。分析线粒体多聚体和线粒体酶谱数据,在玉米和拟南芥中共识别出1 463个与核糖体结合的mcircRNAs;进一步结合基于质谱的蛋白质组学数据进行验证,鉴定出了358个源自mcircRNA的多肽^[89]。

4.6 参与蛋白互作

与蛋白质互作是circRNA的重要生物学功能之一^[48,90-92]。circRNA可以通过识别、捕获和携带不同的蛋白质,并将它们运送到特定的亚细胞位置,以调控靶向mRNA或核糖体生成的方式发挥其功能^[90],也可以与特定的蛋白结合形成circRNA-蛋白复合物,通过改变蛋白质的空间构象来实现调控功能。例如,*ciR-7/CDR1as*可以与AGO2蛋白相互作用,竞争性地结合*miR-7*,从而调节*miR-7*对靶标的调控^[30]。此外,circRNA还可以通过与蛋白质相互作用,参与泛素化、细胞周期、细胞衰老等生命过程^[48]。该类型相互作用不仅影响circRNA的合成和降解,还可调节蛋白质的功能和表达^[91]。Zhou等^[92]研究表明,circRNA的生物合成过程受到多种因素的混合调控,包括转录因子、RNA结合蛋白、剪接因子和顺式调节元件等。由于circRNA与线性RNA在结构上存在明显差异,因此研究circRNA-蛋白质互作的试验方法与线性RNA有所不同。目前主要采用RNA-down、RNase酶保护试验、RNA结合蛋白免疫沉淀、荧光原位杂交法和电泳迁移分析法等研究技术检测circRNA-蛋白质的相互作用,其中荧光原位杂交和RNase两种技术可以精确验证互作circRNA的序列。

5 结 语

circRNA在植物中普遍存在,并具有独特的结

构特征和调控机制。尽管其具体功能和作用机制在植物中仍处于探索阶段,但现有研究表明,circRNA在植物的多个生物学过程中发挥重要作用。植物circRNA在不同时期、组织及胁迫条件下呈现出特异性的表达模式,在生长发育、非生物及生物逆境胁迫调控中发挥关键作用。然而,关于circRNA在这些过程中的具体功能及其与其他非编码RNA(如miRNAs、lncRNAs)的相互作用机制仍需深入研究。此外,与线性RNA相比,circRNA的沉默、过表达和敲除载体构建策略尚不完善,限制了对其功能的深入研究。尽管在人类和动物中已证实circRNA具有翻译能力,但在植物中这一功能尚需试验验证。因此,未来植物circRNA的研究应集中在功能解析、载体构建策略优化及翻译功能验证等方面。

参考文献 References

- [1] Mattick J S, Makunin I V. Non-coding RNA [J]. *Human Molecular Genetics*, 2006, 15 (1): 17-29
- [2] Contreras-Cubas C, Palomar M, Arteaga-Vázquez M, Reyes J L, Covarrubias A A. Non-coding RNAs in the plant response to abiotic stress [J]. *Planta*, 2012, 236 (4): 943-958
- [3] Matsui A, Nguyen A H, Nakaminami K, Seki M. *Arabidopsis* non-coding RNA regulation in abiotic stress responses [J/OL]. *International Journal of Molecular Sciences*, (2013-11-18). DOI: doi. org/10. 3390/ijms141122642
- [4] 王雪松. 大豆干旱响应环状RNA鉴定及非生物胁迫调控途径分析[D]. 哈尔滨: 东北农业大学, 2020
Wang X S. Identification of drought-responsive circRNAs and analysis of regulating pathway under abiotic stress in soybean [D]. Harbin: Northeast Agricultural University, 2020 (in Chinese)
- [5] Sanger H L, Klotz G, Riesner D, Gross H J, Kleinschmidt A K. Viroids are single-stranded covalently closed circular RNA molecules existing as highly base-paired rod-like structures [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 1976, 73 (11): 3852-3856
- [6] Kristensen L S, Andersen M S, Stagsted L V W, Ebbesen K K, Hansen T B, Kjems J. The biogenesis, biology and characterization of circular RNAs [J]. *Nature Reviews Genetics*, 2019, 20 (11): 675-691
- [7] Wang P L, Bao Y, Yee M-C, Barrett S P, Hogan G J, Olsen M N, Dinneny J R, Brown P O, Salzman J. Circular RNA is expressed across the eukaryotic tree of life [J/OL]. *PLoS One*, (2014-03-07). DOI: doi. org/10. 1371/journal. pone. 0090859
- [8] Jeck W R, Sorrentino J A, Wang K, Slevin M K, Burd C E, Liu J Z, Marzluff W F, Sharpless N E. Circular RNAs are abundant, conserved, and associated with ALU repeats [J]. *RNA*, 2013, 19 (2): 141-157

- [9] Liu J J, Ren Y, Xu Y Y, Yin Y G, Han B, Zhang Z, Li J P, Song Y, Zhang L P, Fan D Y, Liu M Y, Wang L J, Teng Y X, Liu H F, Ma C. Investigation of grapevine circular RNA *Vv-circPAS1* revealed the function on root development and salt stress resistance[J/OL]. *Scientia Horticulturae*, (2024-07-23). DOI: doi.org/10.1016/j.scienta.2024.113489
- [10] Zhang Y, Zhang X O, Chen T, Xiang J F, Yin Q F, Xing Y H, Zhu S S, Yang L, Chen L L. Circular intronic long noncoding RNAs [J]. *Molecular Cell*, 2013, 51 (6): 792-806
- [11] Li Z Y, Huang C, Bao C, Chen L, Lin M, Wang X L, Zhong G L, Yu B, Hu W C, Dai L M, Zhu P F, Chang Z X, Wu Q F, Zhao Y, Jia Y, Xu P, Liu H J, Shan G. Exon-intron circular RNAs regulate transcription in the nucleus[J]. *Nature Structural & Molecular Biology*, 2015, 22 (3): 256-264
- [12] Patop I L, Wüst S, Kadener S. Past, present, and future of circRNAs[J/OL]. *EMBO Journal*, (2019-07-25). DOI: doi.org/10.15252/embj.2018100836
- [13] Ashwal-Fluss R, Meyer M, Pamudurti N R, Ivanov A, Bartok O, Hanan M, Evtan N, Memczak S, Rajewsky N, Kadener S. circRNA biogenesis competes with pre-mRNA splicing[J]. *Molecular Cell*, 2014, 56 (1): 55-66
- [14] Wang Y, Wang Z F. Efficient backsplicing produces translatable circular mRNAs[J]. *RNA*, 2015, 21 (2): 172-179
- [15] Liang D M, Wilusz J E. Short intronic repeat sequences facilitate circular RNA production[J]. *Genes & Development*, 2014, 28 (20): 2233-2247
- [16] Conn S J, Pillman K A, Toubia J, Conn V M, Salamanidis M, Phillips C A, Roslan S, Schreiber A W, Gregory P A, Goodall G J. The RNA binding protein quaking regulates formation of circRNAs[J]. *Cell*, 2015, 160 (6): 1125-1134
- [17] Will C L, Lührmann R. Spliceosome structure and function [J/OL]. *Cold Spring Harbor Perspectives In Biology*, (2010-12-30). DOI: doi.org/10.1101/cshperspect.a003707
- [18] Chen L L, Yang L. Regulation of circRNA biogenesis[J]. *RNA Biology*, 2015, 12 (4): 381-388
- [19] Zhang X O, Dong R, Zhang Y, Zhang J L, Luo Z, Zhang J, Chen L L, Yang L. Diverse alternative back-splicing and alternative splicing landscape of circular RNAs[J]. *Genome Research*, 2016, 26 (9): 1277-1287
- [20] Westholm J O, Miura P, Olson S, Shenker S, Joseph B, Sanfilippo P, Celniker S E, Graveley B R, Lai E C. Genome-wide analysis of *Drosophila* circular RNAs reveals their structural and sequence properties and age-dependent neural accumulation[J/OL]. *Cell Reports*, (2014-12-11). DOI: doi.org/10.1016/j.celrep.2014.10.062
- [21] Gao Y, Wang J F, Zhao F Q. CIRI: An efficient and unbiased algorithm for *de novo* circular RNA identification[J/OL]. *Genome Biology*, (2015-01-13). DOI: doi.org/10.1186/s13059-014-0571-3
- [22] Salzman J, Chen R E, Olsen M N, Wang P L, Brown P O. Cell-type specific features of circular RNA expression [J/OL]. *PLoS Genetics*, (2010-12-30). DOI: doi.org/10.1371/journal.pgen.1003777
- [23] Chen L, Yu Y Y, Zhang X C, Liu C, Ye C Y, Fan L J. PcircRNA_finder: A software for circRNA prediction in plants[J]. *Bioinformatics*, 2016, 32 (22): 3528-3529
- [24] Zhang P J, Liu Y J, Chen H J, Meng X W, Xue J T, Chen K S, Chen M. CircPlant: An integrated tool for CircRNA detection and functional prediction in plants[J/OL]. *Genomics, Proteomics and Bioinformatics*, (2020-11-04). DOI: doi.org/10.1016/j.gpb.2020.10.001
- [25] Yin S W, Tian X, Zhang J J, Sun P S, Li G L. PCirc: Random forest-based plant circRNA identification software [J/OL]. *BMC Bioinformatics*, (2021-01-06). DOI: doi.org/10.1186/s12859-020-03944-1
- [26] Zheng Y, Ji P F, Chen S, Hou L L, Zhao F Q. Reconstruction of full-length circular RNAs enables isoform-level quantification [J/OL]. *Genome Medicine*, (2019-01-19). DOI: doi.org/10.1186/s13073-019-0614-1
- [27] Wang K, Singh D, Zeng Z, Coleman S J, Huang Y, Savich G L, He X P, Mieczkowski P, Grimm S A, Perou C M, MacLeod J N, Chiang D Y, Prins J F, Liu J Z. MapSplice: Accurate mapping of RNA-seq reads for splice junction discovery [J/OL]. *Nucleic Acids Research*, (2010-08-28). DOI: doi.org/10.1093/nar/gkq622
- [28] Li X, Wu Y F. Detecting circular RNA from high-throughput sequence data with de Bruijn graph[J/OL]. *BMC Genomics*, (2020-03-05). DOI: doi.org/10.1186/s12864-019-6154-7
- [29] Memczak S, Jens M, Elefantioti A, Torti F, Krueger J, Rybak A, Maier L, Mackowiak S D, Gregersen L H, Munschauer M, Loewer A, Ziebold U, Landthaler M, Kocks C, le Noble F, Rajewsky N. Circular RNAs are a large class of animal RNAs with regulatory potency[J]. *Nature*, 2013, 495 (7441): 333-338
- [30] Hansen T B, Jensen T I, Clausen B H, Bramsen J B, Finsen B, Damgaard C K, Kjems J. Natural RNA circles function as efficient microRNA sponges[J]. *Nature*, 2013, 495 (7441): 384-388
- [31] Chen L L. The biogenesis and emerging roles of circular RNAs [J]. *Nature Reviews Molecular Cell Biology*, 2016, 17 (4): 205-211
- [32] Ghosal S, Das S, Sen R, Basak P, Chakrabarti J. Circ2Traits: A comprehensive database for circular RNA potentially associated with disease and traits [J/OL]. *Frontiers in Genetics*, (2013-12-10). DOI: doi.org/10.3389/fgene.2013.00283
- [33] Ye C Y, Chen L, Liu C, Zhu Q H, Fan L J. Widespread noncoding circular RNAs in plants[J]. *New Phytologist*, 2015, 208 (1): 88-95
- [34] Zheng Q P, Bao C Y, Guo W J, Li S Y, Chen J, Chen B, Luo Y T, Lyu D B, Li Y, Shi G H, Liang L H, Gu J R, He X H, Huang S L. Circular RNA profiling reveals an abundant circHIPK3 that regulates cell growth by sponging multiple miRNAs[J/OL]. *Nature Communications*, (2016-04-06). DOI: doi.org/10.1038/ncomms11215
- [35] Kulcheski F R, Christoff A P, Margis R. Circular RNAs are miRNA sponges and can be used as a new class of biomarker [J]. *Journal of Biotechnology*, 2016, 238: 42-51
- [36] Chen L, Zhang P, Fan Y, Lu Q, Li Q, Yan J B, Muehlbauer G J, Schnable P S, Dai M Q, Li L. Circular RNAs mediated by transposons are associated with transcriptomic and phenotypic variation in maize[J]. *New Phytologist*, 2018, 217 (3): 1292-1306
- [37] Lu T T T, Cui L L, Zhou Y, Zhu C R, Fan D L, Gong H, Zhao Q,

- Zhou C C, Zhao Y, Lu D F, Luo J H, Wang Y C, Tian Q L, Feng Q, Huang T, Han B. Transcriptome-wide investigation of circular RNAs in rice[J]. *RNA*, 2015, 21 (12): 2076-2087
- [38] Sablok G, Zhao H W, Sun X Y. Plant circular RNAs (circRNAs): Transcriptional regulation beyond miRNAs in plants [J]. *Molecular Plant*, 2016, 9 (2): 192-194
- [39] Zeng R F, Zhou J J, Hu C G, Zhang J Z. Transcriptome-wide identification and functional prediction of novel and flowering-related circular RNAs from trifoliate orange (*Poncirus trifoliata* L Raf) [J]. *Planta*, 2018, 247 (5): 1191-1202
- [40] Hong Y H, Meng J, Zhang M, Luan Y S. Identification of tomato circular RNAs responsive to *Phytophthora infestans* [J/OL]. *Gene*, (2020-07-01). DOI: doi.org/10.1016/j.gene.2020.144652
- [41] Wang Y X, Wang Q, Gao L P, Zhu B Z, Luo Y B, Deng Z P, Zuo J H. Integrative analysis of circRNAs acting as ceRNAs involved in ethylene pathway in tomato[J]. *Physiologia Plantarum*, 2017, 161 (3): 311-321
- [42] 尹军良, 马东方, 刘乐承, 夏雨晨, 朱永兴. 环状RNA的生物特征及其在植物中的研究进展[J]. 西北植物学报, 2017, 37 (12): 2510-2518
- Yin J L, Ma D F, Liu L C, Xia Y C, Zhu Y X. Biology features of circular RNAs and their research progress in plants[J]. *Acta Botanica Boreali-Occidentalia Sinica*, 2017, 37 (12): 2510-2518 (in Chinese)
- [43] Meng X W, Li X, Zhang P J, Wang J J, Zhou Y C, Chen M. Circular RNA: An emerging key player in RNA world [J]. *Briefings in Bioinformatics*, 2017, 18 (4): 547-557
- [44] Yin J L, Liu M Y, Ma D F, Wu J W, Li S L, Zhu Y X, Han B. Identification of circular RNAs and their targets during tomato fruit ripening[J]. *Postharvest Biology and Technology*, 2018, 136 90-98
- [45] 殷子贺, 杨成成, 赵钰慧, 赵丽, 吕秀荣, 杨振超, 武永军. 开花期番茄 circRNA 的测序分析及功能分析[J]. 中国农业科学, 2023, 56 (21): 4288-4303
- Yin Z H, Yang C C, Zhao Y H, Zhao L, Lv X R, Yang Z C, Wu Y J. Sequencing and functional analysis of tomato circRNA during flowering stage [J]. *Scientia Agricultura Sinica*, 2023, 56 (21): 4288-4303 (in Chinese)
- [46] Tan J J, Zhou Z J, Niu Y J, Sun X Y, Deng Z P. Identification and functional characterization of tomato circRNAs derived from genes involved in fruit pigment accumulation[J/OL]. *Scientific Reports*, (2017-08-17). DOI: doi.org/10.1038/s41598-017-08806-0
- [47] Zhao W, Cheng Y H, Zhang C, You Q B, Shen X J, Guo W, Jiao Y Q. Genome-wide identification and characterization of circular RNAs by high throughput sequencing in soybean[J/OL]. *Scientific Reports*, (2017-07-17). DOI: doi.org/10.1038/s41598-017-05922-9
- [48] Cheng J P, Zhang Y, Li Z W, Wang T Y, Zhang X T, Zheng B L. A lariat-derived circular RNA is required for plant development in *Arabidopsis*[J]. *Science China Life Sciences*, 2018, 61 (2): 204-213
- [49] Zhou J P, Yuan M Z, Zhao Y X, Quan Q, Yu D, Yang H, Tang X, Xin X H, Cai G Z, Qian Q, Qi Y P, Zhang Y. Efficient deletion of multiple circle RNA loci by CRISPR-Cas9 reveals *Os06circ02797* as a putative sponge for *OsMIR408* in rice[J]. *Plant Biotechnology Journal*, 2021, 19 (6): 1240-1252
- [50] Zuo J H, Wang Y X, Zhu B Z, Luo Y B, Wang Q, Gao L P. Analysis of the coding and non-coding RNA transcriptomes in response to bell pepper chilling[J/OL]. *International Journal of Molecular Sciences*, (2018-07-09). DOI: doi.org/10.3390/ijms19072001
- [51] Wang J X, Lin J, Wang H, Li X G, Yang Q S, Li H, Chang Y H. Identification and characterization of circRNAs in *Pyrus betulifolia* Bunge under drought stress[J/OL]. *PLoS One*, (2018-07-17). DOI: doi.org/10.1371/journal.pone.0200692
- [52] Wang Y X, Yang M, Wei S M, Qin F J, Zhao H J, Suo B. Identification of circular RNAs and their targets in leaves of *Triticum aestivum* L. under dehydration stress[J/OL]. *Frontiers in Plant Science*, (2017-01-05). DOI: doi.org/10.3389/fpls.2016.02024
- [53] Yin J L, Liu Y K, Lu L, Zhang J, Chen S Y, Wang B T. Comparison of tolerant and susceptible cultivars revealed the roles of circular RNAs in rice responding to salt stress [J]. *Plant Growth Regulation*, 2022, 96 (2): 243-254
- [54] Zuo J H, Wang Q, Zhu B Z, Luo Y B, Gao L P. Deciphering the roles of circRNAs on chilling injury in tomato [J]. *Biochemical and Biophysical Research Communications*, 2016, 479 (2): 132-138
- [55] Gao Z, Li J, Luo M, Li H, Chen Q J, Wang L, Song S R, Zhao L P, Xu W P, Zhang C X, Wang S P, Ma C. Characterization and cloning of grape circular RNAs identified the cold resistance-related *Vv-circATS1* [J]. *Plant Physiology*, 2019, 180 (2): 966-985
- [56] Yang Y T, Zhang X, Su Y C, Zou J K, Wang Z T, Xu L P, Que Y X. MiRNA alteration is an important mechanism in sugarcane response to low-temperature environment[J]. *BMC Genomics*, 2017, 18: 1-18
- [57] Gao Z, Sun B Z, Fan Z B, Su Y F, Zheng C C, Chen W P, Yao Y X, Ma C, Du Y P. *Vv-circSIZ1* mediated by pre-mRNA processing machinery contributes to salt tolerance[J]. *New Phytologist*, 2023, 240 (2): 644-662
- [58] Huang J, Wang Y L, Yu J, Li F D, Yi L H, Li Y Z, Xie N, Wu Q, Samarina L, Tong W, Xia E H. Evolutionary landscape of tea circular RNAs and its contribution to chilling tolerance of tea plant [J/OL]. *International Journal of Molecular Sciences*, (2023-01-12). DOI: doi.org/10.3390/ijms24021478
- [59] Pan T, Sun X Q, Liu Y X, Li H, Deng G B, Lin H H, Wang S H. Heat stress alters genome-wide profiles of circular RNAs in *Arabidopsis* [J]. *Plant Molecular Biology*, 2018, 96 (3): 217-229
- [60] Song Y P, Bu C H, Chen P F, Liu P, Zhang D Q. Miniature inverted repeat transposable elements *cis*-regulate circular RNA expression and promote ethylene biosynthesis, reducing heat tolerance in *Populus tomentosa* [J]. *Journal of Experimental Botany*, 2021, 72 (5): 1978-1994
- [61] Sun M Y, Jing Y, Wang X S, Zhang Y Z, Zhang Y H, Ai J, Li J, Jin L G, Li W B, Li Y G. *Gma-miR1508a* confers dwarfing, cold tolerance, and drought sensitivity in soybean [J/OL]. *Molecular Breeding*, (2020-04-16). DOI: doi.org/10.1007/s11032-020-01116-w
- [62] Wang X S, Chang X C, Jing Y, Zhao J L, Fang Q W, Sun M Y, Zhang Y Z, Li W B, Li Y G. Identification and functional prediction of soybean circRNAs involved in low-temperature responses [J/OL]. *Journal of Plant Physiology*, (2020-03-11). DOI: doi.org/10.1016/j.

- jplph. 2020. 153188
- [63] Zhu Y X, Jia J H, Yang L, Xia Y C, Zhang H L, Jia J B, Zhou R, Nie P Y, Yin J L, Ma D F, Liu L C. Identification of cucumber circular RNAs responsive to salt stress [J/OL]. *BMC Plant Biology*, (2019-04-27). DOI: doi.org/10.1186/s12870-019-1712-3
- [64] Li Y Q, Xia W, Li Y, Li X P. Expression and drought functional analysis of one circRNA *PecircCDPK* from moso bamboo (*Phyllostachys edulis*) [J/OL], *PeerJ*, (2024-09-30). DOI: doi.org/10.7717/peerj.18024
- [65] Wang Z P, Liu Y F, Li D W, Li L, Zhang Q, Wang S B, Huang H W. Identification of circular RNAs in kiwifruit and their species-specific response to bacterial canker pathogen invasion [J/OL]. *Frontiers in Plant Science*, (2017-03-27). DOI: doi.org/10.3389/fpls.2017.00413
- [66] Zhou R, Zhu Y X, Zhao J, Fang Z W, Wang S P, Yin J L, Chu Z H, Ma D F. Transcriptome-wide identification and characterization of potato circular RNAs in response to *Pectobacterium carotovorum* subspecies brasiliense infection [J/OL]. *International Journal of Molecular Sciences*, (2017-12-27). DOI: doi.org/10.3390/ijms19010071
- [67] Xiang L X, Cai C W, Cheng J R, Wang L, Wu C F, Shi Y Z, Luo J Z, He L, Deng Y S, Zhang X, Yuan Y L, Cai Y F. Identification of circularRNAs and their targets in *Gossypium* under *Verticillium* wilt stress based on RNA-seq [J/OL]. *PeerJ*, (2018-03-16). DOI: doi.org/10.7717/peerj.4500
- [68] Ghorbani A, Izadpanah K, Peters J R, Dietzgen R G, Mitter N. Detection and profiling of circular RNAs in uninfected and maize Iranian mosaic virus-infected maize [J]. *Plant Science*, 2018, 274: 402-409
- [69] Wang J Y, Yang Y W, Jin L M, Ling X T, Liu T L, Chen T Z, Ji Y H, Yu W G, Zhang B L. Re-analysis of long non-coding RNAs and prediction of circRNAs reveal their novel roles in susceptible tomato following TYLCV infection [J]. *BMC Plant Biology*, 2018, 18: 1-16
- [70] Yin J L, Han X W, Zhu Y X, Fang Z W, Gao D R, Ma D F. Transcriptome profiles of circular RNAs in common wheat during *Fusarium* head blight disease [J/OL]. *Data*, (2022-08-29). DOI: doi.org/10.3390/data7090121
- [71] Fan J, Quan W L, Li G B, Hu X H, Wang Q, Wang H, Li X P, Luo X T, Feng Q, Hu Z J, Feng H, Pu M, Zhao J Q, Huang Y Y, Li Y, Zhang Y, Wang W M. CircRNAs are involved in the rice-*Magnaporthe oryzae* interaction [J]. *Plant Physiology*, 2020, 182 (1): 272-286
- [72] Xia K F, Pan X Q, Zeng X, Zhang M Y. *Xoo*-responsive transcriptome reveals the role of the circular RNA133 in disease resistance by regulating expression of *OsARAB* in rice [J]. *Phytopathology Research*, 2023, 5 (1): 33
- [73] Wang X Y, Li L, Fan R Y, Yan Y J, Zhou R J. Genome-wide identification of circular RNAs and MAPKs reveals the regulatory networks in response to green peach aphid infestation in peach (*Prunus persica*) [J/OL]. *Gene*, (2024-10-11). DOI: doi.org/10.1016/j.gene.2024.148994
- [74] Legnini I, Di Timoteo G, Rossi F, Morlando M, Briganti F, Sthandier O, Fatica A, Santini T, Andronache A, Wade M, Laneve P, Rajewsky N, Bozzoni I. Circ-ZNF609 is a circular RNA that can be translated and functions in myogenesis [J]. *Molecular Cell*, 2017, 66 (1): 22-37
- [75] Pamudurti N R, Bartok O, Jens M, Ashwal-Fluss R, Stottmeister C, Ruhe L, Hanan M, Wyler E, Perez-Hernandez D, Perez-Hernandez D, Ramberger E, Shenzis S, Samson M, Dittmar G, Landthaler M, Chekulaeva M, Rajewsky N, Kadener S. Translation of circRNAs [J]. *Cell Reports*, 2017, 66 (1): 9-21
- [76] Sonenberg N, Hinnebusch A G. Regulation of translation initiation in eukaryotes: Mechanisms and biological targets [J]. *Cell*, 2009, 136 (4): 731-745
- [77] Wang Y, Ding B. Viroids: Small probes for exploring the vast universe of RNA trafficking in plants [J/OL]. *Journal of Integrative Plant Biology*, (2010-01-11). DOI: doi.org/10.1111/j.1744-7909.2010.00900.x
- [78] Chen C Y, Sarnow P. Initiation of protein synthesis by the eukaryotic translational apparatus on circular RNAs [J]. *Science*, 1995, 268 (5209): 415-417
- [79] Shi Y, Jia X, Xu J. The new function of circRNA: Translation [J]. *Clinical and Translational Oncology*, 2020, 22 (12): 2162-2169
- [80] Perriman R, Ares M. Circular mRNA can direct translation of extremely long repeating-sequence proteins in vivo [J]. *RNA*, 1998, 4 (9): 1047-1054
- [81] AbouHaidar M G, Venkataraman S, Golshani A, Liu B L, Ahmad T. Novel coding, translation, and gene expression of a replicating covalently closed circular RNA of 220 nt [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2014, 111 (40): 14542-14547
- [82] Yang Y, Fan X J, Mao M W, Song X W, Wu P, Zhang Y, Jin Y F, Yang Y, Chen L L, Wang Y, Wong C C, Xiao X S, Wang Z F. Extensive translation of circular RNAs driven by N⁶-methyladenosine [J]. *Cell Research*, 2017, 27 (5): 626-641
- [83] Zhou C, Molinie B, Daneshvar K, Pondick J V, Wang J K, Van Wittenbergh N, Xing Y, Giallourakis C C, Mullen A C. Genome-wide maps of m⁶A circRNAs identify widespread and cell-type-specific methylation patterns that are distinct from mRNAs [J]. *Cell Reports*, 2017, 20 (9): 2262-2276
- [84] Meyer K D, Jaffrey S R. The dynamic epitranscriptome: N⁶-methyladenosine and gene expression control [J]. *Nature Reviews Molecular Cell Biology*, 2014, 15 (5): 313-326
- [85] Luo G Z, MacQueen A, Zheng G Q, Duan H C, Dore L C, Lu Z K, Liu J, Chen K, Jia G F, Bergelson J, He C. Unique features of the m⁶A methylome in *Arabidopsis thaliana* [J/OL]. *Nature Communications*, (2014-11-28). DOI: doi.org/10.1038/ncomms6630
- [86] Wan Y Z, Tang K, Zhang D Y, Xie S J, Zhu X H, Wang Z G, Lang Z B. Transcriptome-wide high-throughput deep m⁶A-seq reveals unique differential m⁶A methylation patterns between three organs in *Arabidopsis thaliana* [J]. *Genome Biology*, 2015, 16 (1): 1-26
- [87] Sun P S, Li G L. CircCode: A powerful tool for identifying circRNA coding ability [J/OL]. *Frontiers in Genetics*, (2019-10-10). DOI: 10.3389/fgene.2019.00981
- [88] Han Y, Li X X, Yan Y, Duan M H, Xu J H. Identification, characterization, and functional prediction of circular RNAs in maize [J]. *Molecular Genetics and Genomics*, 2020, 295 (2): 491-503
- [89] Liao X, Li X J, Zheng G T, Chang F R, Fang L, Yu H, Huang J, Zhang

- Y F. Mitochondrion-encoded circular RNAs are widespread and translatable in plants[J]. *Plant Physiology*, 2022, 189 (3): 1482-1500
- [90] Hentze M W, Preiss T. Circular RNAs: Splicing's enigma variations[J]. *EMBO Journal*, 2013 32(7): 923-925
- [91] Du W W, Fang L, Yang W N, Wu N, Awan F M, Yang Z G, Yang B B. Induction of tumor apoptosis through a circular RNA enhancing Foxo3 activity[J]. *Cell Death and Differentiation*, 2017, 24 (2): 357-370
- [92] Zhou W Y, Cai Z R, Liu J, Wang D S, Ju H Q, Xu R H. Circular RNA: Metabolism, functions and interactions with proteins[J/OL]. *Molecular Cancer*, (2020-12-14). DOI: doi.org/10.1186/s12943-020-01286-3

责任编辑:吕晓梅



第一作者简介:李义婷,长江大学农学院作物保护学专业博士研究生。以第一作者身份发表SCI论文3篇,共同一作发表SCI论文2篇,以通讯作者发表SCI论文1篇,以其他身份参与发表论文15篇,授权专利1项。获2021—2023年“湖北省优秀科技论文”。参与国家自然科学基金面上项目(32272500)、湿地生态与农业利用教育部工程研究中心开放基金项目(KFT202305)。获2023—2024年度长江大学“学业一等奖学金”。



通讯作者简介:尹军良,博士,长江大学农学院教授,博士生导师,长江大学“学科菁英人才”。主要从事农作物抗逆基因资源挖掘及其作用机制解析研究。主持国家及省部级各类科研项目17项,授权专利4项,出版专著1部。发表论文150余篇,其中SCI收录111篇,ESI前1%高被引4篇,累计他引2500次,H指数28。获省部级科技奖励6项。指导大学生获各类科技创新奖励13项。