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·专题论坛·

# 植物叶绿体发育及调控研究进展

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**摘要** 植物的光合作用几乎是所有生物生存和发展的物质基础。叶绿体是绿色植物进行光合作用的重要细胞器。尽管叶绿体发育及调控一直受到人们的关注, 但其装备及调控的分子机制尚不完全清楚。该文对叶绿体装备过程、叶绿体发育调控及质体-细胞核反向信号的研究进展进行概述, 以使人们从整体上认识叶绿体发育及调控机制。

**关键词** 叶绿体, 发育调节, 质体-细胞核反向信号

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叶绿体是普遍存在于陆地植物、藻类和部分原生生物中执行光合作用的半自主性细胞器。叶绿体的形状和大小因植物种类不同而具有较大差异, 并受到光照等环境条件的影响从而产生适应性变化。叶绿体的发育受到核基因编码蛋白因子的调控, 同时细胞核接受传递叶绿体发育状况及功能状态的质体反向信号(plastid retrograde signaling), 它们相互协调, 共同促成质体的最佳发育及功能的充分发挥。本文基于前人的研究工作, 对叶绿体发育过程及其调控机制进行综述。

## 1 高等植物叶绿体发育的基本途径

叶绿体的发育在某种程度上代表着进化史上的一个奇迹。种子植物的叶绿体是从一个无光合能力的前驱结构——前质体/原质体发育而来(Waters and Langdale, 2009)。前质体在随后的发育过程中根据所处的位置以及接受光的程度, 分化成为叶绿体、白色体、淀粉质体和有色体等功能各异的质体。

光是叶绿体发育的必要条件, 可被一系列能够感受特定波长的蛋白所感知, 蛋白通过构象变化与下游信号分子相互作用。感受红光和远红光的光敏色素(phytochrome A/B, phyA/B)及感受蓝光和紫外光的隐花色素(cryptochrome, cry)是负责调控光形态建成的两类光受体(Jiao et al., 2007)。光敏色素相互作用因子(phytochrome-interacting factors, PIFs)是一类能够与光敏色素相互作用的螺旋-环-螺旋(helix-loop-helix)家族转录因子, 在光下phyB转移至核内并结合PIF3, 启动自身磷酸化, 进而调节光形态建成相关基因的转录(Huq et al., 2004; Bauer et al., 2004)。研究表明, PIF3负调节编码叶绿素合成调节酶基因*HEMA1*、*GUN5*以及光合系统PSI中*LHCA1*、*PsaE1*基因的表达(Goslings et al., 2004; Shin et al., 2009)。PIF1则能够与原叶绿素酸酯氧化还原酶PORC的启动子相互作用, 部分控制叶绿素的合成(Moon et al., 2008)。也就是说, *PIFs*家族基因强烈抑制光形态建成, 特别是叶绿体的发育。

幼苗一旦能够光合自养, 其光形态建成的下一阶段将是活化顶端分生组织, 进而形成子叶和叶绿体, 实现原质体向叶绿体的转变。在叶出现之前, 暴露于光下的顶端分生组织(shoot apical meristem, SAM)的转录组分析表明, 细胞分裂素(cytokinin, CTK)和赤霉素(gibberellin, GA)正调控相关基因、核糖体相关基因等的表达, 使蛋白翻译及细胞增殖加速。随后这些受诱导表达的蛋白参与叶绿体装备相关基因的表达(López-Juez et al., 2008)。光敏色素和隐花色素在叶原基内带动叶绿体装备过程, 包括核编码蛋白的输入、叶绿素水平上升、类囊体中光合电子传递

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(photosynthetic electron transport, PET)复合物的形成等一系列平行事件的进行。

叶绿体的装备需要从细胞质中输入大量核基因编码的蛋白。大多数核编码的叶绿体蛋白能够被质体膜识别并通过Toc/Tic复合物进行转运(Soll and Schleiff, 2004)。Toc/Tic复合体的主要组分受到光的正调节而且对底物具有特异性。*AtTOC33*在幼苗中强烈表达, 其突变可造成光合蛋白的输入及积累上的缺陷(Kubis et al., 2003)。AtToc159的亚基由*AtTOC-159*、*AtTOC132*、*AtTOC120*及*AtTOC90*编码, 其对底物运输蛋白也表现出强烈的选择性(Bauer et al., 2000)。*Toc*/*Tic*的差异表达可能提供一种叶绿体早期发育阶段光合蛋白输入的有效策略(Jarvis and Soll, 2001; Agne and Kessler, 2009)。除了Toc/Tic复合物参与叶绿体蛋白输入外, 核编码叶绿体蛋白的输入还可通过其它方式实现。一些类囊体功能蛋白, 如形成叶绿素复合体的蛋白(light-harvesting chlorophyll, Lhc)被基质叶绿体信号识别颗粒(cpSRP43/54)所识别, 进而调节蛋白插入内膜。研究表明, Lhc的完全插入需要膜定位蛋白ALB3的协助(Bellafiore et al., 2002)。

类囊体装备是叶绿体组装的重要环节。前质体内膜经过折叠形成囊泡, 囊泡经过聚集、增殖发育成基粒片层或间质片层。在此过程中, 核编码催化类胡萝卜素和叶绿素合成后期阶段的相关酶也出现在质体膜上。同时, 叶绿素与叶绿素结合蛋白形成复合体并插入内膜, 作为蛋白输入过程的持续(Hoober et al., 2007)。许多研究表明, 囊泡似乎更适合携带1个单位的叶绿素、酶和光合蛋白穿越基质融合到发育中的类囊体上(Austin and Staehelin, 2011)。内膜相关蛋白VIPP1等因子驱动囊泡折叠形成类囊体网状结构, GTPases(如拟南芥FZL等)可能在类囊体网状结构装备过程中发挥作用。*VIPP1*突变使植物不能形成正常的类囊体及囊泡(Kroll et al., 2001; Aseeva et al., 2007; Zhang et al., 2012)。THF1(thylakoid formation 1)是位于类囊体和基质中的叶绿素代谢相关蛋白。在*thf1*突变体的叶绿体中出现了许多缺少类囊体膜的囊泡(Wang et al., 2004; Wu et al., 2011)。叶绿体被膜的半乳糖酯在类囊体形成过程中也扮演着重要角色(Kelly and Dormann, 2004; Kobayashi et al., 2007)。成熟叶绿体内膜与类囊体膜之间存在直接的连接点, 表明两者在一定程度上呈现动态连接(Shimoni et al., 2005)。Gao等(2006)的研究表明, 维持动态类囊体结构需要FZL, *FZL*突变使植物产生大而不规则的叶绿体和容易堆积的小囊泡, 但其影响叶绿体发育的机制尚不清楚。

在叶绿体生物组装过程中, 为了与细胞分裂及生长相一致必须进行增殖。研究表明, 叶绿体的分裂发生在叶绿体形成的早期(Pyke, 1999; Okazaki et al., 2009)。FtsZ1和FtsZ2是植物中与细菌分裂蛋白同源的组分(Osteryoung and McAndrew, 2001), 叶绿体分裂初期这2种蛋白共同组成内分裂环。研究表明, DRP5B(dynamin related protein 5B)蛋白围绕在叶绿体外层(Miyagishima et al., 2006), 与叶绿体分裂及大小等发育状况相匹配(Okazaki et al., 2009)。质体分裂蛋白PDV1和PDV2形成一种胞质类组分, 是细胞内叶绿体数量的主要机械性决定因素(Okazaki et al., 2009)。*pdv1*和*pdv2*突变体中含有大且不规则的叶绿体(Miyagishima et al., 2006)。相反, 超表达*PDV1*和*PDV2*的拟南芥叶肉细胞中会产生小而多的叶绿体(Okazaki et al., 2009)。FtsZ参与内圈分裂环的装备, 外圈环部分地被PDV蛋白招募并由锚定于外部膜上的DRP5B蛋白组成(Holtsmark et al., 2013)。这种围绕叶绿体中心相分离的环, 通过二分体产生2个叶绿体。研究发现, 在分生组织中PDV的活性较高, 叶中PDV蛋白的减少与叶龄及叶绿体分裂等因素有关(Okazaki et al., 2009)。

## 2 细胞特异叶绿体的发育

被子植物在进化过程中逐渐发育出分布于不同类型细胞中且具备差异功能的亚型叶绿体。拟南芥(*Arabidopsis thaliana*)和烟草(*Nicotiana tabacum*)的表皮细胞中存在小且未完全发育的叶绿体, 这与表皮细胞具保护功能相一致。气孔保卫细胞叶绿体的光合活性对气孔功能的充分发挥至关重要(Lawson, 2009)。特异细胞中质体发育的差别, 可能是细胞自主因子的正调节和协调作用受抑制的共同结果(Waters and Langdale, 2009)。除了根中具备抑制叶绿体发育功能的光合抑制子COP/DET/FUS家族外(Kwok et al., 1996), 关于特异细胞叶绿体发育机理尚知之甚少。

真叶的叶绿体由分生组织的原质体在叶原基出

现时发育而来, 而子叶中的叶绿体则是由白色体在光下快速转化而成。SCO是叶绿体定位的延伸因子G(elongation factor G, EF-G), 其突变造成子叶颜色改变, 但不影响真叶叶绿体的发育, 表明SCO在子叶的叶绿体发育中扮演重要角色。有研究表明, SCO功能的发挥与蔗糖营养信号有关(Albrecht et al., 2006; Ruppel and Hangarter, 2007)。拟南芥CYO1也参与子叶叶绿体的发育过程, 与大肠杆菌DnaJ类似, 具有预测的锌指结构区域(Shimada et al., 2007), 推测类囊体内, 该区域在富含半胱氨酸残基蛋白(例如光合体系组成蛋白)的折叠过程中起作用。

C4植物(如玉米(*Zea mays*)等)的光合作用由叶肉细胞和维管束鞘细胞共同完成。叶肉细胞的叶绿体主要进行$CO_2$固定, 真正的卡尔文循环在维管束鞘细胞中进行。玉米两种细胞的叶绿体存在明显的差别。叶肉细胞叶绿体富含基质, 积累PSII, 缺少淀粉; 而维管束鞘细胞叶绿体缺少基质, 积累核酮糖-1,5-二磷酸, 包含大量的淀粉颗粒。同时, 两种亚型叶绿体蛋白质组成也都具有各自的特异性(Majeran et al., 2005)。高等植物及苔藓中存在一种编码Myb类转录因子的*GLK*(golden2-like, GLK)家族基因。该家族成员在植物中的功能具保守性, 每种植物至少存在2种*GLK*基因, 其主要功能是调节参与编码植物叶绿素合成组分(包括My-螯合酶亚基等)基因的表达(Papenbrock et al., 1997; Adhikari et al., 2011; de Dios Barajas-López et al., 2013)。*GLK*家族基因在不同类型光合细胞中的表达存在差异(Rossini et al., 2001; Yasumura et al., 2005)。拟南芥和苔藓的GLK家族成员在促进核基因表达上存在功能冗余(Fitter et al., 2002; Yasumura et al., 2005; Waters et al., 2009)。玉米*ZmGLK1*在叶肉细胞中表达, 而同源的*ZmGLK2*在维管束鞘细胞中表达较强。它们在叶肉细胞及维管束鞘细胞中的分化与各自主要功能相一致(Chang et al., 2012)。Langdale和Kidner(1994)的研究表明, *ZmGLK2*的突变特异破坏维管束鞘细胞内光合器官的发育, 但对叶肉细胞中的叶绿体没有影响(Langdale and Kidner, 1994)。推测*GLKs*可能起源于单个的*GLK*基因, 复制促使亚功能出现, 进而在C4植物中促进双态叶绿体的发育(Wang et al., 2013)。基因家族内同源体的差异表达可能与基因调节区的功能选择相关, 不同的启动子识别可能部分负责不同途径的叶绿体生物装备(Sage, 2004)。Covshoff等(2008)的研究表明, *Zmhcf136*突变体幼苗致死, PSII活性丧失, 同时叶肉细胞叶绿体基质匮乏, 但维管束鞘细胞的叶绿体发育不受影响(Covshoff et al., 2008)。玉米中编码DnaJ类蛋白BSD2的基因突变仅在维管束鞘细胞中表现出不规则的叶绿体(Brutnell et al., 1999)。这些叶绿体发育同源基因差异表达的确定, 为揭示亚型叶绿体的不同结构特征及差异功能提供了基础。然而, 已鉴定出的在叶肉细胞和维管束鞘细胞中C4植物特异缺陷突变体仍然很少。

## 3 叶绿体发育过程的调控

核编码蛋白的输入, 为成熟叶绿体的发育提供了物质及功能基础。输入的蛋白参与并调控叶绿体基因的转录、转录后加工及翻译等过程。叶绿体基因转录所需的RNA聚合酶包括质体编码的RNA聚合酶(plasmid encoding RNA polymerase, PEP)和核基因编码的RNA聚合酶(nuclear encoded RNA polymerase, NEP)。研究表明, 核编码的西格玛(SIG)因子在控制叶绿体中RNA聚合酶与启动子结合中起关键作用(Lysenko, 2007)。在光下, SIG因子激活质体基因表达, 引起光合反应核心蛋白(如*PsbD*等)的表达, 同时调节RNA加工和核糖体的装备。在拟南芥中已鉴定出6个编码SIG因子的核基因。这些SIG因子利用质体RNA聚合酶启动特异基因的转录, SIG2和SIG6也被认为在子叶脱黄化中具有特殊的功能(Woodson et al., 2013)。在玉米中已经鉴定出5个ZmSIG因子, 其中前4个定位于质体并作用于质体特异基因的转录, 而ZmSIG2B除了具备叶绿体SIG因子活性外, 也在线粒体基因转录中发挥一定的作用(Beardslee et al., 2002)。SIG家族成员功能上存在冗余, 互补测试、启动子互换及突变分析等都有助于阐明基因组织特异性和功能的差异性。核编码蛋白对叶绿体RNA编辑、转录后加工、维持RNA的稳定性等起重要作用(Vaistij et al., 2000)。陆生植物莱茵衣藻(*Chlamydomonas reinhardtii*)叶绿体基因在翻译的过程中需要进行内含子的剪切和外显子的拼接。研究发现, 这些叶绿体基因转录物的拼接需要来自核编码蛋白质因子的参与。玉米的核基因*CRS1*和*CRS2*发生突变, 会严重影响叶绿体中许多II类内含子的剪切过程(Jenkins et al.,

1997; Vogel et al., 1999; Ostheimer et al., 2003)。某些核编码蛋白通过控制叶绿体核糖体装配等方式调控叶绿体基因的翻译。在低温环境下，拟南芥叶绿体核糖体的组装需要核编码DIM1的参与(Tokuhisa et al., 1998)。研究发现，核基因与叶绿体基因翻译之间存在一一对应的调控关系。如衣藻*tab1-F15*基因的突变导致叶绿体的*psaB* mRNA不能翻译；玉米*atp1*基因突变导致叶绿体*atpB*/*E* mRNA不能翻译。

## 4 叶绿体-细胞核反向信号

一方面，核基因编码的组分参与调控叶绿体基因的表达；另一方面，细胞核也时刻接受来自质体且体现质体自身发育及功能状况的反向信号，使得细胞核编码的叶绿体蛋白种类和数量能够更好地适应质体发育及功能发挥的需求。

研究表明，质体反向信号至少通过包括质体基因表达(plastidial gene expression, PGE)、质体代谢物质(四吡咯等)、质体蛋白输入、活性氧产生和活性氧其它相关过程等在内的多种途径来向细胞核传递质体发育及功能状态信号，进而调节核基因的表达(Pfannschmidt, 2010)。质体基因表达似乎是协调不同质体类型早期发育阶段中核编码质体基因表达所需(Kanervo et al., 2008)。质体基因表达出现缺陷时，多种核编码质体蛋白(如LHCB)受到负调控(Pesaresi et al., 2006; Koussevitzky et al., 2007)。各种研究结果显示，质体基因表达途径只在成熟叶中存在(Pesaresi et al., 2006)。同时，质体基因表达随质体内氧化还原状态的变化而变化。拟南芥PRIN2是质体定位的转录激活蛋白，能够促进被质体编码RNA聚合酶启动的质体基因转录。该基因的突变使得拟南芥对质体氧化还原状态不敏感(Chateigner-Boutin et al., 2008; Arsova et al., 2010)。*prin2*突变体中质体基因较低的表达水平破坏正调节信号或诱导产生核编码质体蛋白表达的负调节信号(Kindgren et al., 2012)。

叶绿体的代谢状况以代谢物为信号调控核基因的表达。研究表明，四吡咯参与叶绿体与细胞核之间的信息交流。叶绿体受到损伤会使四吡咯代谢受影响，且作为一种信号调节相关核基因的表达。在绿藻和高等植物中，四吡咯途径的受损表现为影响光合相关核基因(*PhANGs*)的表达(Cornah et al., 2003; Alawady and Grimm, 2008; von Gromoff et al., 2008; Zhang et al., 2012)。对叶绿体与细胞核之间通讯交流削弱的*gun*突变体的研究表明，Mg-原卟啉IX(Mg-protoIX)和Mg-原卟啉IX单甲基酯(Mg-protoMe)是影响核基因表达的主要卟啉类物质。Mg-原卟啉的积累为叶绿体调控核基因的表达所需(Mochizuki et al., 2001; Gray, 2003)。De Dios Barajas-López等(2013)推测，Mg-原卟啉影响叶绿素合成及扩散，或穿梭于叶绿体被膜至细胞溶质中传递质体信号。同时，Mg-原卟啉的积累与光合相关核基因的表达降低存在相关性(De Dios Barajas-López et al., 2013)。最新研究表明，Mg-原卟啉IX积累的变化与Lhcb表达的变化并不匹配；相反，通过合成酶复合物所产生代谢物的流量可能导致这种信号的产生(Moulin et al., 2008; Pfannschmidt, 2010)。质体中的甲基赤藻糖醇(methylerythritol cyclodiphosphate, MEcPP)是质体甲基赤藻糖醇磷酸盐途径中产生的类异戊二烯前体，诱导核编码的胁迫反应中质体蛋白的表达。近来该物质被证实为重要且特异的反向信号代谢物(Xiao et al., 2012)。

叶绿体的氧化还原状态可激发反向信号调控核基因的表达(Fey et al., 2005; Tadini et al., 2012)。氧化还原状态对核基因的调控被认为是一种适应性的过程，使细胞核基因的表达能够适应外界条件的改变，进而提高光合效率及避免光损伤(Kindgren et al., 2012)。质体醌(plastoquinone, PQ)被认为是影响核基因表达的氧化还原信号产生位点。高等植物中，PQ的氧化还原状态与其它信号结合在一起共同实现对核基因的精细调控(Fernández and Strand, 2008)。研究发现，多种核基因，如质体蓝素基因(*PETE*)、抗坏血酸过氧化酶基因(*APX2*)和早期光诱导蛋白基因(*ELIP2*)等均受到PQ氧化还原状态的调节(Schütze et al., 2008)。2 000多个拟南芥核编码光反应蛋白中，有54个受到PQ氧化还原状态的严格调控(Fey et al., 2005)。叶绿体中主要产生包括$^1O_2$、$O_2^{\cdot-}$、$H_2O_2$和OH·等形式的活性氧，它们可能作为信号分子调节叶绿体及细胞核基因的表达，从而使细胞更好地适应环境。大量的植物抗氧化胁迫基因的表达受到来自叶绿体ROS的调控。同时，PQ氧化还原状态也容易受到外界条件的影响。外源施加$H_2O_2$能够刺激叶绿体*APX2* (chloroplast APX2, cAPX2)和锌指转录因子*ZAT10*

及*ZAT12*的表达, 施加过氧化氢酶则能消除这种效果(Rossel et al., 2007; Fernández and Strand, 2008; Kindgren et al., 2012)。还有研究显示, $^1O_2$和$H_2O_2$相互作用共同影响PQ氧化还原状态调节的信号系统(Laloi et al., 2007)。尽管其作用机制还不甚清楚, 但可以确信叶绿体产生的ROS在调节核基因表达方面发挥了重要作用。

GUN1是质体定位的PPR蛋白, 受到氧化还原、Mg-原卟啉IX及细胞器基因表达调节途径的影响。*GUN1*的突变使细胞器转录翻译抑制子林肯霉素对核表达质体蛋白的抑制受阻, 该基因突变体中*LHCB*的表达较高(Koussevitzky et al., 2007; Cottage et al., 2010; Sun et al., 2011)。越来越多的研究表明, GUN1至少整合了细胞器基因表达及氧化还原调节途径, 为质体产生或传输刺激的公共信号至细胞核中所需。ABI4是参与植物激素ABA反应中具顺式作用元件(*cis*-acting elements)的转录因子。研究证明ABI4作为调节因子作用于*gun*-突变体中受影响基因的上游序列, 在质体反向信号中扮演重要角色(Larkin et al., 2003; Koussevitzky et al., 2007)。*ABI4*的突变引起相对较弱的*gun*表型, 表明其它的调节因子也参与PGE对核编码质体蛋白的调控(León et al., 2012)。同时, ABI4在传递有关抗坏血酸的信息中扮演重要角色, 其具体作用为促进细胞对氧化胁迫的缓冲能力(Foyer et al., 2012)。能够从叶绿体转运至细胞核中的蛋白, 是潜在的质体信号携带者。PTM是一个定位于叶绿体膜上的转录因子, 全长PTM蛋白仅在叶绿体外膜中存在, 且被证实调控PhANG的表达, 进而调节叶绿体信号。PTM蛋白的N端有1个分子量约为58 kDa的区域在细胞器基因表达抑制剂达草灭或质体蛋白合成抑制子林肯霉素的存在下能够在细胞核中积累, 通过蛋白酶体加工, 把来自质体的信号释放到核中(Sun et al., 2011)。*gun1*突变体中PTM的N端(N-PTM)在核中的积累明显弱于野生型, 同时突变体表型被N-PTM的组成型表达所回补, 表明GUN1对PTM功能的发挥很重要(León et al., 2012)。*ABI4*在*ptm*突变体中的表达明显减少, N-PTM在细胞核中的释放与胁迫诱导的*ABI4*表达之间存在联系。PTM的PHD区域结合*ABI4*的启动子, 调节*ABI4*的表达, 这种调节作用与组蛋白的修饰有关(Sun et al., 2011)。对*gun1ptm*和*abi4ptm*两个双突变体的分析显示, GUN1、PTM及ABI4作用于同一信号途径中。也就是说, 叶绿体膜结合转录因子PTM连接叶绿体信号蛋白GUN1和细胞核调节因子ABI4, 进而共同作用于质体信号从叶绿体转向细胞核的过程(De Dios Barajas-López et al., 2013)。这种确认的信号途径中, 仍然存在诸如PTM如何感受反向信号、何种途径依赖于PTM与细胞核进行交流等悬而未决的问题。

总之, 叶绿体-细胞核之间存在着时刻向细胞核传递的能体现叶绿体发育状态及功能状况的逆向信号, 但对这方面的研究却进展缓慢。

## 5 研究展望

经过几十年的努力, 人们对植物叶绿体的发育调控有了比较深入的了解。执行光合作用的同时, 叶绿体在感知并转导环境胁迫信号中也发挥着重要作用。作为重要的植物细胞器, 其发育及调控机制非常复杂, 受到内外多种因素的影响, 其中涉及核编码质体蛋白的输入、质体基因表达的调控、质体-细胞核反向信号途径等多个方面。然而, 一直备受青睐的质体-细胞核反向信号途径的研究进展较慢, 相关过程及调控的分子机制仍不清楚。这将是今后人们努力探寻的重要方向。

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# Research Advances in the Development and Regulation of Plant Chloroplasts

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**Abstract** Photosynthesis is the physical basis of almost all biological survival and development events. Chloroplasts are important organelles in green plants for photosynthesis. Although chloroplast development and regulation has been a research focus, the process and molecular mechanism is not fully clear. This paper summarizes recent studies about chloroplast process, development regulation and chloroplast-to-nucleus retrograde signaling for better understanding chloroplast development and regulation.

**Key words** chloroplast, developmental regulation, plastid-to-nucleus retrograde signaling

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