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光敏色素的生物学功能及其调控

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摘 要 光是影响植物生长发育的重要因素,植物为感受光而进化出光受体。光受体分为 4 类,其中光敏色素研究较为深入,它是红光和远红光受体,在光形态建成过程中发挥着重要作用。近年来的研究阐明了光敏色素的作用模式,以及由其介导的光信号转导途径和植物发育调节过程,如下胚轴延伸、茎分支、生物钟及开花时间控制等。基于目前的研究总结光敏色素的生物学功能及其介导的光信号转导途径,并展望其研究前景,以期对相关领域研究提供参考。

关键词 光敏色素; 光信号途径; 生物学功能; 调控

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植物在整个生命周期中一直处于变化的光环境下,光质、光强及辐照度的改变均对植物生长发育产生影响^[1]。在长期进化过程中,植物在适应光环境变化的同时,还能相互影响改变微生境,即植物能感受光信号也能产生光信号。光信号参与调控种子萌发、幼苗脱黄化、生物钟节律和开花时间等生理过程^[2]。植物通过不同种类光受体(photoreceptors)感知光的方向、波长、强度以及光周期等信号,从而调控体内相关基因的表达,光敏色素(phytochrome, phy)是目前研究最为深入的光受体,其生理作用非常广泛,植物从种子萌发到开花、结果及衰老均受其影响^[3]。

1 光敏色素的结构和分类

1.1 光敏色素的发现

光敏色素是植物体内普遍存在的红光/远红光受体。Flint 等^[4]首次发现红光能促进而远红光则抑制种子萌发。随后 Butler 等^[5]发现在红光/远红光照射下蛋白提取液的吸收光谱有显著差异。1960 年植物学家 Borthwick 和物理化学家 Hendricks 将其正式命名为光敏色素^[6]。

1.2 光敏色素的结构特征

光敏色素是一种易溶于水的色素蛋白质,相

对分子质量为 2.5×10^5 。一个光敏色素单体包含 1 个线性四吡咯生色团和 1 个脱辅基蛋白分子,蛋白分子由 2 个分子质量在 120~127 ku 的多肽聚合而成。如图 1 所示,光敏色素由 2 个结构域构成:一个是位于 N 末端的分子质量为 70 ku 的光感受域,另一个是 C 末端的分子质量为 55 ku 的光调节域^[7]。光敏色素中光感受区包括多个亚结构域。在天然状态下,光敏色素通过 C 末端的氨基酸残基聚合成二聚体^[8]。生色团与高度保守的 GAF (cGMP-specific phosphodiesterase/adenylate cyclases/formate hydrogen lyase transcription)区域相结合,当红光或远红光照射时,生色团的线性四吡咯环发生光质异构化,从而形成红光吸收型或远红光吸收型光敏色素^[9]。PHY (Phytochrome domain) 区域紧邻 GAF 区域的 C 端,是保持吸收光谱完整所必需的组分^[10]。光调节区含有 2 个 PAS(period circadian protein homolog 1 / aryl hydrocarbon nuclear translocator / single-minded gene)同源重复序列和 1 个组氨酸激酶相关结构域 HKRD(Histidine-kinase-related domain),此结构在光信号转导中发挥重要作用^[11]。

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1.3 光敏色素的分类

光敏色素在植物中的存在和作用并不单一。1989 年 Sharrock 和 Quail 首次获得直接证据证明存在多种光敏色素基因^[12]。随后,Clack 等^[13]获得光敏色素 D(phyD)、光敏色素 E(phyE)基因的序列。在玉米、水稻以及小麦中存在 3 类光敏色素,在松树和银杏中分别存在 4 种和 3 种光敏色素^[9,14-16]。研究表明,光敏色素家族最早形成 2 个分支,其中一支很快分成光敏色素 A(phyA)和光敏色素 C(phyC),另一分支分为光敏色素 B(phyB)和 phyE^[11]。phyE 在某些类群(如单子叶植物)中丢失,而 phyD 则起源于 phyB 最近的一次基因复制事件^[11]。不同种类光敏色素基因的进化速率也不同,phyA、phyB 较保守,而 phyC、

phyE 的进化速率是 phyA、phyB 的 1 133 倍^[17]。

光敏色素按其在光下的状态可分为 2 类:光不稳定型(如 phyA)和光稳定型(如 phyB-phyE 等)。其在植物中有 2 种存在形式,分别是红光吸收型(Pr)和远红光吸收型(Pfr)。一般把吸收红光的光敏色素称为 Pr 型光敏色素,其吸收红光后即转变成吸收远红光的 Pfr 型光敏色素。在黑暗条件下,Pfr 会逆转为 Pr,Pfr 浓度降低并被蛋白酶降解^[18]。光敏色素主要有 3 种反应方式,极低辐照度反应(VLFR)、低辐照度反应(LFR)和强辐射反应(HIR)。不同种类光敏色素的反应方式各不相同,其中 phyA 主要调节 VLFR 和 HIR,phyB 则调节 LFR^[19]。

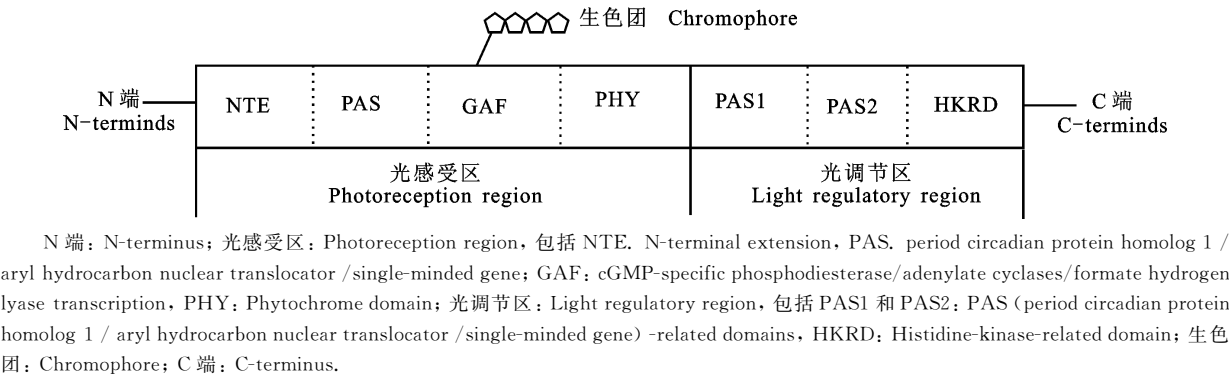


图 1 光敏色素结构域示意图

Fig. 1 The schematic diagram of different domains of phytochrome molecule

2 光敏色素的生物学功能

光敏色素感受光信号并参与调控的生理反应包括种子萌发、幼苗光形态建成、避荫作用、开花时间和昼夜节律响应等^[7](表 1)。此外,近年研究还发现,光敏色素参与调控植物对非生物胁迫的抗性应答^[8]。

2.1 在种子萌发中的功能

Borthwick 等^[20]的研究首次证明红光/远红光受体能调节种子萌发。对拟南芥突变体的研究表明,至少有 3 种光敏色素(phyA、phyB、phyE)参与拟南芥种子萌发的调控。phyA 在不同波长的光照(紫外线、可见光和远红光)下调控不可逆转的 VLFR 反应,而 phyB 则调控红光/远红光受体的 LFRs 反应,2 种反应均能促进种子萌发^[21]。此外,在连续远红光及强辐射条件下,phyA 能促进种子萌发^[22]。phyE 可能直接参与远红光的光受体响应,或协助 phyA 调控种子萌发^[22]。有趣的是,环境温度参与拟南芥种子萌发的光调控,不

同光敏色素在温度变化条件下其功能会相应改变^[23]。

2.2 幼苗去黄化

黑暗中生长的幼苗发生黄化,且下胚轴伸长、子叶不展开、原质体发育成白色体。而光下幼苗则发生去黄化反应,植株形态正常且原质体发育为成熟的叶绿体。不同光敏色素(除 phyE 外)在幼苗去黄化过程中均起到一定作用^[24]。

在白光和红光下,phyA 缺失突变体表现为野生型光形态建成表型;而在连续远红光照射时,该突变体表现为暗形态建成表型,表明 phyA 是感知和调节远红光反应的主要光受体^[25]。此外,试验证明 phyA 在红光处理下的快速调控基因表达响应中起重要作用^[26]。phyB 是主要调控去黄化的光敏色素。但红光处理后,phyB 缺失突变体和野生型在转录水平表达差异不显著^[27];phyA/phyB 双突变体与 phyB 单突变体相比,下胚轴明显增长且子叶扩张减少,进一步揭示 phyA 在红光下的作用。

在红光照射下,phyC 也能调控幼苗去黄化反应^[28]。但 phyC/phyD 双突变体表型与单突变体表型间无明显差异;在远红光下,phyC 则不能调控幼苗去黄化反应^[29]。

此外,phyD 在红光下也能独自调控幼苗去黄化作用^[25]。而 phyE 在此过程中的作用则极其微弱。

2.3 避荫反应

植物发育的调控不仅跟光暗有关,还受光质

量的影响,特别是由其他植物的阴影带来的光质量变化^[30]。因此,植物启动另一种策略即避荫反应,包括茎和叶柄的伸长,开花时间提前,顶端优势增加等^[30]。

phyB 是大多数避荫反应的光受体,而 phyA 是避荫环境中光照辐照度变化的敏感感受器。根据对突变体的研究显示,phyD 和 phyE 帮助 phyB 参与避荫反应。

表 1 不同种光敏色素在植物生长发育及应对逆境胁迫中的作用

Table 1 Different roles of phytochrome family members in plant growth and development

生物学功能	Function	光敏色素	Phytochrome	参考文献	Reference
种子萌发	Seed germination	phyA、phyB、phyD、phyE		22-23, 31-33	
幼苗去黄化反应	Seedling de-etiolation	phyA、phyB、phyC		34	
避荫作用	Shade avoidance	phyA、phyB、phyD、phyE		35	
光合作用	Photosynthesis	phyB		31	
茎的伸长作用	Stem elongation	phyA		35	
开花周期	Flowering	phyC、phyD		36-37	
植物育性	Plant fertility	phyA		35	
叶片发育	Leaf architecture	phyC		36	
生物节律周期	Circadian clock	phyA、phyB、phyC		38-39	
非生物胁迫(盐、旱、冷)	Abiotic stress	phyA、phyB、PhyD、phyE		40-44	

3 光敏色素的调控

目前,已知光信号转导途径的相关基因根据其作用可分为 3 类:

第 1 类,参与光敏色素核定位。光敏色素入核是其发挥作用、调控光信号的关键步骤。但不同光敏色素的核内定位机制各不相同^[45-46]。早期研究^[47-48]显示,持续照射红光和蓝光能有效诱导 phyB-phyE 转移到细胞核内,并可以通过远红光照射逆转。近年来研究发现在由黑暗过渡到远红光照射时,phyB 也能快速移位至细胞核内^[49],与早期结果矛盾,其潜在原因仍需进一步研究。与 phyB-phyE 不同,phyA 入核不仅需要光信号,还需要 2 个同源伴侣蛋白协助,即 FHY1(Far-red elongated hypocotyl 1)和 FHL(fhy1 like)^[48, 50-51]。陈芳等^[52]研究发现,FHY1 是帮助 phyA 入核、转录因子互作、结合基因启动子等的辅助蛋白。Lin 等^[53]发现拟南芥中 2 种光反应关键蛋白:FHY3(far-red elongated hypocotyl3)和 FAR1(Far-red impaired response1),两者通过直接激活 *FHY1/FHL* 基因的表达来共同调控 phyA 在核内的积累。Genoud 等^[54]研究发现细胞核内组成型的 phyA 弥补 fhy3 突变体的表型。拟南芥 phyA 这种特殊的入核调控方式可能与其

适应性进化有关^[55]。其他物种不同光敏色素的入核机理是否与拟南芥一致目前还不清楚。

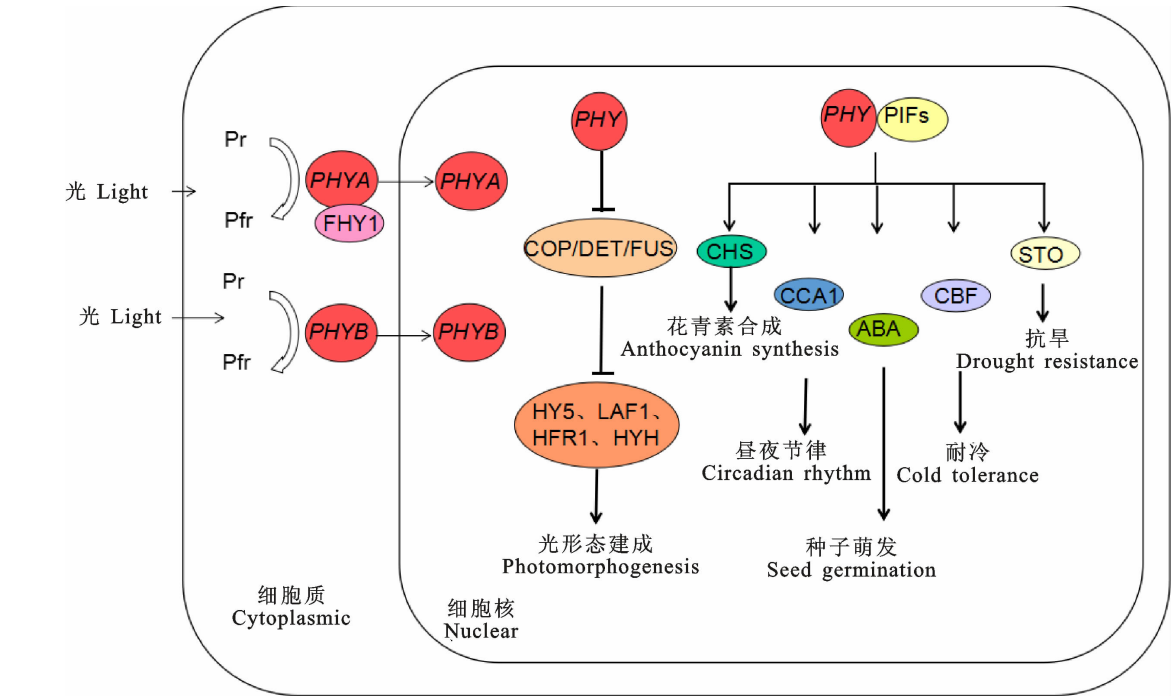
第 2 类,参与光敏色素信号输出。邓兴旺课题组^[56-57]的遗传试验筛选鉴定出一个光形态建成抑制因子,命名为 COP/DET/FUS(CONSTITUTIVE PHOTOMORPHOGENESIS/DE-ETIOLATED/FUSCA)基因,这些因子的突变体在暗环境中呈现光形态建成表型。研究表明,HY5(ELONGATED HYPOCOTYL5)^[58]、HYH(HY5 Homolog)^[59]、LAF1(LONG AFTER FARRIED LIGHT1)^[60]以及 HFR1(LONG HYPOCOTYL IN FAR-RED1)^[61-63]等均促进光形态建成蛋白的表达水平增高,进而促进光敏色素的活化,从而抑制 COP/DET/FUS 的活性。此外,这些因子可在植物体内形成不同的复合体,参与泛素化途径。其中 COP1-SPAs 复合体由 COP1 及 SPAs(SUPPRESSOR OF PHYA1)家族成员构成,其中 COP1 是拟南芥光形态建成的关键抑制因子,在黑暗条件下,能作为 E3 泛素连接酶降解光形态建成的转录因子,但在光下 COP1 活性被抑制且在核内的丰度降低。SPAs 家族是 phyA 信号转导中的另一个负调控因子,通过结合 COP1 对目标蛋白进行水解,且作为一个共同作用因子调节 COP1 的功能^[64]。CSN

(COP9 signalosome),由 8 个高度保守的不同亚基组成,是一个新的 E3 泛素连接酶的调节因子,是细胞对外界刺激或胁迫产生响应的调节成分^[65-66]。CDD 复合体 [COP10, DET1, DDB1 (DNA DAMAGE BINDING PROTEIN1)] 的具体功能还不清楚。此外,光信号导致 COP/DET/FUS 失活的具体分子机制也有待进一步研究。

第 3 类,直接调节光反应。与光受体相互作用因子中,有一类重要的碱性螺旋环螺旋(basic helix-loop-helix, bHLH)类转录因子-PIFs(phytochrome interacting factor)家族蛋白,其主要功能是调节光敏色素介导的暗形态建成到光形态建成转换过程中的信号转导途径^[67]。目前,已知的 PIFs 家族成员有且仅有 PIF1 和 PIF3 可以与活化的 phyA 相互作用,且 PIF1 与 phyA 的结合能力比 PIF3 强^[68-69]。PIF3 能与 phyC 和 phyE 分别形成异源二聚体^[70]。研究发现 PIF3 和 phyB 可以在体外结合至光响应基因启动子的 G-box 区域,表明光敏色素可以将光信号直接靶向目的基因的启动子调控该基因表达^[71-72]。研究证明,

在转录因子 PIF3 或 HY5 的协同作用下,phyA-FHY1 复合物可以结合至编码查尔酮合酶的 *CHS*(CHALCONE SYNTHASE) 基因启动子上,共同调控 *CHS* 的转录^[73]。Chen 等^[74]证明在与 phyA 直接发生相互作用的靶基因启动子上存在大量供 PIFs 识别的顺式作用元件。这一发现说明包括 PIFs 和 HY5 在内的大量转录因子均能以直接或间接的方式在靶基因启动子上与 phyA 发生相互作用,对众多下游基因进行调控,从而对各种内外信号作出快速反应^[75]。拟南芥其他类型的转录因子(如 ARR4,IAAs,ATHB23 等)也能以上述方式与光敏色素发生相互作用^[75-77]。此外,也有研究认为 phyB 会阻碍 PIFs 结合至靶基因的启动子区域^[78],并通过一系列体外试验证明,PIF1 和 PIF4 与靶基因作用后不能与 phyB 或 phyA 同时结合^[79-80],其深层次的机理还有待进一步试验证实。

基于以上分析,笔者绘制光敏色素与各相关因子互作的模式图(图 2)。



Pr. 红光吸收型 Phytochrome red light-absorbing form; Pfr, 远红光吸收型 Phytochrome far-red light-absorbing form; PHYA. Phytochrome A; PHYB. Phytochrome B; FHY1, Far-red elongated hypocotyl 1; PHY. Phytochrome; COP1/DET/FUS. Constitutive photomorphogenesis/de-etiolated/fusca; HY5;Long hypocotyl 5; LAF1;Long after farred light1; HFR1;Long hypocotyl in far-red1; HYH;HY5 Homolog; PIFs; Phytochrome interacting factors; CHS; Chalcone synthase; CCA1;Circadian clock-associated protein 1; ABA;Absciscic acid; CBF.CRT/DRE2 binding factor; STO. Salt tolerance protein;箭头表示正调控作用, T 型线表示负调控作用 Arrow represent positive regulation and T-type line represent negative regulation.

图 2 光敏色素信号转导通路模式
Fig. 2 Simplified model of the phytochrome signaling pathway

4 展 望

不同光敏色素的分子结构和生理功能已得到系统的阐述,其信号传导机制成为近年来研究的重点。目前,基于对光信号、温度及多种植物内源激素共同组成的信号网络有系统认识,一大批与光敏色素相互作用的因子被发现。但因该网络的复杂性,其整体功能以及各信号分子在整个调控网络中的作用还需深入研究。如何系统诠释以光敏色素为中心的信号通路作用机制以及各通路间的相互关系,仍是亟待解决的关键问题。此外,光敏色素还是介导植物应对各种非生物与生物胁迫的重要激素^[32],了解其体内的作用方式将为培育适应不同光环境尤其是弱光下的农作物新品种提供有价值的理论参考依据。

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Biological Functions and Signaling Regulation Network of Phytochromes

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Abstract Light is essential for plant growth and development. Plants have evolved light receptors (LRs) to accept light signal. So far, four different kinds of LR have been reported, among these, phytochromes have been well-studied, which act as red and far-red LR and play vital roles in photomorphogenesis. Currently, the action mode of phytochrome and light signal transduction pathway as well as modulation of plant development have been elucidated, e. g. the hypocotyl extension, stem branching, circadian rhythm and flowering time control, etc. In this review, we summarized the biological functions, regulation of phytochrome, and light signal transduction pathways in plant development, which may provide insight for further study in this field.

Key words Phytochrome; Light signal pathways; Biological functions; Regulation

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