植物生理学报 *Plant Physiology Journal* 2024, 60 (3): 399–429
doi: 10.13592/j.cnki.ppj.600004

植物生物学发展报告(2013—2023)专刊 Special Issue on Advances in Plant Biology (2013–2023)

植物光信号转导研究领域近十年重要研究进展

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摘要: 光是影响植物生长和发育的一种环境信号, 在植物的整个生命周期中发挥关键的调控功能。光信号转导的研究已有一百多年的历史, 一直都是植物生物学研究领域的一个热点。本文从光敏色素、隐花素、紫外B受体等3种信号转导途径、光信号转导的共性调控机制、光信号与内源激素信号和其他环境信号的互作、以及作物光形态建成等方面, 对植物光信号转导研究领域近十年来的重要进展进行了概述。

关键词: 光受体; 光信号转导; 信号互作

Research advances in plant light signaling transduction during the past ten years

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收稿 2023-02-28 修定 2023-04-12

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Abstract: Light is an environmental signal that plays important roles in regulating growth and development of plants during their entire life cycle. The research of light signaling transduction has a history of more than one hundred years and has always been the hot field in plant biology. This review paper mainly summarized important progresses in the area of light signaling transduction of the past ten years, including the light signaling pathways of phytochromes, cryptochromes, and ultraviolet-B photoreceptor, the common regulatory mechanisms of the signaling pathways, the cross-talk between light and endogenous hormonal signals as well as the other environmental signals, and photomorphogenesis in crops.
Key words: photoreceptor; light signaling transduction; signal interaction

植物的生长与发育离不开太阳光。除了光能被吸收用于光合作用, 光的波长、方向、周期、强度等因素都深刻影响植物的地域分布、生长习性、发育与繁衍。光信号由植物体内不同家族的光受体所精确感知, 包括光敏色素(phytochrome, phy)吸收600~750 nm波长的红光和远红光, 隐花素(cryptochrome, cry)和向光素(phototropin, phot)吸收320~500 nm的蓝光和紫外光A, UV RESISTANCE LOCUS 8 (UVR8)吸收280~315 nm波长的紫外光B。这些光受体接收光信号后被激活, 经由复杂的信号通路将光信号传递下去, 最终调节种子萌发、光形态建成、叶绿体发育、避荫反应、生物节律、气孔开闭、开花和衰老等多个生物学过程。在分子与生化层面, 光信号的感知和传递存在多种调控方式和作用机制。同时, 植物生长发育是一个有机的整体, 光信号还需要与外界的其他环境信号以及体内的激素信号相互作用, 共同精确调控植物对环境的响应。

光信号转导一直是植物生物学领域的研究热点之一, 近10年来取得了一系列重要进展。本文从光敏色素、隐花色素、UVR8等3类光受体入手, 从光信号的共性调控机制、光信号与激素信号和其他环境信号的互作机制以及农作物光信号转导的研究进展等几个方向进行了综述。过去该领域发表了大量重要的论文, 但由于篇幅所限, 很多研究成果未能写进本文, 我们深表歉意。

1 光敏色素信号转导途径

早在20世纪中叶, 研究人员就发现红光照射能够促进莴苣(*Lactuca sativa*)种子萌发, 而随后照射远红光能够逆转红光对种子萌发的促进作用。在高密度种植下, 植物因为彼此遮挡造成遮荫环境中红光与远红光的比例发生变化, 被遮挡的植物会产生避荫反应, 以竞争有限的光照。深入研究

红光和远红光信号转导的分子机制, 有助于进一步理解植物如何适应复杂的光环境, 对培育耐密植的作物新品种也具有重要的理论指导意义。

1.1 光敏色素的结构

PhyA与phyB是模式植物拟南芥(*Arabidopsis thaliana*)中最重要、也是研究最为深入的两类光敏色素蛋白(Li等2011)。光敏色素全蛋白是二聚体结构, 其蛋白单体分为N端感光结构域(photosensory module, PSM)和C端信号输出结构域(output module, OPM), 中间以铰链区(hing region)相连。PSM区与生色团PΦB (phytochromobilin)共价连接, 与光受体的感光功能相关, OPM区与光敏色素的二聚化、入核转运、光小体(photobody)形成等功能相关, 铰链区可能参与调控光敏色素的磷酸化(Li等2011; Qiu等2017; Park等2018; Zhou等2018a; Legris等2019; Cheng等2021)。光敏色素有两种能够互相转化的构象形式: 远红光吸收形式(far-red light-absorbing form, Pfr)和红光吸收形式(red light-absorbing form, Pr)。Pr形式的光敏色素吸收红光后向Pfr转变, 而Pfr形式的光敏色素吸收远红光后向PrPr转变(Legris等2019; Cheng等2021)。长期以来, 人们认为Pfr形式的光敏色素是有活性的形式, 而Pr形式无活性,但近来发现位于细胞核中的Pr形式phyA可能具有一定的生物学活性(Sheerin等2015; Zhou等2018a; Menon等2020; Li和Hiltbrunner 2021a)。最新的研究发现, 光敏色素phyB见光由Pr转变为Pfr形式后, 可以通过“光-钙调控环路”, 快速激活两个钙依赖性蛋白激酶, 在Ser80和Ser106位点磷酸化phyB, 控制phyB进入细胞核(Zhao等2023a)。细胞核内的phyB通过液-液相分离过程形成动态可控的光小体, 招募相关组分进行信号转导(Chen等2022a)。

光敏色素可能存在Pr-Pr、Pr-Pfr和Pfr-Pfr等多种形式的二聚化结构, 而不同的二聚化结构可能与光敏色素特异的生化活性相关(Klose等2015)。近期研究揭示了phyB在Pr状态下的二聚体结构: 该结构并非是预期中的平行结构, 其C端HKRD (histidine kinase-related domain)结构域头对头连接, N端感光结构域头对尾连接, 形成了一个近似于平行四边形的不对称结构, 这有助于不同构象的光敏色素与其他信号组分间的相互作用(Li等2022b)。光通过诱导光敏色素构象转变, 调节其与其他蛋白(如转录因子、E3泛素连接酶、激酶等)的相互作用, 并引起大规模的转录重编程, 最终使植物对光做出适应性响应(Legris等2019; Cheng等2021)。

1.2 Phy-PIFs调控模块

光敏色素互作因子PIFs (phytochrome-interacting factors)是一类可以与光敏色素蛋白相互作用的bHLH家族转录因子, 是光信号响应过程中的关键负调控因子。Phy-PIFs是植物红光/远红光信号转导早期重要且快速的调控模块。光敏色素蛋白通过与PIFs互作, 抑制其蛋白丰度, 并改变下游基因的转录水平。红光促进蛋白激酶PPKs (photoregulatory protein kinases)与phyB相互作用, 同时PPKs与PIF3直接互作并介导其磷酸化(Ni等2017)。随后, 磷酸化的PIF3被E3泛素连接酶LRB (light-response bric-a-brack/tramtrack/broad)识别并经由26S蛋白酶体途径降解, 且phyB在该过程中被共同降解(Ni等2014)。此外, 激酶BIN2 (brassinosteroid-insensitive2)、MPK6 (mitogen-activated protein kinase6)以及SPA (suppressor of *phyA-105*)蛋白也被证明可直接磷酸化PIF1/3/4等蛋白(Bernardo-Garcia等2014; Lin等2017; Xin等2018; Paik等2019)。有意思的是, 光敏色素N端的感光模块具备激酶活性, 能够在体外直接磷酸化PIFs蛋白(Shin等2016), 但是光敏色素是否作为激酶发挥功能尚需进一步研究。另一方面, 泛素连接酶EBF1/2 (ethylene-insensitive 3-binding F-box 1/2)、BOP (blade-on-petiole)、CTG10 (cold temperature-germinating 10)同样参与介导PIF1/3/4的泛素化修饰与降解(Dong等2017; Jiang等2017; Zhang等2017a; Majee等2018)。此外, 有研究报道COP1-SPA复合体也促进PIF1/5的降解(Zhu等2015; Pham等2018)。

光敏色素与PIFs相互作用也能抑制PIFs蛋白的转录活性, 且阻断PIFs转录因子结合靶基因启动子序列, 从而促进光形态建成。其中, PIF3蛋白包含一个类似p53的转录激活区域, phyB (包括phyA)受光激活后与之互作并抑制其转录活性, 且该抑制作用主要由phyB的N端结构域介导, 而PIF蛋白的降解主要由phyB的C端结构域控制(Qiu等2017;

Yoo等2021)。在另一研究中, 通过分别突变phyB的N端与C端点, 发现phyB的N端参与调控PIFs的DNA结合能力, C端结构域参与调控PIFs的降解过程(Park等2018)。此外, 光激活的phyB还通过调控*PIF3*转录本的可变剪接来调控其蛋白丰度(Dong等2020a)。总体上, 光敏色素通过调控PIFs蛋白丰度、转录活性及DNA结合能力等多种方式来传递红光/远红光信号。

近期的一些研究发现多个蛋白组分通过与phy-PIFs模块相互作用来调控红光/远红光信号。在红光下, BBX4/11 (B-box containing protein4/11)同时与phyB和PIFs相互作用, 从而降低PIFs的转录活性及其控制的基因表达水平(Heng等2019; Song等2021)。PCH1 (photoperiodic control of hypocotyl 1)以及PCHL (PCH1-like)与PIF1相互作用, 负调控其DNA结合能力, 同时促进光诱导的PIF1降解(Cheng等2020)。同时, PCH1/PCHL还能与光激活的phyB特异互作, 这有助于phyB光小体的形成和稳定, 抑制phyB构象的暗逆转过程以促进光形态建成(Huang等2016; Enderle等2017)。研究发现14-3-3家族的两个成员14-3-3λ/κ与PIF3以及Pfr形式的phyB相互作用, 从而促进phyB-PIF3-PPK复合体的形成并正调控光信号, 而R2R3-MYB家族转录因子MYB30以及植物低温信号重要转录因子CBF1 (C-repeat binding factor 1)通过与phyB和PIF4/5互作, 抑制了phyB-PIFs之间的相互作用, 从而促进PIF4/5蛋白的积累, 负调控光形态建成(Dong等2020b; Yan等2020; Song等2023)。此外, bHLH家族转录因子HEC1/2、G蛋白β亚基AGB1和磷酸酶PP6均被报道通过与PIFs蛋白相互作用来调控PIFs转录因子的活性与丰度(Zhu等2016; Xu等2019; Yu等2019; Kathare等2020)。

1.3 Phy-COP1/SPA调控模块

COP1 (constitutively photomorphogenic 1)作为一类E3泛素连接酶, 在植物光形态建成过程中发挥核心负调控作用。在黑暗下, *cop1*突变体表现出短下胚轴、子叶张开的组成型光形态建成表型。在植物体内, COP1与SPAs蛋白形成四聚体结构, 且SPAs能够促进COP1的E3泛素连接酶活性。转录因子HY5 (elongated hypocotyl 5)作为植物光形态建成的重要正调控因子, 是早期鉴定到的COP1最著名底物。在黑暗下, COP1-SPA复合体介导HY5等光形态建成正调控因子通过26S蛋白酶体途径的降解, 从而抑制光形态建成(Osterlund等2000; Podolec等2018; Han等2020)。Pfr形式phyA和phyB特异与SPA相互作用, 进而阻碍了COP1与SPA形成复合体, 最终抑制了COP1的E3泛素连接酶活性(Lu等2015; Sheerin等2015)。同时, 光激活的光敏色素也能快速诱导SPA2降解, 该调控作用进一步加快了COP1-SPA复合体的失活(Chen等2015a; Schenk等2021)。因此, 光敏色素通过抑制COP1-SPA复合体的功能, 间接促进了HY5等蛋白的积累, 正调控植物的光形态建成。

另一方面, 其他信号组分也能调控COP1-HY5模块。其中, DET1 (de-etiolated 1)促进COP1与HY5的相互作用, 从而降低HY5蛋白水平以促进暗形态建成(Canibano等2021)。Ser-Arg-Asp富含的蛋白SHW1 (short hypocotyl in white light 1)与COP1及HY5均相互作用并促进COP1介导的HY5降解, 从而负调控光形态建成(Srivastava等2015)。多个B-box家族转录因子(包括BBX20、BBX21以及BBX22等)被证明作为HY5的辅助因子并促进其功能(Xu等2016a; Bursch等2020; Song等2020; Zhao等2020)。此外, 染色质重塑因子PKL (pickle)、组蛋白去乙酰化酶HDA15 (histone deacetylase 15)/19、钙调蛋白CAM7、冷响应因子COR27 (cold regulated 27)/COR28均能与HY5相互作用并影响其下游基因的表达, 最终调控光形态建成(Jing等2013, 2021; Abbas等2014; Zhao等2019; Kahle等2020; Li等2020c; Zhu等2020)。

1.4 红光/远红光信号的其他调控组分

磷酸化修饰、SUMO化修饰以及可变剪接等也参与调控光敏色素介导的光形态建成, 多个与这些过程相关的新调控组分也陆续得到鉴定。例如, TZP (tandem zinc-finger/plus 3)能够与phyA相互作用并调控phyA的磷酸化, 而磷酸化的phyA可能是活性更强的形式, 在远红光信号转导中发挥重要功能(Zhang等2018a; Zhou等2018a)。此外, TZP与phyB直接互作并促进phyB蛋白的积累以及phyB光小体的形成, 且通过抑制COP1与HY5间的互作

来促进HY5积累(Kaiserli等2015; Li等2022a; Fang等2022)。目前发现有三类蛋白参与调控光信号组分的SUMO修饰: SIZ1 (sap and miz1 domain-containing ligase 1)促进COP1的SUMO化, 从而提高其E3连接酶活性(Lin等2016); OTS1 (overly tolerant to salt 1)促进phyB蛋白去SUMO化, 从而抑制phyB与PIF5的结合, 最终负调控phyB介导的红光信号(Sadanandom等2015); ASP1 (*Arabidopsis* SUMO protease 1)在远红光下促进FHY1 (far-red elongated hypocotyl1)蛋白去SUMO化, 提高FHY1的稳定性, 从而促进phyA介导的远红光信号(Qu等2020)。另外, 近期的研究揭示红光激活的phyB与剪接因子SFPS (splicing factor for phytochrome signaling)、RRC1 (reduced red-light responsies in *cry1 cry2* background 1)、SWAP1 (suppressor-of-white-apricot/SURP RNA-binding domain containing protein 1)等相互作用, 共同调控大量光响应基因pre-mRNA的可变剪接, 从而优化植物的生长(Xin等2017, 2019; Kathare等2022)。另一项全基因组水平的分析发现光敏色素还参与调控启动子的选择性使用, 这使得被调控基因能够根据光信号的改变转录出不同版本的pre-mRNA (5′端核酸序列不同), 由此翻译出的蛋白根据其N端序列差异定位至不同细胞区域并发挥功能, 以适应光环境的变化(Ushijima等2017)。

2 隐花素信号转导途径

2.1 CRY的结构及其蛋白稳定性和光受体活性的调控

蓝光受体隐花素在模式植物拟南芥中首先被发现, 后被证实广泛存在于微生物、动物和植物中。拟南芥基因组编码三个CRY同源蛋白, 其中CRY1定位于细胞核和细胞质, 而CRY2只定位于细胞核, 它们分别主要调控植物的光形态建成与光周期开花(Guo等1998; Lin等1998; Liu等2016)。CRY3虽被命名为第三个CRY, 但因其缺乏CRY1和CRY2的C端延伸区而与光裂解酶存在更高的相似性。生化研究表明CRY3在体外具有修复单链DNA中嘧啶二聚体的活性(Kiontke等2020), 但目前尚无遗传学证据表明其参与DNA损伤修复或其他生长发育过程。

CRY1和CRY2虽与光裂解酶具有同源性, 但缺少DNA修复活性(Krischer等2022; Vechtomova等2020)。CRY的N-端功能区(CNT)是光裂解酶的同源区域, 故又称为PHR (photolyase-homologous region)结构域。PHR结构域与黄素腺嘌呤二核苷酸(FAD)非共价结合, 以其作为生色团感应蓝光信号。CRY的C-端结构域(CCE或CCT)的保守性较低, CNT和CCT都能介导CRY与下游因子互作进行光信号转导(Mao等2021; Wang等2018a; Xu等2018; Yang等2000)。植物CRY被蓝光激活后经历光还原、光寡聚化和信号转导来调节下游基因表达(Wang和Lin 2020e)。CRY的二聚化反应是原初光反应的关键步骤, 并进一步形成四聚体(Ma等2020a; Shao等2020)。CRY2的抑制因子BIC1 (blue-light inhibitor of cryptochromes 1)和BIC2通过与之结合阻断其蓝光依赖的二聚化, 并抑制其光小体的形成、磷酸化、降解等生理生化过程(Kruusvee等2022; Wang和Lin 2020e; Wang等2016)。对BIC2-CRY2N复合物晶体结构的解析发现BIC2表现出延展结构并缠绕在CRY2的N端周围, 抑制光还原期间电子和质子从CRY2转移到FAD, 使CRY2低聚物回复为单体形式(Ma等2020b)。CRY的光寡聚化是其功能发挥的必要非充分条件, 即光寡聚化后可能存在构象上的进一步改变来影响CRY与其他蛋白质的相互作用(Liu等2020)。

植物中存在多种机制调节CRY的活性和丰度。比如, CRY对蓝光的敏感性受到CRY-BIC负反馈环的调节: 蓝光激活的CRY通过抑制COP1的活性保护下游转录因子HY5, 从而促进*BIC*基因的转录来抑制CRY自身的活性(Wang等2017)。此外, COP1和E3泛素连接酶LRBs分别与CRY1和CRY2互作并促进其降解, 来调节它们在不同光照或温度条件下的的丰度(Chen等2021; Liu等2022; Ma等2021; Miao等2022)。同时, CRY依赖蓝光介导的磷酸化修饰来调控其生物活性和蛋白水平, 在CRY2的CCT结构域上的三个丝氨酸残基(包括S598、S599和S605)参与了蓝光依赖性的磷酸化过程(Wang等2015)。光激活的CRY2有至少24个不同的氨基酸残基在体内被磷酸化, 4个光调控相关的酪蛋白激酶PPK1-4功能冗余地参与CRY1和CRY2的磷酸化修饰, 调节其生化活性并促进CRY2进入泛素化

降解途径(Liu等2017a)。此外酪蛋白激酶CK1.3和CK1.4可以在体外磷酸化CRY2 (Tan等2013)。

2.2 CRY调控光形态建成、光周期开花和避荫反应的分子机制

COP1-SPAs是抑制光信号转导的关键复合体, 在黑暗中该复合体作为$CUL4^{COP1\text{-}SPAs}$ E3泛素连接酶的底物适配器降解下游靶蛋白, 从而抑制光形态建成和开花(Liu等2008b, 2011b; Stawska和Oracz 2019; Wang等2018a)。CRY1与CRY2均与SPA1发生蓝光特异性的互作, 并抑制COP1的活性, 来分别促进HY5和CO (CONSTANS)蛋白的稳定性, 从而促进光形态建成(Huang等2014; Lian等2011; Liu等2011a)和开花(Zuo等2011)。此外, CRY1与SWR1 (SWI2/SNF2-related1)复合体亚基SWC6 (SWR1 complex 6)和ARP6 (actin-related protein 6)互作, 促进H2A.Z在HY5靶基因上的占位来调控其表达, 进而调控光形态建成(Mao等2021)。CRY1还可以与G-蛋白β亚基AGB1 (GTP-binding protein beta1)互作, 促进HY5与AGB1的解离, 正向调节HY5的DNA结合活性, 从而促进光形态建成(Lian等2018)。

除COP1-CO途径, CRY通过多种机制调控拟南芥开花时间。CRY2以蓝光依赖的方式与bHLH转录因子CIB1结合, 上调其转录激活活性和*FT* (*flowering locus T*)基因表达, 从而调控光周期开花(Liu等2008a; Meng等2013)。CRY2还通过与开花负调控因子TOE1 (target of early activation tagged 1)和TOE2发生蓝光依赖的互作, 来促进CO的功能及*FT*的转录, 从而促进开花(Du等2020)。CRY2可以通过与CIS1 (CRY2-interacting splicing factor 1)的蓝光依赖性互作, 促进低温长日照条件下的开花(Zhao等2022b)。此外, 蓝光激活的CRY2表现出类似转录因子的活性并直接结合DNA来激活*FT*转录, 进而促进开花(Yang等2018b)。高氮可能通过上调AMPK激酶的活性, 促进定位于细胞核内的CRY1的磷酸化和降解, 而抑制开花(Yuan等2016)。

CRY通过直接或间接影响PIF蛋白的活性介导弱蓝光诱导的避荫反应(de Wit等2016b; Pedmale等2016)。首先, CRY能直接与PIF4和PIF5发生蓝光特异的互作, 在弱蓝光条件下, 由于CRY的活性降低而释放了对PIF的直接抑制作用, 从而促进避荫反应(Ma等2016; Pedmale等2016)。PIF4蛋白能够直接靶向并促进其自身基因表达, CRY1功能缺失导致*PIF4*转录水平上调, 这种正反馈调控有可能增加植物避荫反应对弱蓝光的敏感性(Zhai等2020)。其次, CRY在蓝光下能够通过与SPA1互作抑制COP1的活性, 从而保护转录因子HFR1 (long hypocotyl in far red 1) (Liu等2011a; Pacin等2016)。而HFR1能直接与PIF发生蛋白互作并抑制PIF的转录活性(de Wit等2016a)。因此, 在弱蓝光条件下, CRY失去对COP1的抑制作用而导致HFR1的降解, 结果进一步释放PIF的转录活性并促进避荫反应。

2.3 CRY介导蓝光信号与植物激素和温度信号互作的分子机制

蓝光信号一方面通过促进CRY1与AUX/IAA (auxin/indole-3-acetic acid)蛋白互作, 来抑制生长素诱导的AUX/IAA蛋白降解(Xu等2018), 另一方面通过促进其与ARF6 (auxin response factor 6)和ARF8互作来抑制对下游靶基因的结合能力, 从而抑制生长素信号转导(Mao等2020); CRY1通过与BES1 (BRI1-EMS-suppressor 1)互作来抑制其DNA结合能力和靶基因的表达, 从而实现蓝光信号对油菜素内酯BR信号转导的抑制 (Wang等2018b); CRY1还可以与DELLA蛋白和赤霉素GA受体GID1 (GA-insensitive dwarf1)互作, 抑制GA-GID1-DELLA复合体形成, 解除GA诱导的DELLA蛋白的降解, 进而实现蓝光信号对GA信号转导的抑制(Xu等2021; Zhong等2021)。

CRY1在高温下以蓝光依赖的方式与PIF4互作来下调其活性和生长素合成, 抑制拟南芥下胚轴伸长(Ma等2016)。冷胁迫相关蛋白COR27和COR28与HY5互作平衡植物发育与抗寒性(Li等2020c)。低温增强CRY2与COP1的互作, 从而减弱对HY5的泛素化降解, 同时导致B-box转录因子BBX7和BBX8大量表达增强植物的抗冻性(Li等2021c)。CRY2在参与温度响应的同时其丰度也受到温度调控, 低温导致CRY2与E3泛素连接酶LRB的相互作用增强和蓝光依赖性的泛素化降解(Ma等2021)。

2.4 CRY调控生物钟和对地磁场响应的分子机制

在调控生物钟节律方面, CRY2直接与生物钟核心组分PRR9 (pseudo response regulator 9)以蓝光

依赖的方式发生互作(He等2022), 或者通过与转录因子TCP22 (teosinte branched 1-cycloidea-PCF 22)互作在植物细胞中形成蓝光依赖的光小体, 间接调节生物钟核心组分*CCA1* (*circadian clock associated 1*)基因的表达(Mo等2022)。此外, CRY2通过影响信使RNA的m^6A甲基化修饰参与调节昼夜节律。蓝光激活的CRY2经历液-液相分离(LLPS)凝聚成光小体, CRY2同源四聚体与m^6A甲基化读写器亚基MTA、MTB和FIP37 (FKBP12-interacting protein 37)互作调节生物钟相关基因的m^6A甲基化修饰。CRYs和MTA功能缺失均加速*CCA1*基因的mRNA降解并导致生物钟周期延长(Wang等2021b)。

与动物相似, 植物也对地球磁场的变化产生应激反应(Paponov等2021), CRYs被认为是负责动物光依赖性磁接收的候选蛋白(Karki等2021)。有证据表明, 植物CRY参与静磁场(SMF)促进的根生长(Jin等2019)。外部施加磁场增加了CRY的磷酸化水平, 从而增强了对下胚轴伸长的抑制作用(Pooam等2019)。借助量子生物学的研究手段预测地球磁场(MF)可能通过调节活性氧来调节CRY的功能(Pooam等2020)。磁受体*MagR*基因广泛存在于人类、植物和微生物的基因组中, 其编码蛋白与CRY的相互作用是高度保守的, 在鸽子体内会形成磁传感器复合物(MagS)来感知地磁。拟南芥中至少存在四种MagR同源蛋白ISCAs, 并可能与CRY互作形成植物磁感应的蛋白复合体(Parmagnani等2022)。

3 紫外光B信号途径

紫外光是太阳光组分之一, 根据波长不同分为三种: 315~400 nm的UV-A、280~315 nm的UV-B [其中311~313 nm的波段被称为窄波段(narrowband) UV-B, 全波段被称为broadband UV-B]、波长<280 nm的UV-C。UV-B对植物来说是把双刃剑, 低强度的UV-B能够调控植物光形态建成, 如促进子叶张开和花青素积累, 抑制下胚轴伸长等, 而高强度的UV-B则造成植物胁迫和损伤, 如抑制光合作用等, 严重影响植物生长发育。

3.1 UV-B受体UVR8的发现及其感知UV-B的分子机制

UVR8是一个β螺旋蛋白, 是UV-B的光受体, 最先在筛选拟南芥对UV-B超敏感突变体里被发现。在没有UV-B的条件下, UVR8以同源二聚体形式存在, 接受UV-B照射后, UVR8二聚体迅速解离, 形成单体, 这一过程依赖于UVR8生色团上的一个色氨酸残基(Heijde和Ulm 2013)。2012年, UVR8的晶体结构被解析, 揭示了UVR8受体感知UV-B信号的机制(Wu等2012; Christie等2012)。UV-B诱导UVR8单体化后, UVR8能够由单体重新聚合成二聚体, 从而关闭UV-B的信号通路(Heijde和Ulm 2013; Heilmann和Jenkins 2013)。

3.2 UVR8介导的UV-B信号转导

UVR8定位于细胞质和细胞核, 蛋白总量不受UV-B和其他光质的影响。当植物受到UV-B照射后, UVR8二聚体会解聚形成单体并在细胞核内积累。URV8-COP1-HY5是研究早期发现的UVR8介导UV-B信号通路的经典途径(Heijde和Ulm 2012)。UV-B促进UVR8核内积累需要COP1。细胞核中的UVR8单体与COP1互作, 解除COP1对HY5的降解, HY5作为转录因子调控UV-B响应基因的表达。UV-B激活的UVR8单体与COP1-SPAs复合体的底物HY5竞争性结合COP1-SPAs复合体。UVR8与COP1的WD40结构域形成两个互作界面, 这两个互作界面是UVR8和COP1互作以及竞争COP1-SPA底物HY5所必需的(Wang等2022f)。

UVR8能够直接与转录因子相互作用来调节转录。UVR8能够和BR信号通路中的重要转录因子BES1/BES1-INTERACTING MYC-LIKE 1 (BIM1)结合, 进而抑制它们的DNA结合能力而抑制基因表达及下胚轴伸长(Liang等2018)。UVR8还可以通过直接结合转录因子WRKY36而调控*HY5*基因转录及下胚轴伸长, 在UV-B条件下, UVR8的C端可以和WRKY36的C端互作解除WRKY36对*HY5*的抑制, 从而表现为UV-B下下胚轴短的表型, 促进UVR8介导的光形态建成(Yang等2018d)。UV-B还可以通过调控MYB13转录因子的转录活性从而促进UV-B下子叶发育和植物对UV-B的耐受性(Qian等2020)。UVR8能够快速且持续地与多个转录因子共同调控下游基因表达(Qian等2020)。研究发现UV-B不仅调控植物地上部的光形态建成, 还可以调控地下部分侧根的生长发育。UV-B激活的

UVR8直接结合并抑制转录因子MYB73/77对下游生长素相关基因的结合, 从而抑制生长素响应及侧根的发育, 调控植物地下部对UV-B的响应(Yang和Liu 2020c; Yang等2020d)。这些新调控因子的发现也暗示了UV-B光信号和激素信号通路密切相关, 共同调控植物生长发育和环境适应性。

BR信号通路中激活的BES1不仅调控了UV-B光形态建成, 而且可以介导植物生长和UV-B胁迫反应之间的平衡。当植物受到宽波段的UV-B辐射后, UV-B胁迫不仅可以通过依赖UVR8的形式激活UVR8-COP1-HY5通路, 还能以不依赖UVR8的方式抑制*BES1*基因表达, 从而解除BES1对*PFG* (*production of flavonol glycosides*)基因的抑制效应, 进而促进黄酮类等防晒化合物的积累, 从而保护植物免受UV-B胁迫(Liang等2020)。

UV-B信号通路也存在负反馈调控, WD40蛋白RUP1 (repressor of UV-B photomorphogenesis 1)和RUP2是高度同源的两个蛋白, 它们都受UV-B的诱导, 是UVR8介导的UV-B信号通路中的负调节因子, 它们都能够直接通过其WD40结构域和UVR8相互作用(Gruber等2010)。RUP1和RUP2蛋白可以促进UVR8单体聚合为二聚体。在UV-B照射下, UVR8二聚体会解聚形成单体, 但二聚体和单体的转换是动态的过程, 在UV-B照射一段时间后UVR8单体又能重新二聚化, RUP1和RUP2参与UVR8的重新二聚化, 其对UV-B响应形成一个负反馈机制(Heijde和Ulm 2012; Jenkins 2014)。研究发现RUP2与持续激活单体形式的$UVR8^{W285A}$有两个互作界面, RUP2的WD40结构域与UVR8的C27 (UVR8蛋白C端27个氨基酸)结构域为第一个互作界面, RUP2的WD40结构域与UVR8核心结构域为第二个互作界面, 这两个互作界面对RUP2与UVR8互作及促进UVR8由单体向二聚体转变非常重要(Wang等2022d)。RUP1/RUP2和HY5蛋白互作, 并且RUP1/RUP2可以和CUL4-DDB1 (cullin 4-damaged DNA-binding protein1)组装成泛素连接酶复合体从而介导HY5蛋白降解, 抑制光形态建成(Ren等2019)。同时RUP2是植物开花途径中的负调控因子, RUP2可以和CO蛋白互作, 抑制CO对*FT*启动子的结合活性与转录, *rup2*突变体表现在短日照早花, 这一表型受到UV-B诱导但不依赖于UVR8 (Arongaus等2018)。

3.3 UV-B信号通路和其他信号通路的联系

一方面UV-B抑制生长素合成基因YUC (*YUCCA*)和响应基因*IAA29* (*indole-3-acetic acid inducible 29*)的表达抑制生长素信号通路, 另一方面UVR8和COP1通过调控HY5/HYH进而调节*GA2ox1* (*GA2 oxidase 1*)基因的表达, 抑制GA的产生, 稳定了DELLA蛋白, 进而促进PIF蛋白的降解, 并且UV-B本身就可以促进PIF蛋白降解, 故而UV-B通过抑制生长素和赤霉素信号通路抑制植物避荫反应(Sharma等2019; Tavridou等2020)。TPI (trypsin proteinase inhibitor)蛋白是JA (jasmonic acid)信号途径中的关键抵御蛋白, UV-B可以促进*TPI*基因的转录, 不影响JA的含量, 但是可以通过提高植物对JA的敏感性帮助植物抵抗虫子进食的伤害(Demkura等2010)。

植物在高温下呈现热形态建成的表型, 在20℃下, UV-B通过UVR8-COP1抑制*PIF4*的转录和PIF4蛋白积累, UV-B也会促进HFR1蛋白的积累。在28℃下, 高温促进HFR1蛋白的积累, UV-B通过UVR8-COP1稳定HFR1蛋白, HFR1蛋白进而抑制PIF4的转录活性, 因此, UV-B通过抑制PIF4的蛋白积累和转录活性进而调控热形态建成(Hayes等2017)。

植物和动物细胞感受UV-B后会引起脱落酸(ABA)浓度的增加, 细胞质中钙离子浓度升高, 钙离子作为第二信使会提高NOS (NO synthase)合成酶的活性从而促进一氧化氮(NO)的合成。NO在动植物对UV-B的适应和抗氧化反应发挥重要作用(Tossi等2012)。UV-B通过UVR8促进气孔关闭, 这一过程通过调节硝酸还原酶活性来调控植物体内NO含量, NO通过抑制保卫细胞质膜上的钾离子通道, 促进氯离子通道的打开从而促进气孔关闭(Tossi等2014)。UV-B可以通过UVR8的信号通路来调节ABA信号通路中的响应因子, 从而调节植物体内H_2O_2和NO含量, 具体和ABA信号通路存在怎样的联系仍有待研究。

4 光信号转导中的共性调控机制

近十年, 大量文献报道了光信号可作用于多个分子层面, 包括转录水平、转录后水平、蛋白质翻译及翻译后水平调控基因表达, 从而影响植物生长发育。

4.1 转录水平调控

光信号主要通过介导染色质结合因子的表达、亚细胞定位与活性调控下游靶基因转录。已发现的重要染色质结合因子主要包括转录因子与转录共调控因子、组蛋白修饰调控因子与染色质重塑因子、非编码RNA与RNA结合蛋白三类。

HY5/HYH、PIF家族转录因子和BBX家族转录因子等可同时作用于多个光信号转导通路调控基因表达。转录因子可通过与靶基因区DNA直接互作, 调控光信号相关基因表达。研究发现HY5/HYH (HY5 homolog)可识别靶基因启动子含有G-box (CACGTG)或E-box (ACGT)等顺式作用元件区域, 在已发现的上千个靶基因中, HY5还可以结合在*COP1*和*SPAs*等基因的启动子上, 促进这些基因的转录。此调控可与已知的COP1/SPA复合体调控形成负反馈, 共同影响植物幼苗见光过程中子叶开角、延展与变绿速率及下胚轴伸长抑制等(Huang等2012; Xu等2016b; Zhang等2017c; Burko等2020)。PIF家族转录因子在光信号介导的基因转录调控中, 既有功能冗余也有单个PIF蛋白的独特作用(Oh等2014; Pfeiffer等2014; Paulisic等2021; Burko等2022)。PIF蛋白能够特异性识别G-box顺式作用元件, 在黑暗条件下结合并促进靶基因转录, 进而调控暗形态建成。人们发现了一系列影响PIF转录活性的调控因子。例如: 光激活型phyB可阻碍PIFs对于靶基因的结合, 从而抑制PIFs转录激活活性(Park等2012); ABI5 (ABA insensitive5)可促进PIF1与G-box所在染色质区域的结合(Kim等2016); 黑暗条件下, PIFs可促进*PIL1* (*PIF3-like 1*)和*HEC2* (*HECATE 2*)转录; 而光照条件下, PIL1和HEC2可通过直接互作阻碍PIFs结合靶基因(Luo等2014; Zhu等2016)。TCP4与PIF3可特异性调控黄化幼苗子叶见光打开进程(Dong等2019)。BBXs可作为HY5的转录共调控因子, 促进HY5转录激活作用(Xu等2016a; Bursch等2020)。由此可见, 不同类型的转录因子之间, 可协同、拮抗或以反馈环路方式参与光信号介导的转录调控。

表观修饰因子可由特定转录因子招募至靶基因位点进而参与光信号介导的转录调控。组蛋白修饰酶可参与光信号介导的基因转录调控。组蛋白去乙酰化酶HDA15可分别由PIF1、PIF3、HY5和NF-YC等招募至靶基因, 降低其乙酰化水平, 调控特定光信号相关基因转录, 实现光控种子萌发和幼苗下胚轴生长与叶绿素合成等进程的调控作用(Liu等2013b; Gu等2017; Tang等2017; Zhao等2019)。HY5可招募组蛋白去乙酰化酶HDA9至细胞自噬相关基因并抑制其转录, 从而抑制光照条件下细胞自噬过程(Yang等2022); 组蛋白变体可参与光信号介导的基因转录调控。已发现INO80、PIF7-EEN、phyB-SWC6/ARP6和CRY1-SWC6/ARP6等调控模块, 可介导组蛋白变体H2A.Z在靶基因染色质区的掺入, 能够参与光信号相关基因的转录调控, 实现对于下胚轴长度的控制(Yang等2020a; Mao等2021; Wei等2021; Willige等2021)。染色质重塑因子可参与光信号介导的基因转录调控。在光照下, CHD3类染色质重塑因子PKL与HY5直接互作, 调控靶基因H3K27me3甲基化修饰水平; 在黑暗下, PKL则可与PIF3和BZR1 (brassinazole-resistant1)等直接互作, 调控靶基因H3K27me3修饰水平, 从而平衡幼苗见光过程中相关基因的转录水平, 实现不同光照环境下对幼苗下胚轴长度的调控(Jing等2013; Zhang等2014a)。SWI/SNF类染色质重塑因子BAF60 (BRG1/BRM-associated factor 60)可在光照条件下结合在含有G-box的低核小体密度染色质区, 阻碍PIF4对下游靶基因的结合, 实现下胚轴伸长抑制作用(Jegu等2017)。NuA4复合体亚基EPL (enhancer of polycomb)可在光合组织中受光信号诱导表达, 提高叶绿体转录相关基因H4K5ac乙酰化修饰水平, 实现对于叶绿体发育进程的调控(Barrero-Gil等2022)。

microRNA (miRNA)和长链非编码RNA (lncRNA)可参与植物光信号介导的转录调控。miRNA可通过序列互补与靶基因直接互作, 以介导靶基因转录本切割和翻译抑制两种方式, 在转录后水平调

控靶基因表达。PIFs可直接结合到特定miRNA如miR156基因启动子区并调控其表达(Xie等2017)。光信号可通过光受体促进维持miRNA稳定性的HEN1 (HUA enhancer1)表达进而促进miRNA的积累, 同时miRNAs前体及加工复合体核心组分的表达也受到光信号的调控(Tsai等2014; Choi等2020)。水稻(*Oryza sativa*)光敏色素OsphyB可调控miRNAs表达, 影响水稻生长(Sun等2015b)。植物特有的非编码RNA *HID1* (*hidden treasure1*)可参与光控种子萌发、幼苗暗见光变绿和光控幼苗下胚轴伸长抑制等调控(Wang等2014, 2018c, 2023c)。

4.2 转录后水平调控

转录后层面的调控主要包括mRNA前体的可变剪接、mRNA的修饰及稳定性和RNA编辑三个方面。

可变剪接是增强生物蛋白质组多样性的一种主要转录后调控机制。光作为重要的环境因子参与调控植物基因组可变剪接(Mancini等2016; Zhang等2017b; Cheng和Tu 2018; Kathare和Huq 2021)。红光处理1 h, 拟南芥基因组6.9%的基因可变剪接发生改变, 且大多为剪接因子和转录因子(Shikata等2014)。在小立碗藓(*Physcomitrella patens*)光形态建成过程中, 光可调控内含子保留这一类别的可变剪接事件促进光合及翻译相关因子表达(Wu等2014)。光信号可通过调控光受体与剪接因子的互作及转录延伸的速率两种方式调控基因可变剪接(Godoy Herz等2019), 例如小立碗藓光受体PpPHY4 (phytochrome 4)与剪接因子PphnRNP-H1 (heterogeneous nuclear ribonucleoprotein H1)互作会影响U1 snRNP (U1 small nuclear ribonucleoproteins)的组装(Shih等2019); PpPHY4和PphnRNP-F1互作调控光响应基因的内含子保留促进其表达, 进而正调控光形态建成(Lin等2020); 拟南芥活化形式phyB与剪接因子SFPS、SWAP1及RRC1互作形成复合体调控*PIFs*、*COP1*和*PHOT1*等靶基因剪接(Xin等2019; Kathare等2022); 光下PHYB与SMP2 (swellmap 2)互作通过调控*REV8* (*reveille 8*)剪接间接促进*PIF4*表达, 进而促进下胚轴伸长(Yan等2022); CRY2与剪接因子CIS1 (CRY2-interacting splicing factor 1)互作调控*FLM* (*flowering locus M*)剪接进而调控植物开花(Zhao等2022b)。此外, 剪接因子UAP56 (U2AF65 associated protein56)可在核内与COP1互作, 结合小核RNA共同调控可变剪接参与拟南芥光暗形态建成(Li等2022d)。

m^6A (N^6-methyladenosine)是生物体内广泛存在且可逆的一种RNA修饰, 对于植物生长发育非常重要。研究发现FIONA1 (U6 small nuclear RNA (adenine-(43)-N6)-methyltransferase)可作为甲基转移酶对底物mRNA进行m^6A修饰, 调控*PIFs*基因mRNA的稳定性, 进而调控持续红光及远红光条件下的下胚轴伸长(Wang等2022b); 另一个m^6A甲基转移酶VIR (virilizer)介导*HHL1* (*hypersensitive to high light1*)、*MPH1* (*maintenance of PSII under high light1*)和*STN8* (*state transition8*)等光保护基因的m6A修饰, 增加mRNA稳定性并促进蛋白翻译, 帮助植物完成强光条件下的光保护(Zhang等2022)。甲基转移酶MTA (mRNA adenosine methylase)、MTB (methyltransferase B)和FIP37 (FKBP12-interacting protein 37)可与活化的CRY2在核内互作, 通过调控底物*CCA1*的m^6A修饰水平参与调控植物昼夜节律(Wang等2021b)。

RNA编辑是广泛存在于生物体的一种核苷酸插入、缺失或替换的现象, 其中植物叶绿体基因组C→U的替换较为典型。叶绿体RNA编辑对于基因正常表达非常重要, 且编辑位点主要位于基因编码区。研究表明PPR (pentatricopeptide repeat protein)、MORF (multiple organellar RNA editing factor)、ORRM (organelle rna recognition motif protein)、PPO1 (protoporphyrinogen IX oxidase 1)和OZ1 (organelle zinc finger 1)等因子参与调控叶绿体RNA编辑, 叶绿体RNA编辑异常会影响细胞器的生物发生, 使植物出现叶片白化、生长速率减慢和光合效率下降等多种表型(Zhang等2014b; Sun等2015a; Hackett等2017; Yan等2017, 2018; Small等2020)。

4.3 翻译水平调控

随着核糖体印记与蛋白质组学等分子生化技术在植物研究体系中的发展与完善, 直到2012年人们才开始在组学水平系统发现光信号可介导数千个基因在翻译水平上的表达变化(Liu等2012; Juntawong和Bailey-Serres 2012)。光信号在翻译层面

的调控主要分为翻译组学水平的调控和选择性调节特定类别蛋白质翻译两个方面。

已有报道显示光信号可介导蛋白翻译组变化调控植物幼苗的光形态建成。利用核糖体图谱技术鉴定了拟南芥黄化幼苗经短暂光照后翻译发生显著变化的mRNA, 发现光可优先增强核糖体蛋白编码基因与光合相关基因的翻译, 这可能是光促使幼苗发育早期整体翻译效率增强的原因之一(Liu等2012, 2013a; Akagi等2023)。光信号转导中的核心抑制因子COP1在光诱导的翻译调控过程中发挥重要作用。COP1可通过抑制生长素对雷帕霉素靶标TOR的激活进而抑制其下游信号分子RPS6 (ribosomal protein S6)的磷酸化, 最终阻碍了mRNA的翻译起始和蛋白质合成。而当植物感受到远红光或者蓝光信号时, 活化形式的phyA和CRY通过抑制COP1的活性间接促进了“生长素-TOR-S6K-RPS6”信号通路, 从而提高新生蛋白质的合成效率以促进植物光形态建成(Chen等2018)。一些基因5′UTR区域包含短开放阅读框(uORF), 可以通过竞争性结合核糖体等方式抑制下游编码区的翻译效率, 研究发现uORF可作为一个光信号响应开关介导植物光形态建成中蛋白翻译组变化(Liu等2013a; Kurihara等2018)。

另外, 光信号可以通过选择性精细调控蛋白翻译影响植物幼苗的生长发育。如Paik等人证实, 光敏色素phyA和phyB通过与细胞质定位的锌指蛋白PENTA1 (PNT1)相互作用进而抑制原叶绿素氧化还原酶A (PORA, protochlorophyllide oxidoreductase A)基因mRNA的翻译, 以控制黄化幼苗子叶的正常变绿(Paik等2012)。另外, 胞质中由mRNA和核糖核蛋白聚集组成的复合物“P小体” (processing bodies)通过选择性调控光形态建成促进因子的蛋白翻译来精确调控幼苗发育(Jang等2019)。光信号还可以通过促进HYL1 (hyponastic leaves1)和DCL1 (dicer-like1)的蛋白翻译来调节miRNA加工, 从而精确调节光形态建成(Kurihara等2019)。此外, 强光胁迫也参与了植物体内蛋白质的翻译调控。当植物突然遭到强光照射时, 植物吸收的光能远超光合作用的消耗就会导致叶绿体产生大量过氧化氢, 而这部分积累的活性氧则会快速激活GCN2 (general control non-derepressible2)的活性, GCN2作为翻译起始因子eIF2α的磷酸化激酶, 显著影响胞质中mRNA的翻译, 使得植物适应过量光照的胁迫(Lokdarshi等2020)。

4.4 翻译后水平调控

光信号可在蛋白翻译后水平调控基因表达, 主要通过泛素化修饰、磷酸化和SUMO化修饰影响蛋白亚细胞定位、蛋白稳定性与体内功能发挥。

蛋白质泛素化修饰在植物光信号转导中发挥重要作用。一系列光形态建成抑制因子COP/DET/FUS可在植物体内形成COP1复合体、CSN复合体(COP9 signalosome, CSN)和CDD (COP10、DDB1和DET1)复合体, 通过泛素/26S蛋白酶体途径降解HY5、LAF1 (long after far-red light1)和HFR1等光形态建成促进因子(Lau和Deng 2012)。近年来的研究不断拓展与完善人们对于COP1-SPA复合体蛋白的表达与活性调控机制。例如, 暗中E3泛素连接酶CSU1 (COP1 suppressor1)可在细胞核降解COP1 (Xu等2014b)。暗中COP1在细胞核内的表达不依赖SPA蛋白, 但光下COP1从细胞核向细胞质转运依赖SPA蛋白(Balcerowicz等2017)。此外, 光下乙烯可促进COP1入核, 降解HY5进而促进下胚轴伸长(Kieber等2013)。同时, 一系列COP1的调控因子被鉴定, 例如: CSU2可在核内与COP1互作抑制COP1泛素化的功能, 从而促进HY5积累(Chen等2015b); PIF1可与COP1/SPA复合体互作增强COP1对底物的招募和泛素化能力(Xu等2014c); PID (pinoid)可与COP1互作并磷酸化COP1第20位丝氨酸进而抑制COP1的活性(Lin等2017); SIZ1可介导COP1第193位赖氨酸发生SUMO 化修饰, 进而增强COP1的活性(Fang等2021)。同时, COP1可介导SIZ1泛素化修饰, 促进SIZ1降解(Lin等2016)。此外, COP1除以E3连接酶发挥功能外, 还可与BIN2互作, 抑制BIN2对PIF3的磷酸化修饰, 进而增强PIF3蛋白稳定性, 促进暗形态建成(Ling等2017)。

蛋白磷酸化和SUMO化修饰在植物光信号转导调控中非常重要。活化形式的光敏色素可在自磷酸化后介导PIF蛋白降解(Shin等2016)。此外, PPKs、SPAs、BIN2和MPK6等也可作为激酶在光照条件下介导PIF蛋白磷酸化降解(Ling等2017; Ni

等2017; Xin等2018;Paik等2019)。光受体和转录因子也会受到SUMO化修饰调控。研究表明SIZ1通过介导phyB的SUMO化修饰来抑制phyB和PIF蛋白的互作(Bernula等2021); SUMO化的PIF3蛋白活性减弱从而促进植物光形态建成; 远红光下SUMO蛋白酶ASP1通过调控FHY1去SUMO化, 增加FHY1蛋白在细胞核的积累, 进而促进拟南芥下胚轴伸长(Qu等2020; Bernula等2021)。

5 光信号与激素信号互作

光信号通路与多种植物激素信号通路存在多个层面的紧密联系, 共同调控植物对光环境变化的响应。光与激素的交叉反应研究也极大提高了人们对植物如何在生长发育中整合外源环境信号与内源激素这一机制的认识。

5.1 光与乙烯

在土壤中萌发生长的拟南芥幼苗处于黑暗环境, 表现出顶端弯钩、闭合的子叶和伸长的下胚轴等结构特征, 这些特征能够保护植物幼苗的子叶和顶端分生组织等重要结构安全、快速地突破土壤。研究表明, 在土壤覆盖下幼苗产生大量乙烯气体稳定乙烯信号通路关键转录因子EIN3 (ethylene-insensitive 3)蛋白, *ein3*缺失突变体幼苗表现出明显的出土缺陷(Zhong等2014)。土壤覆盖的暗环境下, COP1通过降解EBF蛋白, 稳定EIN3, 促进植物幼苗在土壤中出土的存活能力(Shi等2016a)。EIN3和光信号通路的转录因子PIF3表现出了高度的协作, 以相互独立、互不依赖的方式调控暗形态建成(Shi等2018); EIN3和PIF3共同促进*HLS1* (*hookless1*)基因的转录, 促进暗下黄化苗的顶端弯钩结构的形成(Shi等2018; Zhang等2018b)。此外, 乙烯和PIF3可以促进微管结合蛋白MDP60 (microtubule-destabilizing protein 60)的表达, 从而调控下胚轴细胞中微管的排布方向和方式以及下胚轴的伸长(Ma等2018)。

当植物幼苗破土而出接受光照后, 表现出子叶打开并扩展、子叶变绿、顶端弯钩打开等特征, 在这些形态变化调控过程中, 光信号通路和乙烯信号通路同样存在复杂的相互作用。研究发现, 红光受体phyB在见光后进入细胞核, 通过增强EBFs与EIN3的相互作用, EIN3蛋白迅速降解, 促进了子叶的打开和发育(Shi等2016b)。进一步研究发现, 幼苗突破土壤的过程中一类微蛋白miP1a/b蛋白表达量迅速上升, 并通过解聚转录因子PIF3和EIN3四聚体的方式抑制了转录因子与启动子区域结合的能力, 从而促进光形态建成(Wu等2020); phyB可以通过抑制顶端弯钩形成的重要因子HLS1蛋白多聚体的产生, 抑制HLS1的功能, 促进顶端弯钩的打开(Lyu等2019)。在调控子叶变绿方面, PIF3和EIN3相互作用形成调控复合体, 以相互依赖的方式在黑暗下抑制各类光合作用相关基因的表达, 保证了子叶中质体能够以适应环境的方式发育, 促进植物的变绿(Liu等2017b)。此外, 在植物营养生长过程中, 光信号通路的FHY3和EIN3可以共同调控*PHR1* (*phosphate starvation response 1*)基因的表达水平, 促进磷饥饿反应(Liu等2017c); 在低温胁迫的反应中, PIF3和EBF1共同参与低温反应重要的组分CBF家族基因的转录水平, 从而调控植物在低温环境下的生长(Jiang等2017)。

5.2 光与生长素、赤霉素

生长素与赤霉素对植物形态建成具有重要调控作用。近年研究发现, 光信号通过PIFs调节下胚轴中生长素的水平, 调控幼苗去黄化过程中下胚轴生长和子叶打开(Sun等2016)。SAURs (small auxin-up RNAs)拮抗PP2C-D1的活性, 调节幼苗去黄化过程中顶端弯钩打开和子叶扩展(Wang等2020c)。UDP-糖基转移酶能够促进生长素合成前体IPyA的糖基化, 调节生长素水平进而调控生长素稳态, 该过程受到PIF4负调控(Chen等2020)。SEU (seuss)转录调控因子与PIF4互作促进PIF4与生长素相关基因的结合, 调节IAA水平, 整合光温信号控制植物生长(Huai等2018)。光与生长素的交叉互作还发生在受体层面, 研究发现CRY1/phyB与TIR1 (transport inhibitor response1)竞争性结合AUX/IAA, 增加AUX/IAA稳定性, 激活生长素信号, 调节植物在光下生长(Xu等2018)。phyA与TIR1竞争结合AUX/IAA, 激活生长素信号, 调节植物在避荫条件下生长(Yang等2018a)。在高红光/远红光比例条件下, COL7 (CO-like7)以phyB依赖的方式, 促进生长素合成抑制因子SUR2 (superroot 2)的表达, 促进植物的分枝(Zhang

等2014d)。此外, 光通过HY1-HY5/HYH-PIN1/2模块调控生长素转运蛋白在细胞内的定位和表达, 促进生长素积累进而调节侧根的形成(Duan等2021), 而紫外光调控UVR8与MYB73/77互作抑制MYB73/77对生长素相关基因*IAA19*的转录激活, 抑制生长素反应调节侧根生长(Yang等2020d)。PIF5/4和ARF2互作, 调控衰老通路基因表达进而调节植物衰老过程(Xue等2022)。

赤霉素是促进种子萌发的主要内源激素, 研究发现phyB介导的光促进种子萌发可以被转录因子REVs抑制, REVs通过抑制赤霉素的生物合成影响种子萌发(Jiang等2016)。蓝光下, CRY1通过蛋白互作促进DELLA积累, 抑制PIFs对生长相关基因的转录激活, 促进光形态建成(Xu等2021)。染色质重塑因子PKL与PIF3互作, 调控植物暗形态建成; GA_3通过DELLA抑制PKL与细胞伸长基因的互作, 调控植物光下生长发育(Zhang等2014a)。CRY1以蓝光依赖的方式与GID1互作, 促使DELLA蛋白积累降解PIFs, 抑制细胞伸长基因表达进而促进植物光形态建成(Zhong等2021)。大豆(*Glycine max*)蓝光受体GmCRY1s增加bZIP转录因子STFs (soybean TGACG-motif binding factors)的丰度, 上调编码GA2氧化酶基因表达, 使GA_1失活并抑制茎伸长(Lyu等2021)。

5.3 光与脱落酸、茉莉酸

脱落酸(ABA)是抑制种子萌发的主要内源激素。研究发现, 远红光可以通过phyB-PIF1模块和phyB-RVE1/2模块调节脱落酸和赤霉素之间的拮抗作用, 进而调控种子休眠与萌发; 当植物处于黑暗时, COP1通过转录和翻译后的调节机制介导ABA诱导下游转录因子ABI5的积累, 抑制种子萌发(Shi等2013, 2015; Jiang等2016; Yang等2020b)。黑暗条件下COP1能够泛素化ABD1 (ABA-hypersensitive DCAF1)从而促进ABI5的积累, 且ABA可以促进黑暗下COP1的入核, 进一步加强ABI5的积累(Peng等2022)。同时, ABA在光照下促进COP1的核积累, 暗示着在不同光照条件下, ABA可能通过不同方式调控COP1的定位(Chen等2022c)。此外, 黑暗下积累的PIF4能够直接结合*ABI5*的启动子正调控其表达, 并且ABA受体PYL8/9能与PIF4直接互作并影响PIF4转录活性(Qi等2020)。BBX21通过与HY5和ABI5蛋白直接相互作用, 抑制二者结合*ABI5*启动子的能力, 从而负调控*ABI5*表达(Xu等2014a)。幼苗去黄化是植物从异养型转为自养型的关键过程。光形态建成负调控因子DET1通过与FHY3相互作用结合在*ABI5*的启动子区, 并招募去乙酰化酶HDA6抑制*ABI5*的表达, 进而促进幼苗转绿(Tang等2013; Xu等2020)。同样, *COP1*的表达受ABI4和HY5转录模块拮抗调控, 而COP1能够在光照下直接与ABI4互作并对其降解, 从而正调控去黄化过程(Xu等2016b)。此外, ABA激活的SnRK2s可以磷酸化SWEET11/12促进其自身相互作用和转运能力, 从而促进糖分从地上部分向地下部分的转运(Chen等2022b)。

近年来, 茉莉酸(JA)在植物光形态建成的调控作用也备受关注。远红光下, phyA可以促进FIN219 (far-red insensitive 219)/JAR1 (jasmonate resistant1)的积累, 负调控COP1蛋白丰度并抑制其入核, 抑制下胚轴伸长(Wang等2011)。此外, JA通过抑制COP1与SPA1的相互作用来调控下胚轴伸长和子叶打开(Zheng等2017); MYC2促进EIN3降解并抑制其转录活性来减少*HLS1*的表达, 进而抑制乙烯介导的顶端弯钩形成(Song等2014; Zhang等2014c)。JA还参与调控光诱导的代谢物合成, 在拟南芥中, COP1抑制JA诱导的花青素积累(Li等2014); 在黄花蒿(*Artemisia annua*)中, AaMYB108可以通过和AaCOP1和AaJAZ8 (*Artemisia annua* jasmonate-zim-domain protein 8)相互作用从而整合光信号和JA信号调控青蒿素生物合成(Liu等2023)。JA是调控遮荫下生长和防御平衡的重要植物激素。FHY3与MYC2/3/4直接相互作用促进JA下游防御反应, 同时JAZ1可以与FHY3和FAR1 (far-red impaired response 1)直接相互作用并抑制其转录活性, 从而介导JA抑制的遮荫响应(Liu等2019)。遮荫下的生长和防御平衡还可以被一种磺基转移酶ST2a调控, 该酶通过催化非活性HSO4-JA的形成来减少JA下游响应, 植物通过phyB-PIF模块直接激活*ST2a*的表达, 从而促进避荫生长(Fernandez-Milmanda等2020)。

5.4 光与其他激素

油菜素内酯(BR)促进植物暗形态建成。黑暗

中BR和乙烯通过PIF、EIN3/EIL1和BZR1复合物促进维持顶端结构的基因*SAUR17*的表达(Wang等2023b)。BR缺失突变体和BR不敏感突变体幼苗转绿能力降低, 该过程需要BZR1、PIFs和GRF7 (growth-regulating factor 7)/GRF8协同调控编码叶绿素生物合成关键酶基因的表达, 进而促进幼苗变绿(Wang等2020d)。在暗下BR抑制BIN2, 在光下BIN2与转录因子GLK1 (golden-like 1)/GLK2互作并将其磷酸化, 增强其蛋白稳定性和转录活性, 激活叶绿体合成相关基因正调叶绿体发育(Zhang等2021a)。蓝光下, CRY1一方面与去磷酸化的BES1相互作用, 导致下游靶基因的转录抑制, 抑制下胚轴伸长(Wang等2018b), 另一方面, CRY1可以促进BIN2与BZR1的互作使其磷酸化抑制BZR1的功能(He等2019)。紫外光下, UV-B激活的UVR8与有功能的去磷酸化的BES1和BIM1相互作用抑制其下游调控基因的表达抑制细胞伸长(Liang等2018)。水稻细胞壁连接的受体激酶OsWAK11可以整合光信号和BR信号调控植物的昼夜生长和细胞伸长(Yue等2022)。最新一项有意思的研究发现, 绿光能够促进拟南芥下胚轴伸长, 而这一过程需要BR信号中BES1介导(Hao等2023)。

此外, HY5可以增强BR信号通路中抑制子BIN2的激酶活性从而抑制细胞伸长(Li等2020a)。E3泛素连接酶SINAT在暗下降解而光下稳定, 它降解BES1蛋白水平从而抑制BR信号通路, 促进光形态建成(Yang等2017)。有研究表明BR能够促进BBX28/29蛋白稳定性, BBX28/29与BEE1 (BR enhanced expression 1)/2/3互作正调控BR信号通路(Cao等2022)。BR信号组分也参与到了光周期调控的开花过程, BES1通过下游靶基因BEE1正调控开花, 并且BEE1可以和CRY2直接互作(Wang等2019a)。丝氨酸蛋白酶DEG9调节了细胞分裂素响应元件ARR4 (*Arabidopsis* response regulator 4)的稳定性, 作用在ARR4的上游整合细胞分裂素和光信号通路(Chi等2016)。此外, 光通过FHY3/FAR1与SPL9 (squamosa promoter binding protein-like 9)和SPL15相互作用, 抑制SPL9/15对*BRC1* (*branched 1*)的转录, 调控遮荫条件下的分枝(Xie等2020)。

6 光信号和其他环境信号互作

光照与其他的环境因子, 包括温度、水分、盐碱等, 共同影响并调控植物的生长发育。

6.1 光信号与温度形态建成

相对较高的环境温度可以调控植物的形态建成, 称为温度形态建成, 它与光形态建成存在密切的联系。phyB不但是红光受体, 而且是温度感受器。正常温度下, phyB由钝化状态Pr向活性状态Pfr转化, 抑制温度形态建成; 温度升高时, phyB由Pfr状态向Pr转化, 在细胞核中的核小体体积和数量减少, 促进温度形态建成(Jung等2016; Legris等2016)。但是人们对于phyB如何区分光照和温度两种独立信号并不清楚。最新研究表明, phyB蛋白的N端含有一段固有无序区IDR (intrinsically disordered region)即NTE, C端具有很强的寡聚化能力, 可自我聚集, 并且NTE是phyB感知温度的特异序列, 并通过液液相分离形成光小体, 实现phyB感知温度的能力(Chen等2022a)。植物生物钟EC (evening complex)复合体成员之一ELF3 (early flowering 3)也可以作为温度传感器发挥作用, 其PrD结构域(prion domain)可介导ELF3形成液-液相分离。高温促进ELF3呈液滴状分布, 由此缓解了对其靶基因的抑制作用; 当温度下降时, ELF3又可以快速由相分离状态中释放出来, 抑制其靶基因的转录(Jung等2020)。

PIF4是温度形态建成的中心枢纽因子, 形成了转录水平调控、蛋白水平调控及启动子结合和竞争等复杂的信号调控网络。高温诱导*PIF4*基因表达, PIF4蛋白可以直接激活生长素合成以及信号转导等相关基因, 例如*YUC8*和*IAA29*等, 促进下胚轴的伸长。*PIF4*在表皮中特异性的表达会诱导较长的下胚轴, 而在维管组织中的特异性表达则对于下胚轴的生长没有影响, 同时高温会增加表皮中*PIF4*的转录及其蛋白的DNA结合能力, 说明表皮中PIF4-生长素通路对于植物的温度响应是必需的(Kim等2020)。PIF4调控植物地上组织的温度形态建成, 而HY5调控根的温度形态建成, SPA1介导的磷酸化调控PIF4和HY5的蛋白稳定性, 磷酸化的PIF4蛋白更容易被降解, 而磷酸化的HY5更加稳定并可以从植物地上部分被运输到根部(Lee等2020,

2021)。该研究揭示了植物通过利用不同的转录因子以及组织特异性的方式调控温度形态建成的机制。DET1-COP1-HY5信号级联通路调控PIF4的基因表达, 从而调节温度形态建成(Delker等2014)。又有研究表明, DET1/COP1与HY5通过独立的通路调控温度形态建成, DET1/PIF4可以稳定PIF4蛋白, 并促进温度形态建成, HY5与PIF4竞争结合其靶基因的启动子, 从而抑制温度形态建成(Gangappa和Kumar 2017)。

蓝光受体CRY1也参与温度形态建成。蓝光抑制高温导致的下胚轴伸长, 这一过程依赖于CRY1, CRY1通过与PIF4以蓝光依赖的方式互作, 并抑制PIF4的转录活性, 从而影响PIF4对其靶基因*YUC8*、*IAA19*以及*IAA29*的调控(Ma等2016)。高温条件下, HEMERA蛋白也可以与PIF4互作, 促进PIF4蛋白积累及对其靶基因的激活, 从而促进温度形态建成(Qiu等2019)。

BBX18和BBX23也是温度形态建成的正向调控因子(Zhang等2017c; Ding等2018)。BBX18和BBX23与ELF3以及COP1互作, BBX18/BBX23在高温条件下可帮助COP1降解ELF3, 从而解除ELF3对PIF4的抑制作用, 促进PIF4调控温度形态建成(Ding等2018)。BBX18也可以招募E3泛素连接酶XBAT31以及XBAT35, 对ELF3进行泛素化并促进ELF3的降解, 从而解除ELF3对PIF4的抑制作用(Zhang等2021b, c)。SEU是一个新的参与光形态建成和温度形态建成的转录调控因子, 通过与PIF4互作形成转录调控复合物, 实现对植物生长发育的调控(Huai等2018)。

TCP转录因子家族TCP5、TCP13以及TCP17可以结合PIF4的启动子, 调控植物的避荫反应(Zhou等2018b)。TCP5、TCP13以及TCP17还是温度形态建成的正向调控因子, *tcp5 tcp13 tcp17*三突变体的下胚轴伸长对高温处理不敏感, 在高温条件下, TCP除了可以促进PIF4的表达, 还可以与PIF4互作并促进PIF4的转录活性(Han等2019; Zhou等2019)。另外, 正常温度下, CRY1与TCP17互作, 从而抑制TCP17-PIF4的互作, 而高温可以解除CRY1对TPC17的抑制作用, 并促进TCP17与PIF4的互作从而促进温度形态建成(Zhou等2019)。ABT1即WRKY14是一个新的温度形态建成负调控因子, 它一方面与TCP5互作, 抑制TCP5对*PIF4*的转录, 另一方面与PIF4竞争结合TCP5并抑制TCP5-PIF4复合体的形成和活性(Qin等2022)。

过去关于光温度形态建成的研究多侧重于下胚轴的伸长, 最近一项研究表明, PIF4和TCP4在环境高温下调控子叶生长(Saini等2022)。TCP4主要在子叶表达, 黑暗中, PIF3抑制TCP4对*SAUR16*及*SAUR50*的结合, 促进子叶闭合; 见光后, PIF3迅速降解, 促使TCP4结合靶基因启动子, 促进子叶展开(Dong等2019)。高温条件下, PIF4与TCP4互作, 促进细胞周期抑制基因*KRP1* (*KIP-related protein 1*)的表达, 从而在高温下抑制子叶生长(Saini等2022)。另外, 高温下, PIF4可以抑制*SPCH* (*SPEECHLESS*)基因的表达从而抑制气孔发育(Lau等2018), 这有利于人们更好地理解高温下气孔减少与散温以及过量失水的平衡。

PIF7也是一个参与温度形态建成的因子。高温条件下, PIF7可以结合到*YUC8*和*IAA29*等基因的启动子区, 从而促进下胚轴伸长(Fiorucci等2020)。PIF7蛋白合成受高温诱导, 这依赖于PIF7的5′非翻译区形成的RNA发卡结构, 这种特殊的RNA构象可随温度变化而逆转(Chung等2020)。最新研究发现, PIF7在避荫和高温双重作用下发挥主要功能(Burko等2022), 该研究为人们研究作物避荫、高温响应、密植及产量影响提供了启示。

6.2 光信号与低温信号

一些光信号因子也参与低温信号转导, 使植物更好地适应低温环境。早在2002年就有研究指出, phyB通过调控*CBF*的表达, 激活下游含*C*/*DRE*基序的低温调控基因*COR*的表达, 从而促进植物对低温胁迫的抗性(Kim等2002)。低温促进EBFs蛋白降解, 从而稳定PIF3蛋白, 而PIF3可以直接结合*CBFs*基因的启动子区, 抑制*CBFs*及其下游冷响应基因的表达(Jiang等2017)。在低温条件下, CBFs与PIF3也可以互作, 稳定PIF3与phyB蛋白。phyB稳定后, 促进了低温信号负调控因子PIF1、PIF4及PIF5的降解, 正调控植物的抗冻性, 该研究发现了CBFs蛋白通过负反馈整合光信号调控植物抵御低温的机制(Jiang等2020)。在17和24°C条件下,

CBF1促进PIF4和PIF5蛋白的积累以及下胚轴伸长, 在4℃下却不能发挥此作用, 表明CBF1对于光信号的调控依赖于温度(Dong等2020b)。

蓝光受体CYR2也参与植物的冷信号转导。低温条件下, 受蓝光激活的CRY2蛋白更加稳定, 与COP1的互作增强, 抑制了COP1对HY5蛋白的降解, HY5可以结合到*BBX7*和*BBX8*的启动子区, 激活*BBX7*和*BBX8*的基因表达, 调控下游花青素基因的表达, 从而提高植物的抗冻能力(Li等2021c)。在冷处理下, 拟南芥PFD (prefoldin)蛋白通过DELLA蛋白进入细胞核, 与HY5互作, 介导HY5的泛素化和降解, 从而抑制花青素合成相关基因的表达, 而PFD蛋白介导的HY5泛素化降解是独立于COP1降解通路的(Perea-Resa等2017)。

光信号因子在作物耐寒过程中也起着重要的作用。辣椒(*Capsicum annuum*)*PIF8*基因可以被冷和盐诱导, 在辣椒冷胁迫和盐胁迫中起着重要的作用(Yang等2021)。敲除*SlPIF4*后番茄(*Solanum lycopersicum*)植株对低温敏感, 而过表达*SlPIF4*可提高番茄的耐寒性。低温条件下, SlPIF4可激活*CBFs*以及*SlGAI4*的表达, 促进ABA、JA以及GA的生物合成及信号传递, 提高番茄的耐寒性(Wang等2020b)。冷处理也能诱导*SlHY5*、*SlMYB15*以及*SlCBFs*的表达, SlHY5及SlMYB15可以共同精确调控*SlCBFs*的表达并增强番茄的耐寒性(Zhang等2020)。在低温处理下, 远红光对番茄*SlHY5*的诱导更加明显, 沉默*SlHY5*使番茄植株对冷处理敏感, 而过表达*SlHY5*则增强其对低温的抗性(Wang等2019b)。低温、短日照以及低R/FR光比例, 也会诱导番茄*SlFHY3*的表达。SlFHY3与SlHY5互作促进了SlHY5对肌醇-1-磷酸合成酶基因*SlMIPS3*的转录激活, 从而诱导了番茄体内肌醇的积累, 肌醇可以产生多重衍生物, 增强番茄的耐寒性(Wang等2022c)。最新的GWAS分析发现番茄*SlBBX31*基因启动子区的27 bp碱基缺失突变与番茄的耐寒性有密切关系, 并且这27 bp碱基的自然缺失与番茄的长期驯化有关系。SlHY5促进*SlBBX31*的转录, 但是这27 bp的片段会干扰SlHY5对*SlBBX31*的激活(Zhu等2023)。此外, 水稻phyB负调控水稻对低温的抗性(He等2016)。

6.3 光信号与高温胁迫

高温胁迫影响植物的生长发育并减少作物产量, 关于光信号与高温胁迫的报道并不多。研究表明, *phyB*突变体可以增强拟南芥对高温的抗性, 但是具体的调控机制并不清楚(Song等2017)。在低R/FR光下, 由于phyB活性降低, PIFs丰度增高, 植物受热胁迫的损伤较小。高温胁迫下, phyB蛋白增强植物质膜的热损伤以及多不饱和脂肪酸的含量(Arico等2019)。在质膜上, 多不饱和脂肪酸含量降低有利于植物在高温下的生长。PIF4和PIF5在高温诱导的叶片衰老过程中也起着重要的调控作用。*pif4pif5*突变体延缓了高温胁迫诱导的衰老过程, 而过表达植物在高温处理下表现出早衰表型。转录组实验结果表明, PIF4和PIF5可以直接调控*NAC019*、*SAG113*及*IAA29*、*CBF2*及*BRI1*等基因的表达(Li等2021b)。研究表明, 与野生型相比, 在种子萌发以及营养生长阶段, 由于番茄*SlphyA*和*SlphyB1 B2*突变体细胞膜的稳定程度以及保水能力较强, 热应答基因均上调, 因此其抗高温的能力较强(Abdellatif等2022)。

6.4 光信号与干旱胁迫

光信号与干旱胁迫信号之间也存在紧密联系。胡萝卜(*Daucus carota*) *DcPIF3*基因受干旱和ABA诱导, 在拟南芥中过表达*DcPIF3,* 干旱处理后, 转基因植株的抗氧化能力增强, 丙二醛含量降低。*DcPIF3*促进ABA相关基因的表达并提高内源ABA的含量, 从而提高转基因拟南芥抵抗干旱的能力(Wang等2022e)。玉米(*Zea mays*) *ZmPIF1*的表达受干旱和ABA诱导, 在水稻和拟南芥中过表达*ZmPIF1*均可以减少气孔的开度以及蒸腾率, 提高转基因植株的抗旱能力。同时, 增加转基因水稻的分蘖数和穗数并提高产量(Gao等2018)。在水稻中过表达*ZmPIF3*提高了转基因水稻的相对水含量、叶绿素含量以及叶绿素荧光, 增加了细胞膜稳定性, 从而增强转基因水稻的抗旱及抗盐能力(Gao等2015)。在干旱胁迫下, 番茄*SlphyA*和*SlphyB1 B2*突变体中离子渗透率、丙二醛、过氧化氢量以及氧化损伤均降低, 相对含水量增加, 表明番茄*SlphyA*和*SlphyB1 B2*突变体提高抗旱能力主要是通过阻止

膜损伤以及增加保水量实现的(Abdellatif等2023)。

6.5 光信号与盐胁迫

高盐胁迫导致植物渗透胁迫, 造成细胞死亡, 抑制植物生长发育。最近研究表明, 光温信号关键调控因子SEU作为感受器感知渗透胁迫信号(Wang等2022a)。正常条件下, SEU处于均匀分布状态; 而高渗条件下, SEU的N端无序结构域IDR1可以迅速响应渗透胁迫, 在细胞核内发生相分离聚集成液滴, 其凝聚体可以促进渗透胁迫基因的表达, 从而提高植物抗盐及干旱的能力(Wang等2022a)。盐胁迫下, 烟草(*Nicotiana tobacum*) *NtphyA*、*NtphyB*以及其双突变体的离子渗漏率和丙二醛含量较低, 一些防御相关基因以及抗氧化酶活性较高, 因此突变体抗盐能力更强(Yang等2018c)。在水稻中过表达*OsPIL14*可以促进黑暗中水稻中胚轴的伸长, 并增强了水稻对盐的抗性以及水稻的出苗率。DELLA蛋白SLR1 (slender rice 1)与OsPIL14互作, 抑制了OsPIL14对下游细胞伸长相关基因的激活能力。盐处理促进了OsPIL14的降解, 稳定了SLR1的蛋白活性。该研究揭示了OsPIL14整合光信号和赤霉素信号调控水稻中胚轴伸长以及耐盐的分子机理, 为提高水稻耐盐性及出苗率提供了理论基础(Mo等2020)。

深入研究光信号与环境其他环境信号之间的互作, 不仅有助于完善光信号的调控网络, 还有助于通过分子设计提高植物抵抗和适应逆境的能力, 为提高作物产量提供重要的理论基础。

7 作物光形态建成

光信号对作物的生态适应性、株型、生育期、产量和品质也都具有重要的影响。自20世纪80年代以来, 模式植物拟南芥的研究为作物中的光信号研究奠定了理论基础。最近几年, 研究人员通过对作物如水稻、大豆和玉米等的关键调控因子的功能鉴定和分子机制的研究, 解析了光信号在作物中的重要作用, 为未来的分子育种以及农业生产实践提供重要指导。

光信号在水稻的形态建成和开花等生物学过程具有关键的调控作用。水稻光敏色素基因家族包括三个成员: *OsPHYA*、*OsPHYB*和*OsPHYC*。它们均参与调控水稻开花。水稻开花调控途径主要包括与拟南芥相似的保守*GI* (*GIGANTEA*)-*CO-FT*途径以及水稻特有的*OsPHYB-ELF3-Ghd7* (*grain number*, *plant height*, *and heading date 7*)/*OsPRR37-Ehd1* (*early heading date 1*)-*Hd3a* (*heading date 3a*)/*RFT1* (*rice flowering locus T1*)途径(Wang等2023a)。*OsphyA*单突变体开花时间大致与野生型相同, 说明*OsPHYA*对开花时间影响很小, 但是当*OsPHYB*与*OsPHYA*同时缺失时, *OsPHYA*主要通过在短日照条件下诱导*OsGI*的表达来促进开花和在长日照条件下诱导开花抑制因子*Ghd7*的表达来抑制开花(Lee等 2016)。最近的研究表明, OsphyB在长日照条件下被激活促进OsELF3的降解, 进一步释放OsELF3对*Ghd7*和*OsPRR37*的抑制作用从而抑制开花(Andrade等2022)。此外, OsphyA和OsphyB通过与Ghd7互作来拮抗OsGI对Ghd7的降解作用从而稳定Ghd7 (Zheng等2019)。*OsPHYC*在水稻光周期开花调控过程中功能尚不明确。*OsphyC*突变体在长、短日照条件下均呈现晚花的表型, 且*Ehd1*表达量显著降低。因此, *OsPHYC*可能通过*Ehd1*途径调控水稻开花(Lin等2022b)。蓝光受体也在调控植物开花过程中起到关键作用。研究发现OsCRY1调控水稻幼苗生长, 然而OsCRY1是否调控水稻开花尚不明确。水稻OsFKF1可以与OsGI以及OsCDF1互作来调控开花, OsZTL1和OsZTL2参与水稻开花调控的功能尚未见报道(Han等2015)。

植物通过光受体来感知邻近植物的遮荫环境。水稻中*PIF*同源基因有6个, 分别为*OsPIL11-OsPIL16*。过表达*OsPIL13*可以促进水稻节间伸长(Todaka等2012)。过表达*OsPIL14*可以促进黑暗中水稻中胚轴的伸长, 并增强了水稻对盐的抗性以及水稻的出苗率(Mo等2020)。而过表达*OsPIL15*可以抑制水稻黄化苗生长, 表明不同的*OsPIL*功能可能有差异(Zhou等2014)。

大豆是古四倍体, 具有复制而且复杂的基因组, 大豆中75%的基因都具有多重拷贝。大豆共有8个光敏色素蛋白, 包含4个GmphyA、2个GmphyB和2个GmphyE (Wu等2013)。在持续红光条件下, *GmphyB1*表现为上、下胚轴伸长, 表明*GmphyB1*参与调控红光条件下的幼苗光形态建成(Zhao等

2022a)。以上结果表明大豆的光敏色素具有和拟南芥的光敏色素保守的功能。

不同于水稻和拟南芥等其他物种以phyB为主要的调控开花途径, 大豆是基于GmphyA为主识别光周期信号调控开花的途径。GmphyA2在各种光(特别是红光)下都不稳定。GmphyA3在持续红光的条件下缓慢降解, 并且可以持续存在。长日照条件下, GmphyA3和GmphyA2通过直接结合EC复合体成员LUX (LUX arrhythmo)来降解LUX蛋白, 从而解除LUX对大豆特有的光周期调控核心基因*E1*的抑制作用, 进而延迟开花。LUX1、LUX2和J蛋白形成夜间复合体, 是调控大豆开花、光周期敏感性和光周期现象的核心(Nusinow等2011; Lu等2017; Bu等2021)。GmphyA3和GmphyA2还能与GmEID1蛋白发生光依赖的互作, 而GmEID1能与EC复合体成员J蛋白互作并促进其积累。光激活的GmphyA3和GmphyA2可以竞争性抑制GmEID1-J的互作来促进J蛋白降解, 进而上调E1的表达延迟大豆开花(Qin等2023)。此外, GmphyA2和GmphyA3还可以与E1及其同源蛋白互作来稳定E1蛋白(Lin等2022a)。在短日照条件下, GmphyA2和GmphyA3功能受到抑制, 解除GmphyA2和GmphyA3对*GmLHY1a*和*J*的抑制作用, 释放的GmLHY1a和J进一步抑制大豆开花抑制因子*E1*的表达从而促进开花(Lu等2017; Dong等2021)。大豆GmCRY2a与bHLH类型转录因子GmCIB1在蓝光下发生特异的相互作用抑制叶片衰老(Meng等2013)。GmCRY1s通过促进大豆特异的bZIP转录因子STF1/2积累, 降低内源赤霉素GA1的含量, 从而抑制大豆的避荫反应(Lyu等2021)。

大豆能够通过与根瘤菌互作形成根瘤, 进而进行共生固氮。光是影响大豆结瘤的重要因素, 大豆光受体通过捕捉光信号, 将信号转移到可移动的蛋白并运输到根瘤, 通过整合根瘤菌诱导的结瘤信号通路来调控根瘤的形成(Taylor和Menge 2018)。蓝光是促进根瘤形成的关键因子, 敲除*GmCRY1s*可以抑制根瘤的形成, 而过表达*GmCRY1s*可以促进根瘤的形成(Wang等2021a)。蓝光诱导的光信号是在茎部起源的, 并最终移动到根部。HY5与成花素FT都可以进行长距离移动, 从叶片移动到根部(Kong等2010; Chen等2016; Ji等2022; Li等2022c)。大豆中HY5的同源基因有4个, 分别为*GmSTF1~4*, 而*FT*的同源基因有十多个。研究表明*GmCRY1s*介导蓝光信号, 促进光诱导的信号蛋白GmSFT2a、GmSFT5a、GmSTF3和GmSTF4从茎部移动到根部, 相互作用调控结瘤形成(Wang等2021a; Ji等2022)。

玉米作为典型的单子叶植物, 其中胚轴在功能上类似于双子叶植物的下胚轴, 可作为光形态建成的指标。玉米基因组包含两个*ZmPHYA*, 两个*ZmPHYB*和两个*ZmPHYC*。*ZmPHYB1*在红光下对中胚轴伸长有显著的抑制作用, 而*ZmPHYB2*主要介导了玉米中光周期依赖的开花转变(Yang等2016)。当*ZmPHYB1*和*ZmPHYB2*均突变时, 玉米呈现避荫反应的特征, 即节间距变长, 早花和易倒伏的表型; 而过表达*ZmPHYA1*则导致玉米的株高和穗高增加(Sheehan等2007; Yu等2018)。过表达*ZmPHYCs*可有效降低田间玉米的株高和穗位高(Li等2020b)。*ZmPHYCs*在长日照条件下是开花抑制因子。ZmphyC可以与ZmphyB相互作用, 并且*ZmPHYBs*功能丧失后, 玉米开花时间显著提前, 表明*ZmPHYCs*被敲除后, 可能通过影响*ZmPHYBs*的功能继而促进玉米开花(Li等2020b)。此外, *zmpifs*突变体呈现出避荫反应减弱、株高和穗位高降低的表型(Wu等2019)。*ZmELF3.1*是控制玉米开花期一个主效QTL的候选基因, ZmELF3.1与多个蛋白(ZmELF4和ZmLUX)互作形成EC复合体促进玉米开花。研究还发现*ZmELF3.1*上游启动子区存在两个紧密连锁的逆转录转座子可以调控其表达, 并且在玉米由热带(低纬度)到温带(高纬度)的扩张过程中受到正向选择, 可能是玉米由热带向温带地区扩张的重要驱动力之一(Zhao等2023b)。三个同源的SPL家族转录因子UB2 (unbranched2)、UB3和TSH4 (tasselsheath4)可以响应密植带来的光信号变化, 并通过调控下游植物激素途径和其他转录因子来调控雄穗和果穗的发育, 是玉米育种的重要靶标基因(Kong等2023)。研究还发现光信号转导及开花期调控通路相关的基因在现代玉米育种过程的选择基因中明显富集, 并证明了*ZmPIF3.3*和*ZmTSH4*分别在调控玉米株高(穗位高)和雄穗分枝数方面发挥重要作用(Wang等2020a)。

8 总结和展望

光是影响植物生长发育最重要的环境信号因子之一, 不仅调控植物形态建成, 而且影响植物次生代谢、营养品质和抗性。因此, 光信号调控植物生长和发育的分子机制研究一直是植物学研究的重要科学问题。在过去十年里, 该领域的研究取得了一系列重要突破, 为进一步完善植物光信号调控网络奠定了坚实基础, 并为设计和培育具有耐密植理想株型和高光效的作物新品种提供理论指导。同时, 植物光信号转导研究为植物工厂光谱配方的打造提供理论基础和技术支撑。高度集约化和资源高效利用的植物工厂是未来农业的一个重要发展方向, 光谱配方的设计与光调控技术是植物工厂的核心。通过LED光源的光质光量光周期配比, 可以为不同植物/作物(包括蔬菜、水果、农作物、药用植物、观赏植物等)以及同一植物/作物的不同生长时期量身打造最适的光谱(Thoma等2020; Appolloni等2022), 从而在有限的能源供给下, 生产最优的植物工厂产品。因此, 今后迫切需要开展对不同植物光生物学基本规律和调控机制的深入研究, 以支撑植物工厂和未来智慧农业的发展(Van Delden等2021)。

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