

· 专题论坛 ·

细胞核质转运及其受体在植物抗病防御反应中的调控作用

石添添¹, 高英^{1*}, 王欢^{2,3}, 刘君^{1*}

¹中国农业科学院作物科学研究所, 农作物基因资源与基因改良国家重大科学工程, 北京 100081

²中国农业科学院生物技术研究所, 北京 100081; ³国家成都农业科技中心, 成都 610213

摘要 植物病害严重威胁全球粮食生产, 研究植物对病原菌防御机制和病原菌对寄主作物的侵染过程和分子机制, 有助于改良植物种源使其获得持久抗性。近年来, 日渐增多的研究表明, 一些抗病蛋白需要转移到细胞核内才能启动免疫反应, 进而发挥抗病防御作用, 而细胞核质转运受体是实现这些抗病蛋白核质转运必不可少的“载体”。因此, 细胞核质转运及转运受体在抗病防御中发挥重要作用。该文在介绍植物抗病防御反应机制的基础上, 综述了细胞核质转运及核质转运受体在植物抗病防御反应中的作用研究进展, 并对未来的研究方向进行了展望。

关键词 植物抗病防御反应, 细胞核质转运, 细胞核质转运受体

石添添, 高英, 王欢, 刘君 (2021). 细胞核质转运及其受体在植物抗病防御反应中的调控作用. 植物学报 56, 480–487.

植物病原体严重威胁全球粮食生产, 全球农作物因病害损失预计达20%–30%, 且在粮食短缺地区病害发生更为严重(Savary et al., 2019)。虽然农药的使用和抗病基因的选育有助于缓解病害威胁, 但是病原菌抗性和毒力的迅速进化, 加上宿主范围的扩大和宿主的跳跃, 极有可能导致严重的病害爆发(McDonald and Stukenbrock, 2016; Vannier et al., 2019)。植物因无法通过逃避避开不利环境或危害, 为了生存只能靠其先天免疫来主动防御这些不利因素(Jones and Dangl, 2006; Saijo and Loo, 2020; Wang et al., 2020)。因此, 了解植物对病原菌的防御机制以及病原菌对寄主作物的侵染过程和分子机制至关重要, 这有助于我们掌握设计植物持久抗性所必需的知识, 进而为改善和提高作物对不利环境的抵抗能力提供策略及应对方案(Malik et al., 2020)。目前, 越来越多的数据表明, 细胞核质转运对调控植物抗病防卫极其重要, 不少植物调控抗病的蛋白质, 在核糖体合成后转运至细胞核才能发挥作用(García and Parker, 2009; Deslandes and Rivas, 2011)。因而, 细胞核质转运是实现植物抗病过程中的一道重要关卡, 而核质转运

受体又是实现转运必不可少的载体。本文在简要概述植物抗病防御机制的基础上, 重点对细胞核质转运及转运受体在植物抗病防御反应中的作用研究进展进行综述。

1 植物抗病防御反应

植物和病原菌协同进化, 形成一种识别与被识别、免疫与被免疫的竞争对抗局面。目前, 植物进化出2层免疫系统, 并且这2层免疫系统相互协作来识别和抵御病原体(图1)。病原菌在植物侵染位点表面释放大量保守的病原体相关分子模式(pathogen-associated molecular patterns, PAMPs)或微生物相关分子模式(microbe-associated molecular patterns, MAMPs)。针对这些分子模式, 植物进化出与之对应的质膜定位的模式识别受体(the plasma membrane (PM)-localized pattern recognition receptors, PRRs)来感知这些PAMPs/MAMPs信号, 并与共受体结合来磷酸化激活胞质型类受体激酶(如BIK1 (botrytis-induced kinase 1)和BSK1 (BR-signaling kinase 1)), 进而引

收稿日期: 2021-02-08; 接受日期: 2021-05-28

基金项目: 国家重点研发计划(No.2018YFD1000702, No.2018YFD1000700)和国家自然科学基金(No.31470367)

* 通讯作者。E-mail: gaoying@caas.cn; liujun@caas.cn

发一系列下游免疫反应,如活性氧(reactive oxygen species, ROS)喷发、钙离子流产生、丝裂原激活蛋白激酶(mitogen-activated protein kinase, MAPK)激活和防御基因表达上调(咎新丽等, 2013; Wu and Zhou, 2013; Couto and Zipfel, 2016; Tang et al., 2017; Wang et al., 2020; Zhou and Zhang, 2020; 王伟和唐定中, 2021), 这类免疫反应称为模式触发免疫(pattern-triggered immunity, PTI), 是植物形成的第1层免疫防御系统。

PTI能有效阻止大多数病原微生物的入侵。为对抗植物PTI的防御作用,病原体又进化出效应蛋白并通过其分泌系统注入植物细胞内,从而去抑制PTI使植物产生感病反应。而为了应对效应因子对PTI反应的抑制,植物在不断进化过程中又形成了第2层免疫反应系统,通过识别效应因子的抗病蛋白(R蛋白)开启植物的免疫反应(Jones and Dangl, 2006; Cui et al., 2015; Li et al., 2015), 即效应子触发免疫(effector trigger immunity, ETI) (Cesari, 2018; Monteiro and Nishimura, 2018; Alhoraibi et al., 2019)。研究表明, PTI和ETI并不是独立平行的2条免疫通道,二者可强强联手促进植物的免疫反应, ETI可调动PTI免疫通路来放大PTI反应,而PTI的激活促进ETI免疫反应的加强(王伟和唐定中, 2021; Yuan et

al., 2021; Ngou et al., 2021)。

目前,针对不同物种和病原菌已鉴定克隆出大量的R蛋白。一些研究表明, R蛋白对病原体效应分子的识别会引发大量病原相关蛋白的细胞核转移,进而启动植物细胞的转录重编程,激活防御信号(Jacob et al., 2018; Lolle et al., 2020), 暗示细胞核质转运在植物抗病防御反应中发挥重要作用。

2 细胞核质转运调控抗病防御反应

许多功能蛋白是在细胞质核糖体中合成,运输到细胞核行使功能。核膜的存在形成了细胞质与细胞核之间的交流屏障,小分子物质可自由穿越核孔复合物,一些大分子物质(如蛋白质和RNA)则必须借助核质转运受体穿越核孔复合物,才能够实现细胞核质的转运(Merkle, 2001; Sloan et al., 2016)。

研究表明,细胞核质转运对调控植物抗病防卫反应至关重要,许多蛋白质和RNA等大分子物质通过在细胞核与细胞质之间的转运来调控抗病防御反应(Wiermer et al., 2007; Deslandes and Rivas, 2011; Teh and Hofius, 2014; Gu et al., 2016; Wang et al., 2016)。核质转运过程介导免疫受体的激活、防御信号的产生以及胞内的防御蛋白转运至病原菌侵染位

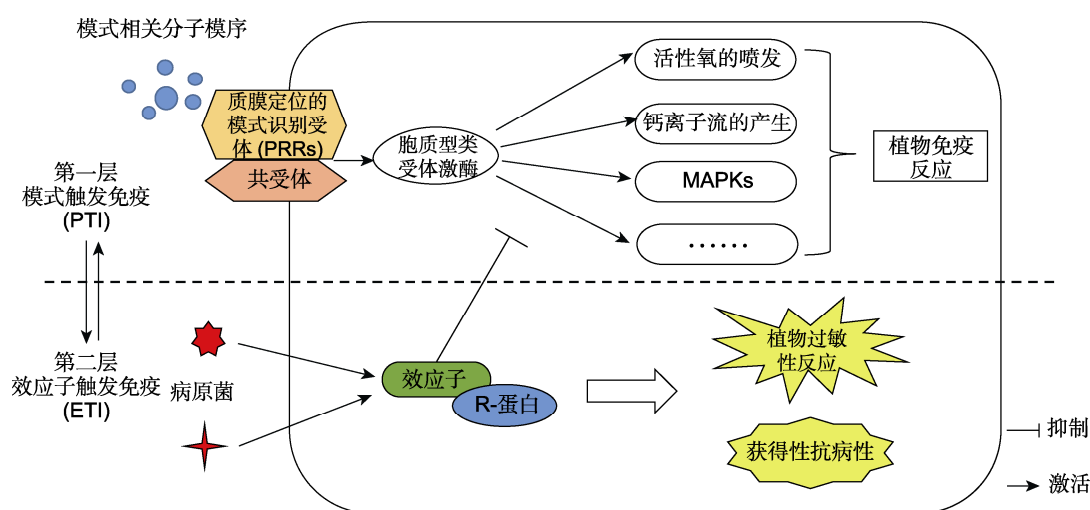


图1 植物免疫机制

PTI: 模式触发免疫; ETI: 效应子触发免疫; PRRs: 质膜定位的模式识别受体; MAPKs: 丝裂原激活蛋白激酶

Figure 1 Mechanism of plant immunity

PTI: Pattern-triggered immunity; ETI: Effector trigger immunity; PRRs: The plasma membrane (PM)-localized pattern recognition receptors; MAPKs: Mitogen-activated protein kinase

点,进而激发感染位点的细胞程序化死亡反应等生理过程(Zhang and Li, 2005; Liu and Gitta, 2008; Park and Ronald, 2012)。植物中,多种核质转运途径参与植物的先天免疫,包括mRNA的细胞核输出和免疫相关蛋白的细胞核输入。

2.1 mRNA的细胞核输出

真核生物中,mRNA从细胞核到细胞质的输出不仅是基因表达的关键过程,也对植物免疫具有重要贡献(Xie and Ren, 2019)。研究发现,一些阻碍mRNA细胞核输出的突变体会减弱植物对病原菌的抗性(Germain et al., 2010; Pan et al., 2012)。例如,拟南芥(*Arabidopsis thaliana*) *MOS3*基因编码保守的核孔蛋白,*MOS11*编码一种与RNA结合蛋白同源的核蛋白,研究发现*MOS3*和*MOS11*突变导致mRNA的输出明显受影响,经检测发现在*mos3*和*mos11*突变体中大多数含有poly(A)的mRNA信号都保留在细胞核内,证明mRNA在细胞核内积累,结果导致抗病突变体*snc1*对病原菌的抗性丧失(Zhang and Li, 2005; Germain et al., 2010; Dong et al., 2016)。Pan等(2012)筛选到1个拟南芥抗病突变体*edr2*的抑制子HPR1-4,*hpr1-4*突变体部分抑制*edr1*突变体介导的对白粉病病原菌和霉菌的抗性;同时发现*hpr1-4*突变体mRNA的细胞核输出明显受阻。这些研究表明,*MOS3*、*MOS11*和HPR1蛋白可能通过介导一些抗病因子的mRNA细胞核输出,进而调控植物的免疫,可见mRNA的细胞核输出在植物免疫中发挥重要作用。

2.2 免疫相关蛋白的细胞核输入

一些R蛋白移位到细胞核调节抗病防御基因的表达,如烟草(*Nicotiana tabacum*) N蛋白、大麦(*Hordeum vulgare*) MLA、拟南芥RPS4和马铃薯(*Solanum tuberosum*) RX抗病蛋白在细胞质中识别病原体效应蛋白,然后转移到细胞核中启动植物细胞的转录重编程,激活防御信号(Burch-Smith et al., 2007; Shen and Schulze-Lefert, 2007; Tameling and Baulcombe, 2007; Wirthmueller et al., 2007)。水稻(*Oryza sativa*) XA21受体对水稻黄单胞杆菌具有广谱抗性,其通过裂解以释放带核定位信号的胞内结构域,该结构域转运至细胞核与OsWRKY62互作进行转录调节,表明XA21受体在体内裂解并将胞内结构

域转运到细胞核是XA21调控免疫反应必需的生物学过程(Park and Ronald, 2012)。拟南芥RRS1-R蛋白对青枯病病原菌具有广谱抗性,而效应蛋白PopP2是被RRS1-R识别的无毒蛋白,效应蛋白PopP2携带核定位信号并被转运至细胞核与RRS1-R互作以提高植物对青枯病的抗性反应,表明效应蛋白PopP2的入核是RRS1-R发挥抗病反应所必需(Deslandes et al., 2003)。

Froidure等(2010)揭示AtsPLA2- α 和AtMYB30相互作用,而AtMYB30是拟南芥中超敏反应(hypersensitive response, HR)和抗病反应的正向调节因子,AtsPLA2- α 从细胞质到细胞核的特异性重新定位,导致AtMYB30的转录活性被抑制,抗病反应丧失,说明AtsPLA2- α 通过细胞核输入介导AtMYB30的抗病反应。Shi等(2010)研究发现,拟南芥NPR1基因编码一种转录共激活因子,在病原体感染后,为应对水杨酸(salicylic acid, SA)的积累,NPR1从细胞质转移至细胞核,并与其它转录因子相互作用,导致2 000多个植物防御基因的表达增强,促进了对病原体的抗性反应。Lee等(2015)证明独立于SA的系统信号诱导的基因SnRK2.8磷酸化NPR1是其细胞核输入所必需,即在SA信号诱导下,SnRK2.8介导的磷酸化与NPR1细胞核输入的协同作用是NPR1诱导获得性抗病性(SAR)的基础。上述研究结果暗示,细胞核质转运在植物先天免疫反应中发挥重要作用,是实现植物抗病过程中的一道重要关卡。

作为核质转运通道,核孔蛋白在调控植物抗病防御反应中同样具有重要作用。研究表明,拟南芥核孔蛋白Nup88、Nup96和Nup160等在植物防御反应中行使重要功能(Zhang and Li, 2005; Cheng et al., 2009; Roth and Wiermer, 2012)。Gu等(2016)报道了CPR5是一种新型的跨膜核孔蛋白,其作为同源复合物存在于核孔复合物(nuclear pore complexes, NPC),与核膜的选择性屏障紧密相关。当受到免疫受体激活时,CPR5会被特异性破坏且其协调的NPC构象发生转变,这种转变可使参与PCD信号转导的CKI(细胞周期蛋白依赖性激酶抑制剂)从NPC上释放,进而细胞周期调节剂诱导防御基因的表达;这种构象转变还可重新调整NPC的选择性屏障以允许各种应激相关信号的底物进入细胞核中发挥作用。因此,CPR5协调NPC介导的核质转运是ETI/PCD诱导中的重要机制。

3 细胞核质转运受体在抗病防御反应中的作用

3.1 植物细胞核质转运受体

一些核膜定位的受体蛋白能够识别并运输生物大分子,使其通过细胞核膜在细胞核与细胞质之间转运(Merkle, 2001, 2003; Palma et al., 2005)。许多蛋白质大分子需要在细胞核与细胞质之间来回穿梭才能发挥重要作用,携带核定位信号(nuclear localization signal, NLS)或核输出信号(nuclear export signal, NES)的底物蛋白可通过入核转运受体或出核转运受体实现核质转运(图2)(Yoshimura et al., 2014)。因此,核质转运受体根据其携带底物进出细胞核的方向不同被分别命名为importins和exportins, importins包括importin α 和importin β 。蛋白质的入核过程需要importin α 或importin α 与importin β 协同配合。其中,importin β 是首先从人类细胞中发现的细胞核输入受体,它与携带底物的importin α 形成复合物并将底物输入细胞核。之后鉴定的转运受体与importin β 具有同源性,被命名为类importin β (importin β -like)转运受体。Importin β 家族成员是一类真核生物中广泛分布的核质转运受体蛋白,这些家族成员功能上高度保守,能在细胞核与细胞质之间穿梭,能与RanGTP相

互作用,且识别特异的转运底物和接头蛋白。其共同结构特性是,有一系列非常相似的HEAT重复螺旋(HEAT repeats)。HEAT重复超螺旋结构的延展性与接头蛋白的多样性,使得一个受体可以结合广泛的底物类型(Merkle, 2001, 2003; 高英等, 2010)。这些转运受体介导的转运过程在生物有机体之间高度保守,动物和酵母中调控核质穿梭以及各个信号过程的组分及分子机制研究得较为清楚,植物中仍有待深入探索。

3.2 核质转运受体在抗病防御反应中的作用

许多功能性抗病蛋白需要在importin β 家族蛋白的协助下转运至细胞核来诱发一系列的防御反应(图2),因而importin β 家族蛋白在抗病防御中具有重要地位(Xu et al., 2011, 2013; Kimura and Imamoto, 2014)。例如,一个与importin- β 超家族成员TRN-SR蛋白高度相似的MOS14蛋白基因突变导致2个R基因SNC1和RPS4的剪接方式改变, SNC1和RPS4介导的抗病性受损,说明MOS14蛋白的细胞核输入对2个R基因SNC1和RPS4的正确剪接是必需的(Xu et al., 2011)。SAD2基因编码一个具有importin β 典型结构域的蛋白,其在拟南芥中由At2g31660基因编码。我们的研究发现, SAD2蛋白参与钙和过氧化氢介导的细胞程

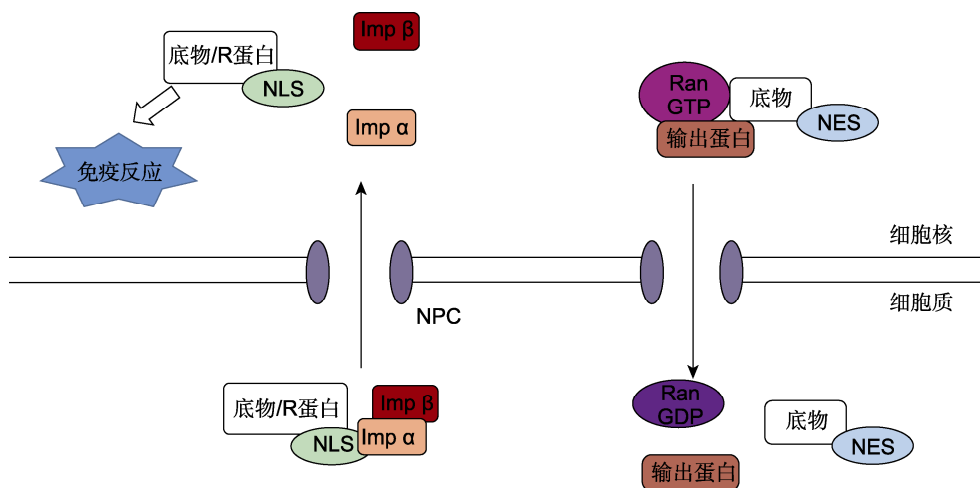


图2 核质转运及转运受体

NLS: 核定位信号; NPC: 核孔复合物; NES: 核输出信号

Figure 2 Nucleocytoplasmic transport and nucleocytoplasmic transport receptors

NLS: Nuclear localization signal; NPC: Nuclear pore complexes; NES: Nuclear export signal

序性死亡反应(Zheng et al., 2020)。进一步研究发现,其突变体和过表达株系分别对假单胞杆菌 *Pst* DC-3000 呈现出感病和抗病表型,推测其作用机制可能是通过调控特异转录因子在细胞核定位,进而影响植物的抗病性反应(数据未发表)。该结果证实了核质转运受体在植物抗病防御反应中的重要作用。

Importin α 是重要的核输入受体,其通过 importin β 上的 IBB 结构域(importin β binding domain)与 importin β 形成稳定的细胞核输入受体复合体协助底物运输(高英等, 2010; Yoshimura et al., 2014)。Palma等(2005)和Lüdke等(2021)研究发现,拟南芥抗病突变体 *snc1* 的抑制因子 *MOS6* 编码 importin $\alpha 3$, 其突变体 *mos6* 可回复 *snc1* 对毒性病原体的抗性反应和免疫,并且 *mos6-1* 单突变体表现出对毒性病原体易感,表明 *MOS6/importin $\alpha 3$* 参与调控植物对病原菌的防御。Roth等(2017)鉴定出 TN13 是核输入蛋白 *MOS6/importin $\alpha 3$* 参与防御反应的作用底物和互作蛋白, *tn13* 突变体对病原菌的抗性减弱,说明 TN13 和 *MOS6* 在抗病防御反应中协同作用。Lüdke等(2018)通过烟草瞬时表达和 Co-IP 验证了 TN13 与 *MOS6/importin $\alpha 3$* 互作,而不与 importin $\alpha 3$ 的同源物互作。亚细胞定位结果显示, TN13 定位于内质网(endoplasmic reticulum, ER)膜上。研究还发现, TN13 响应病原体刺激后从 ER 膜释放进行核转位,这对于植物防御信号转导非常重要。该研究揭示了拟南芥 importin 家族在植物抗病防御信号相关蛋白的细胞核输入中起作用。

4 小结与展望

病害对农业生产的影响极大,导致农作物产量损失严重。解析作物对病害的防御机制有助于改善和提高作物对不利环境的抵抗能力,这是农业生产亟待解决的问题,也是科学家高度关注和关心的问题。

尽管病原菌的防御机制研究已经取得很大进展,然而效应子触发核苷酸结合寡聚化结构域样受体(nucleotide-binding oligomerization domain like receptors, NLRs)以及 NLRs 激活下游事件的机制仍然模糊不清。防御调节因子与抗性(R)蛋白在细胞质和细胞核间的转运说明,细胞核输入输出在植物先天免疫中发挥重要作用。但事实上核质转运是植物中一个

新兴的领域,我们对其在信号传递中的调控作用研究才刚刚起步。随着核质转运受体蛋白的陆续鉴定和克隆,及对这些受体作用机制的深入解析,植物核质转运受体在防御反应中的作用将不断被揭示,这一方面可丰富我们对作物抗病防御反应的认识,另一方面可为未来抗病作物育种提供对策。核质转运受体靶标(如转录因子)基因对信号转导调控起着至关重要的作用,对转运底物的进一步鉴定和调控途径的揭示必将为作物的抗病防御对策提供助力。

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Nucleo-cytoplasmic Transport and Transport Receptors in Plant Disease Resistance Defense Response

Tiantian Shi¹, Ying Gao^{1*}, Huan Wang^{2,3}, Jun Liu^{1*}

¹National Key Facility for Crop Gene Resources and Genetic Improvement (NFCRI), Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS), Beijing 100081, China; ²Biotechnology Research Institute, Chinese Academy of Agricultural Sciences (CAAS), Beijing 100081, China; ³Chengdu National Agricultural Science and Technology Center, Chengdu 610213, China

Abstract Plant pathogens pose a constant and major threat to global food production, so understanding plant's defense mechanism against pathogen and pathogen's infection mechanism against host crops and their molecular mechanisms will be helpful to design protection strategies for durable resistance of plant. Until now, a growing number of studies have shown that some disease resistant proteins need to be transferred to the nucleus to initiate an immune response. Nucleocytoplasmic transport receptors are essential "carrier" for nuclear transport. Therefore, nucleocytoplasmic transport and receptors play important role in disease resistance. Based on the introduction of plant disease defense response mechanism, this paper focuses on research progress of nucleocytoplasmic transport and nucleocytoplasmic transport receptors in disease resistance and proposes a prospect.

Key words plant disease resistance defense response, nucleocytoplasmic transport, nucleocytoplasmic transport receptors

Shi TT, Gao Y, Wang H, Liu J (2021). Nucleo-cytoplasmic transport and transport receptors in plant disease resistance defense response. *Chin Bull Bot* **56**, 480–487.

* Authors for correspondence. E-mail: gaoying@caas.cn; liujun@caas.cn

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