植物核孔蛋白研究进展

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摘要 核孔复合物(nuclear pore complex, NPC)位于核膜, 是控制细胞核与细胞质之间进行蛋白质和mRNA等大分子物质转运的唯一通道。模式植物拟南芥的核孔复合物由30多种多拷贝的核孔蛋白(nucleoporins, NUPs)构成, 根据它们参与形成的亚基可分为外环、内环、连接、跨膜、中心FG(phenylalanine-glycine)和核篮核孔蛋白。核孔蛋白不仅介导核质转运, 而且在植物多个生命进程中发挥重要作用。该文综述了植物核孔蛋白参与核质转运、激素信号响应、生长发育、环境胁迫应答、免疫防御等的研究进展, 为植物核孔蛋白生物学功能的系统认知及深入探索提供参考。

关键词 核孔复合物; 核孔蛋白; 核质转运; 生物学功能

Advances in Plant Nucleoporins

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Abstract NPC (nuclear pore complex), embedding in the nuclear envelope, is the sole gateway channel that controls the trafficking of macromolecules such as proteins and mRNA between nucleus and cytoplasm. In *Arabidopsis thaliana*, the NPC consists of approximately 30 NUPs (nucleoporins) with multiple copies, which can be divided into outer ring, inner ring, linker, transmembrane, central FG (phenylalanine-glycine) and nuclear basket NUPs according to the sub-complex they formed. The NUPs not only modulate nucleocytoplasmic transport, but also play important roles in various biological processes. This review summarized the biological functions of plant NUPs involved in nucleocytoplasmic transport, hormone signaling, growth and development, responses to the environmental stress, plant immunity, which would lay the foundation for systematic cognition and further study on the biological functions of plant NUPs.

Keywords nuclear pore complex; nucleoporins; nucleocytoplasmic transport; biological function

核孔复合物(nuclear pore complex, NPC)即镶嵌在真核细胞核膜中的核孔, 是保障细胞核功能和细胞活动正常运行的关键亚细胞结构。二十一世纪初, 人们利用蛋白质组学手段检测了酵母和动物细胞中核孔复合物的构成, 发现核孔复合物大约由30多种多拷贝的核孔蛋白(nucleoporins, NUPs)、近200多个蛋白质共同组成[1-2]。一些核孔蛋白的序列在不同生物间存在较大差异, 赋予了核孔蛋白功能的有机

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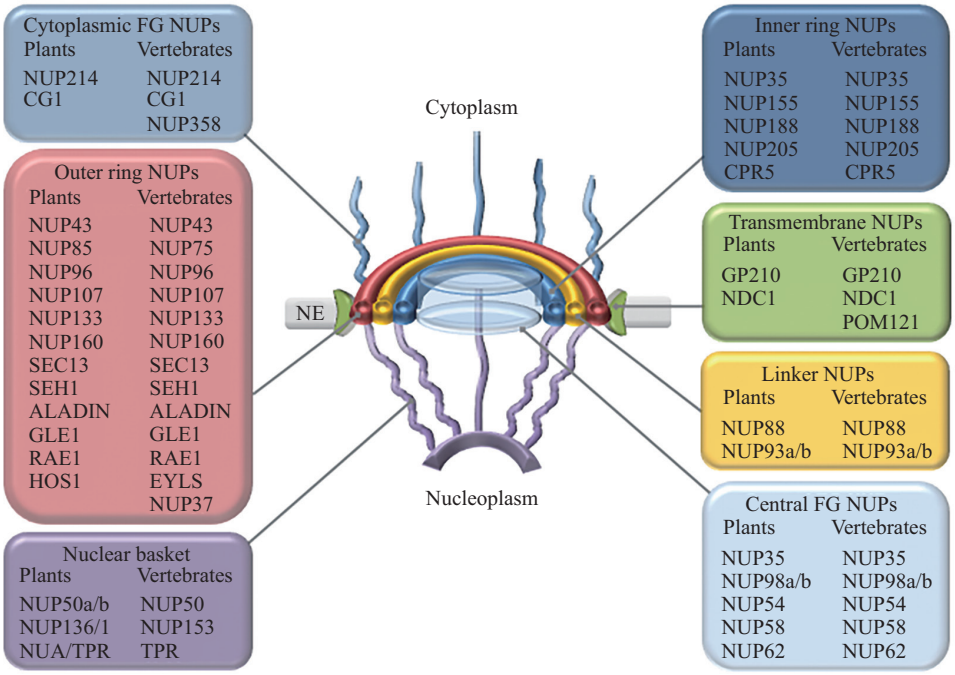
体特异性[3]。另外, 在人类和烟草细胞中均发现, 核孔复合物中的核孔蛋白组分在细胞不同分化期和植物不同发育阶段存在动态变化[4-5]。由此可见, 核孔复合物及核孔蛋白所具有的生物学功能远远超出了我们的原有认知。探究核孔蛋白的功能, 将有利于我们深入认识核孔复合物在真核生物中的作用及工作机制。

蛋白质和mRNA等大分子通过核孔蛋白和核转运蛋白的协助, 穿过核孔在细胞核和细胞质之间进行物质交流[6]。在不同真核生物包括植物中的遗传学研究显示, 核孔蛋白具有多重生物学功能, 目前仍有多个核孔蛋白的功能还不明确, 且存在未知成员有待鉴定。植物细胞组分复杂, 核孔又是细胞中分子量最大的蛋白质复合物, 因此分离纯化核孔和全面鉴定植物核孔复合物成员面临巨大挑战。近些年, 免疫沉淀联合质谱分析技术的成熟, 推动了模式植物拟南芥(*Arabidopsis thaliana*)中核孔蛋白成员的初步鉴定[7-8]。随着核孔蛋白成员逐步明晰及其生物学功能研究的不断深入, 人们了解到核孔蛋白不仅介导核质转运, 而且在植物多个生命进程中发挥重要作用。本文从植物核孔蛋白的分类及其在核质转运、激素信号响应、生长发育、环境胁迫应答、免疫防御等途径中的作用进行综述, 为系统认识和深入探索植物核孔蛋白生物学功能提供参考。

1 植物核孔蛋白的分类

二十世纪中期, 通过透射电子显微镜观察两栖类动物卵母细胞的核膜, 首次发现了核孔结构[9], 而后在豌豆(*Pisum sativum* L.)中观察到相似的结构[10], 从而开启了人们对植物核孔复合物的研究。核孔复合物的组建过程则通过冷冻电子显微镜技术, 在原生生物盘基网柄菌(*Dictyostelium discoideum*)中首次被观察到, 而后在人类细胞中以更高分辨率清晰地获得了核孔复合物组建的完整三维过程, 为获得核孔晶体结构奠定重要基础[11-13]。核孔复合物的形态在真核生物中相对保守, 在植物中的三维结构与动物、酵母相似, 呈现八角状对称的“篮子”结构, 但构成核孔复合物的成员在不同生物间存在差异[14-15](图1)。TAMURA



NE: 核膜; NUP: 核孔蛋白; CG1: 锌指CCCH型家族蛋白1; SEC13: 分泌蛋白13; SEH1: sec13同源蛋白1; ALADIN: 贲门失弛缓症–肾上腺功能不足神经系统紊乱; GLE1: glfg致死因子1; RAE1: RNA输出因子1; HOS1: 渗透响应高表达基因1; ELYS: 来自卵黄囊的胚胎大分子; NUA: 核孔锚定蛋白; TPR: 易位启动子区; CPR5: 组成型表达PR基因5; GP210: 210 kDa糖蛋白; NDC1: 核分裂周期1; POM121: 孔膜蛋白121。

NE: nuclear envelope; NUP: nucleoporin; CG1: Zinc finger CCCH type family protein 1; SEC13: secretory 13; SEH1: sec13 homologue 1; ALADIN: alacrima-achalasia-adrenal insufficiency neurologic disorder; GLE1: glfg lethal 1; RAE1: RNA export factor 1; HOS1: high expression of osmotically responsive gene 1; ELYS: embryonic large molecule derived from yolk sac; NUA: nuclear pore anchor; TPR: translocated promoter region; CPR5: constitutive expresser of PR genes 5; GP210: glycoprotein of 210 kDa; NDC1: nuclear division cycle 1; POM121: pore membrane protein 121.

图1 核孔复合物结构及其亚基的核孔蛋白成员构成

Fig. 1 Molecular architecture of nuclear pore complex and the nucleoporin members of the sub-complex

等[7]利用互作蛋白质组学方法首次鉴定了拟南芥核孔复合物组分, 初步明确了植物核孔蛋白成员的构成(图1)。根据其形成的复合物亚基, 可以将NUPs分为外环、内环、连接、跨膜、核篮和FG(phenylalanine-glycine)核孔蛋白6类[16]: (1) 外环NUPs(outer ring NUPs)由ALADIN(alacrima-achalasia-adrenal insufficiency neurologic disorder)、GLE1(glfg lethal 1)、RAE1(RNA export factor 1)、HOS1(high expression of osmotically responsive gene 1)以及包含NUP43、NUP85、NUP96、NUP107、NUP133、NUP160、SEC13(secretory 13)和SEH1(sec13 homologue 1)的NUP107-160亚复合体组装而成[7]; (2) 内环NUPs(inner ring NUPs)由NUP35、NUP155、NUP188、NUP205以及CPR5(constitutive expresser of PR genes 5)组成[17]; (3) 连接NUPs(linker NUPs)位于外环NUPs和内环NUPs之间, 包括NUP88/MOS7和NUP93a/b[16]; (4) 跨膜NUPs(transmembrane NUPs)包含GP210(glycoprotein of 210 kDa)[18-19]和NDC1(nuclear division cycle 1)[20]; (5) 核篮(nuclear basket)包括NUP50a/b、NUP136/NUP1和NUA(nuclear pore anchor)/TPR(translocated promoter region); (6) FG NUPs包括胞质FG(cytoplasmic FG)和中心FG(central FG)蛋白, 含NUP214[21]和CG1(Zinc finger CCCH type family protein 1)、NUP35、NUP98a/b和NUP62亚复合体, 其中NUP62亚复合体的成员有NUP54、NUP58和NUP62[1,15]。

2 植物核孔蛋白的生物学功能

介导核质转运是核孔蛋白的保守生物学功能, 近些年的研究发现, 核孔蛋白在植物激素信号响应、生长发育、环境胁迫应答、免疫防御中也发挥着重要作用(表1)[3,22-25]。

2.1 植物核孔蛋白与核质转运

核质转运是mRNA和蛋白质等生物大分子物质在细胞核和细胞质之间进行的单向运输活动, 具体

表1 植物核孔蛋白的生物学功能

Table 1 The biological functions of plant nucleoporins

核孔蛋白 Nucleoporins	所属亚基 Sub-complex	参与的生物学过程 Biological processes	参考文献 References
NUP85	Outer ring NUPs	Salt stress, high temperature stress, ABA (abscisic acid) signaling, nodule symbiosis (**Lotus japonicas*)	[38,49,51]
NUP96	Outer ring NUPs	mRNA nuclear export, leaf growth, hypocotyl elongation, flowering time, high temperature stress, immune defence, auxin signaling, ABA (abscisic acid) signaling	[26,38,41,51]
NUP133	Outer ring NUPs	High temperature stress, nodule symbiosis (**Lotus japonicas*)	[41,50]
NUP160	Outer ring NUPs	mRNA nuclear export, protein nuclear import, leaf growth, hypocotyl elongation, flowering time, cold stress, salt stress, immune defence, auxin signaling, ABA (abscisic acid) signaling	[26-27,29,38,41,52]
SEH1	Outer ring NUPs	mRNA nuclear export, immune defence	[8,52]
HOS1	Outer ring NUPs	mRNA nuclear export, leaf growth, hypocotyl elongation, flowering time, cold stress, high temperature stress, salt stress, auxin signaling, ethylene signaling, ABA (abscisic acid) signaling	[30,36-38,41,43,47-48]
RAE1	Outer ring NUPs	mRNA nuclear export (**Nicotiana benthamiana*)	[32]
CPR5	Inner ring NUPs	Protein nuclear import, leaf growth, immune defence, auxin signaling, ABA (abscisic acid) signaling	[17,40,53]
NUP205	Inner ring NUPs	mRNA nuclear export, immune defence	[31]
NUP88	Linker NUPs	Protein nuclear import, immune defence	[33]
NUP98a/b	Central FG NUPs	Flowering time	[44]
NUP54	Central FG NUPs	Leaf growth, flowering time	[8]
NUP58	Central FG NUPs	Leaf growth, flowering time, auxin signaling	[8,34]
NUP62	Central FG NUPs	Leaf growth, flowering time, auxin signaling	[8,35,42]
NUP136/NUP1	Other NUPs	mRNA nuclear export, leaf growth, flowering time	[7]
NUA/TPR	Other NUPs	mRNA nuclear export, leaf growth, flowering time, auxin signaling	[28,39]

除特殊标记植物种属外, 其余均为在模式植物拟南芥中的研究。

All the studies were performed in the model plant *Arabidopsis thaliana*, except of these marked with asterisk.

包括mRNA的核输出和蛋白质的核输入。核孔复合物是控制核质转运的唯一通道, 主要是通过位于细胞质中的输入蛋白(importin)以及在细胞核中的输出蛋白(exportin)特异性识别mRNA和蛋白质等分子, 再由核孔蛋白将这些分子物质输入或输出到细胞核[6]。

植物核孔蛋白介导mRNA核输出的功能研究多集中在拟南芥中。通过mRNA原位杂交检测, 发现NUP96、NUP136、NUP160、SEH1、HOS1和NUA等是植物mRNA核输出所需的关键核孔蛋白, 其功能缺失后mRNA在细胞核中大量滞留[7-8,26-30]。LEONE等[31]证明, *EDS4*(enhanced disease susceptibility 4)负责编码NUP205, *eds4*突变体中mRNA核积累增强, 表明NUP205在mRNA的核输出中也发挥重要作用。另外, 在烟草(*Nicotiana benthamiana*)中, *NbRAE1*的缺乏导致多聚腺苷酸mRNA在细胞核中积累, 揭示烟草核孔蛋白RAE1也参与了mRNA核输出的调控[32]。

人们目前对于直接参与调控蛋白质核输入的核孔蛋白认识还很有限, 仅有NUP160、NUP88/MOS7和CPR5被鉴定出参与特定蛋白质的核输入。PARRY等[26]在*nup160*突变体中观察到转录抑制因子IAA17(indole-3-acetic acid inducible 17)和植物免疫正调控因子EDS1(enhanced disease susceptibility 1)蛋白的核积累减少[29]。研究表明, *nup88*/*mos7-1*(modifier of snc1,7)突变体存在免疫缺陷, 在*mos7-1*突变体中, 抗病蛋白SNC1(suppressor of npr1-1, constitutive 1)以及EDS1和NPR1(non-expresser of PR genes 1)蛋白的核积累显著减少, 而其他蛋白则不受影响[33], 表明NUP88参与调控这些免疫相关蛋白在细胞核中的积累且其积累丰度关系着植物的免疫防御能力。此外, 跨膜核孔蛋白基因*CPR5*过度表达后导致NPR1、JAZ1(jasmonate-zim-domain protein 1)和ABI5(abscisic acid insensitive 5)在细胞质中滞留[17], 揭示CPR5反向调控上述免疫应激和植物激素相关核蛋白的核输入。

2.2 核孔蛋白与植物激素信号响应

植物的生长发育受到多种激素的调节, 核孔蛋白NUP58、NUP62、NUP85、NUP96、NUP160、HOS1、NUA和CPR5参与调控植物激素信号通路。人们以生长素抗性突变体axr1(auxin-resistant1)为背景, 通过正向遗传筛选, 鉴定到了与生长素IAA信号转导有关的核孔蛋白NUA、NUP96和NUP160, 在*axr1*突变体背景下, *NUA*、*NUP96*和*NUP160*的功能缺失会使植物对生长素的敏感性增强[26,28]。人们最初认为这可能是由于核孔蛋白突变体中mRNA的核滞留, 有助于生长素信号途径中负调控因子的转录。然而, 进一步研究表明, 它们对生长素敏感性的增强主要归因于核孔蛋白缺失后生长素转录抑制因子Aux/IAA蛋白的核积累减少[29]。研究发现, *NUP58*和*NUP62*的功能缺失突变体无mRNA核输出缺陷[8], 但突变体植株对生长素敏感性增强[34-35]。LEE等[36]的研究表明, HOS1在控制下胚轴伸长中负调控生长素的生物合成, 并且HOS1同时也参与乙烯(ethylene)信号转导, 在环境胁迫条件下调控叶片的生长[37]。

除参与生长素、乙烯信号外, 脱落酸ABA信号通路也受到核孔蛋白的调控。ZHU等[38]发现, *nup85*、*nup160*和*hos1*突变体对外源ABA处理敏感, 表明NUP85、NUP160和HOS1可能参与调控ABA信号通路。此外, Microarray数据显示, *CPR5*功能缺失后, ABA信号通路基因显著上调表达, 且过表达*CPR5*使ABI5等激素相关核蛋白在细胞质中大量滞留, 表明CPR5负调控ABA信号途径[17]。

2.3 核孔蛋白在植物生长发育中的作用

许多核孔蛋白在控制植物营养生长, 如叶片生长和下胚轴伸长以及开花时间中, 均发挥重要作用。研究证明, 拟南芥核孔蛋白NUP54、NUP58、NUP62、NUP96、NUP136、NUP160、HOS1、NUA和CPR5均参与调控植物叶片的生长, 其功能缺失后莲座叶明显小于野生型, 叶片生长呈现缺陷表型[7-8,26,37,39-40]。ZHANG等[41]研究发现, 高温条件下与野生型相比, *nup96*和*nup160*突变体的下胚轴较短, *hos1*突变体的下胚轴较长, 而*nup85*和*nup133*并无明显下胚轴发育缺陷的表型, 表明不同核孔蛋白在维持植物营养生长中所发挥的作用不尽相同。另外, 大多核孔蛋白在调控植物开花时间中十分关键, 如*NUP54*、*NUP58*、*NUP62*、*NUP96*、*NUP136*、*NUP160*、*NUA*、*HOS1*和*NUP98a/b*功能缺失后, 植物表现出早期开花表型[7-8,26,28,42-44]; 其中, *NUA*功能缺失突变体早花并伴随着*FLC*(flowering locus c)、*MAF4*(mads affecting flowering 4)基因表达水平降低, 而*FT*(flowering locus t)、*SOC1*(suppressor of overexpression of co1)、*MYB33*(myb domain protein 33)、*MYB65*和*LFY*(leafy)基因表达水平增加[41]。此外, *nup98a1*、*nup98a2*单突变体(T-DNA分别插入在*NUP98a*基因第二和第三个外显子上)和*nup98b*单突变体并未出现早花表型, 只有*nup98a1 nup98b1*和*nup98a2 nup98b1*双突变体开花时间明显早于野生型, 表明它们可能在调控开花时

间中存在功能冗余[44]。

2.4 核孔蛋白在环境胁迫应答中的作用

一些核孔蛋白在植物应对环境胁迫的复杂信号网络中也具有重要作用, 正向或负向调控植物应答逆境胁迫。拟南芥响应逆境的基因表达谱显示, 多个核孔蛋白参与非生物胁迫如低温胁迫、高温胁迫和盐胁迫的应答[45-53]。

2.4.1 低温胁迫响应 拟南芥核孔蛋白HOS1和NUP160参与调控植物应答低温胁迫。通过将拟南芥低温响应基因*RD29A*(responsive to desiccation 29a)启动子连接到*LUC*(luciferase)报告基因上, ISHITANI等[45]发现, 低温条件能够诱导*LUC*基因在*hos1-1*突变体中的表达, 而在野生型植株中不能诱导其表达, 初步判断HOS1可能是植物响应低温胁迫的负调控因子[45-46]。在低温响应中, *HOS1*的缺失导致低温胁迫应答调控因子CBFs(c-repeat-binding factors)及其下游冷响应基因的表达上调[45], 而*HOS1*的过度表达则抑制了CBFs和其下游基因的表达, 从而使得植物对低温胁迫更加敏感[47]。此外, HOS1还参与植物在低温条件下的开花过程。HOS1依赖FVE/MSI4(msi1-like 4)蛋白与*FLC*染色质结合, 并且在低温胁迫下HOS1与*FLC*位点的结合显著提高。HOS1还与组蛋白去乙酰化酶HDA6(histone deacetylase 6)相互作用, 抑制HDA6与*FLC*位点的结合, 从而诱导低温条件下*FLC*表达, 控制开花时间[48]。转录激活因子ICE1(inducer of CBF expression 1)对CBFs的低温诱导至关重要, HOS1编码E3泛素连接酶, 研究证明HOS1通过泛素化修饰ICE1使其降解从而来减弱低温信号转导, 调节植物响应低温胁迫[47]。同时, DONG等[27]通过*CBF3-LUC*报告基因, 筛选低温条件下其诱导表达发生缺陷的拟南芥突变体, 发现在*atnup160-1*突变体中低温胁迫应答基因的表达量显著下降, 并导致植物对低温胁迫异常敏感, 表明NUP160正向调控植物应答低温胁迫。

2.4.2 高温胁迫响应 人们最初是在百脉根(*Lotus japonicas*)中发现, 核孔蛋白NUP85和NUP133是植物在高温条件下控制根瘤共生所必需的调控因子, 较高温度使得*nup85*和*nup133*突变体中的根瘤生长明显受到抑制[49-50]。最近研究表明, 拟南芥核孔蛋白NUP85、NUP133、NUP96和HOS1均参与了植物对高温条件的应答[41]。研究人员以多个拟南芥核孔蛋白功能缺失突变体为材料, 从植物生长和免疫防御等方面分析了核孔蛋白在正常和高温条件下的作用。其中, *NUP96*的缺失使植物产生非常明显的高温敏感生长表型, 而在抗病蛋白SNC1介导的植物免疫中, *NUP85*和*NUP133*突变后抑制了SNC1介导的抗病性。深入研究发现, 在高温条件下*nup85*和*nup133*突变体中mRNA在细胞核中大量滞留。另外, 大部分高温应答基因在*nup96*和*hos1*突变体中表达失调, 且高温应答关键调控因子PIF4(phytochrome interacting factor 4)在两者突变体中的核积累明显减少[41], 表明不同核孔蛋白在植物应答高温过程中的多个生理进程如生长发育、核质转运及基因表达调控中发挥不同且至关重要的作用。

2.4.3 盐胁迫响应 ZHU等[38]通过正向遗传筛选的手段, 发现拟南芥核孔蛋白NUP85、NUP160与HOS1参与调控植物响应盐胁迫。当*NUP85*、*NUP160*与*HOS1*功能缺失后, 植物呈现盐胁迫敏感生长表型, 并且*RD29A*、*COR15A*(cold-regulated 15a)和*COR47*等胁迫应答基因的表达也受到明显抑制。

以上核孔蛋白在植物环境胁迫应答中的研究表明, 尽管一些核孔蛋白如NUP160和HOS1响应多个环境因子, 但其所发挥的功能重要性和作用机制不尽相同, 而另有一些核孔蛋白如NUP96和NUP133仅响应某个环境因素, 体现了核孔蛋白功能在环境胁迫应答中的广谱性和专一性。这可能与在植物响应不同环境胁迫下的核质转运过程中, 核孔蛋白特异性识别参与信号转导的功能分子有关, 在未来研究中关注核孔蛋白的特殊作用机制, 将有助于我们认识它们是如何有选择性地、精密地调控植物对环境变化的应答的。

2.5 核孔蛋白在植物免疫防御中的作用

除非生物胁迫外, 核孔蛋白对植物应对生物胁迫时所引发的免疫防御也至关重要。已有报道显示, 拟南芥NUP88、NUP96、NUP160、NUP205、SEH1和CPR5等多个核孔蛋白在植物免疫中发挥重要作用。*NUP96*、*NUP160*和*SEH1*突变后会导致拟南芥对病原菌的敏感性增强[29,51-52]。*NUP88*突变使植物失去抗病蛋白SNC1介导的抗病性[33], 并且qRT-PCR分析表明, 在*snc1*突变体背景下, *NUP96*和*NUP88*功能缺失会导致*PR-1*(pathogenesis-related 1)和*PR-2*基因的表达被抑制[33,51]。CPR5则通过核孔复合物释放ETI(effector-triggered immunity)效应物, 抑制植物的防御反应[17,53]。最新研究表明, *nup205*突变体被病原菌侵染后, 会抑制拟南芥*LNK*(night light-

inducible and clock-regulated)基因表达, 从而导致植物更易感病[31]。

3 结语和展望

迄今为止, 利用模式植物拟南芥, 我们已经对植物核孔蛋白功能有了基本认识。植物核孔蛋白在核质转运、激素信号响应、生长发育、环境胁迫应答、免疫防御中发挥重要功能。然而, 目前关于植物核孔蛋白的研究还处于初级阶段, 现有的认知距离我们系统阐明核孔蛋白在植物中的生物学功能, 深入解析核孔蛋白参与各项生命进程的调控机制仍有一定距离, 许多关于植物核孔蛋白的问题还有待解答, 例如植物核孔复合物中核孔蛋白成员的全面鉴定、不同核孔蛋白生物学功能的冗余与非冗余以及它们在调节植物生命进程中的作用机制。

针对以上问题, 未来的研究工作可从以下几个方面开展: (1) 利用现代互作蛋白质组学研究手段, 结合已有真核生物核孔蛋白数据, 全面鉴定构成植物核孔复合物的核孔蛋白成员; (2) 以单一或多个突变体生长及应激表型观察为基点, 筛查核孔蛋白之间的共同或特异互作因子, 明确核孔蛋白在核质转运大分子物质中的广谱性及特异性, 阐明其在各生物学途径中所发挥功能的冗余与非冗余; (3) 其他真核生物的研究表明, 当生物体处于不同生长阶段或面临不同生存环境时, 核孔复合物组分可能发生动态变化, 如核孔蛋白表达丰度或组成的变化可能启动特殊作用[54], 关注特定条件下核孔复合物中的核孔蛋白组分差异, 有助于深入理解核孔及核孔蛋白在调节植物生命进程中的作用机制。因此, 关于植物核孔蛋白全面深入的研究, 对解读核孔蛋白在植物中的生物学功能及参与各项生命进程的调控机制等方面将有极大的促进作用。

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