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·特邀综述·

光受体介导信号转导调控植物开花研究进展

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摘要 光照是影响植物生长发育的重要环境因子，开花是高等植物生活史上最重要的事件。植物通过光受体感知外界环境中的光照变化，激活一系列信号转导过程从而适时开花。该文介绍了高等植物光受体的种类、结构特征和生理功能的研究进展，并系统阐述了红光/远红光受体光敏色素、蓝光受体隐花色素以及FKF1/ZTL/LKP2等介导光信号调控植物开花的分子机制，包括光受体对*CO*转录及转录后水平调控和对*FT*转录水平的调控等。此外，还介绍了光受体整合光信号与温度和赤霉素等信号调控植物开花的研究进展，并展望了未来的研究方向。

关键词 光受体，开花，光敏色素，隐花色素

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高等植物从营养生长向生殖生长的成花转变和花器官的形成在物种发育、繁殖和进化中发挥核心作用(Teotia and Tang, 2015)。在长日照(LD)植物拟南芥(*Arabidopsis thaliana*)中已探明至少有6种开花调控途径：光周期途径(photoperiod pathway)、春化途径(vernalization pathway)、温度途径(thermoresponsive pathway)、赤霉素途径(gibberellin pathway)、年龄途径(age pathway)和自主途径(autonomous pathway) (Blümel et al., 2015)。在这些途径中，植物通过光受体等感受外部环境信号，历经一系列基因调控的信号转导，将信号传递到*CO* (*CONSTANS*)等成花整合子基因，进而激活成花素基因*FT* (*FLOWERING LOCUS T*)的转录并最终实现开花(Andrés and Coupland, 2012)。CO属于B-box锌指蛋白家族(BBX)成员，其N端具有B-box B1和B2结构域，C端可结合CCT (CO、CO-like及TOC1)结构域。CO在叶片韧皮部伴胞中激活*FT*的转录和*TSF* (*TWIN SISTERS OF FT*)的微弱表达(Samach et al., 2000; Yamaguchi et al., 2005)。FT是1个RAF (Rapidly Accelerated Fibrosarcoma)相关的激酶抑制蛋白，通过韧皮部运输到茎尖分生组织，与分生组织特异性的bZIP转录因子FD (FLOWERING LOCUS D)和FD PARALOGUE相互作用，激活成花整合子基因*SOC1* (*SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1*)、花分生组织特征基因*LFY* (*LEAFY*)和花器官特征基因*AP1* (*APETALA 1*)的表达，并引起下游基因的级联反应，进而调控花发育过程(Corbesier et al., 2007)。本文重点介绍模式植物拟南芥中光受体的结构特征和开花调控等生理功能的研究进展，并对光敏色素(phytochromes, PHYA–PHYE)、隐花色素(cryptochromes, CRY1/CRY2)和ZTL (zeitlupe)/FKF1 (Flavin binding, Kelch repeat, F-box protein 1)/LKP2 (Lov Kelch Protein 2)等通过光周期途径或整合其它成花途径调控植物开花的分子机制进行了综述。同时，指明光受体调控植物开花机制研究中存在的问题，并对未来的研究方向进行了展望。

1 光受体的种类、结构特征与生理功能

1.1 光受体的种类

植物通过3类光受体(photoreceptor)来感知红光、蓝光和紫外光UV-B并进行信号转导，包括5个红光/远红光受体光敏色素(Chen and Chory, 2011); 7个蓝光受体，其中2个隐花色素(Chaves et al., 2011)、3个

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LOV/F-box/Kelch结构域蛋白即ZTLs家族成员FKF1、ZTL及LKP2 (Suetsugu and Wada, 2013), 2个向光素(phototropins, PHOT1–2) (Christie, 2007)和1个UV-B受体UVR8 (UVB-resistance locus 8) (Rizzini et al., 2011)。

1.2 光受体的结构特征

光敏色素是主要的红光/远红光感受器，是植物自身合成的水溶性色素蛋白。功能性光敏色素由2个单体组成，每个单体又含有2个结构域，其中N端的光感受结构域可共价结合生色团，与光敏色素的光化学特性相关，而C端的光调节结构域主要参与光敏色素二聚体的形成及下游信号转导过程(Matsushita et al., 2003; Rockwell et al., 2006)。光敏色素N端功能域又分为4个亚功能域: P1、P2/PAS、P3/GAF和P4/PHY; C端功能域可分为PAS (包括PAS-A和PAS-B)和HKRD (histidine kinase-related domain)两个亚功能域(Bae and Choi, 2008) (图1)。光照会触发光敏色素蛋白在具有生物活性的远红光吸收型Pfr (phytochrome FR-absorbing isomer)和无活性的红光吸收型Pr (phytochrome R-absorbing form)之间相互转化。一般认为，光敏色素生色团与高度保守的GAF区域结合，以Pr形式存在于细胞质中。接收红光刺激后，生色团的线性四吡咯环发生光质异构化，Pr转变为Pfr，并从细胞质转移到细胞核中，直接与PIFs (Phytochrome Interacting Factors)或其它信号转导组分互作，进行光信号的放大和传递(Leivar and Monte, 2014)。在远红光下, Pfr又转变为Pr构象。

隐花色素是一种类光解酶(photolyase)的蓝光受体，在动植物中均有存在(Cashmore, 2003)，但植物中隐花色素不具有催化紫外光损伤DNA修复的功能(Chaves et al., 2011)。CRYs具有2个重要的结构域, N端为非共价结合生色团黄素FAD (Flavin Adenine Dinucleotide)和叶酸MTHF (methenyltetrahydrofolate)的光裂解酶相关PHR (photolyase-homologous region)结构域, C端为不具有光裂解酶活性，但对蛋白互作和信号转导十分重要的CCE (Cryptochrome C-terminal Extension)结构域(Cashmore et al., 1999; Yang et al., 2000) (图1)。

向光素(phototropins)是光活化的丝氨酸/苏氨酸蛋白激酶。目前，在拟南芥中仅发现2种向光素，即PHOT1和PHOT2 (Briggs and Christie, 2002)。PHOT1和PHOT2通过2个N端的LOV (Light, Oxygen, Voltage)结构域(LOV1和LOV2)结合生色团黄素单核苷酸FMN (Flavin Mononucleotide)来感知光信号，并通过LOV结构域与辅因子结合或与其它蛋白发生互作(Christie, 2007) (图1)。LOV结构域最早来自PAS大家族的一个亚家族(Ito et al., 2012a)，该结构域不仅存在于向光素中，还存在于植物、真菌和细菌的其它蓝光感受器中。

ZTLs是一类新发现的蓝光受体蛋白。拟南芥中已知的ZTLs家族包括FKF1、ZTL和LKP2。这3个蛋白都含有3个重要的功能保守结构域: N端的LOV结构域、中间的F-box基序和C端的Kelch重复序列(Somers et al., 2000; Schultz et al., 2001; Ito et al., 2012a)。值得注意的是，拟南芥中ZTLs家族仅有1个LOV结构域，而向光素有2个LOV结构域。ZTLs家族成员均以LOV结构域结合生色团黄素单核苷酸FMN (Nelson et al., 2000; Schultz et al., 2001)。Kelch结构域则与蛋白质的相互作用相关(Ito et al., 2012a) (图1)。

UVR8参与调控植物对UV-B辐射的响应。拟南芥*UVR8*编码440个氨基酸残基，分子量为47 kDa。目前已获得在N端缺少11个氨基酸且在C端缺少59个氨基酸的UVR8蛋白核心的高分辨率晶体结构，其由7个片状的β螺旋构成，但C端和N端的位置、功能结构域特征以及UVR8蛋白从二聚体到单体如何变化尚不清楚(Jenkins, 2014)。

1.3 光受体的生理功能

拟南芥光敏色素基因家族有5个成员: *PHYA*、*PHYB*、*PHYC*、*PHYD*和*PHYE*，不同成员间既相互独立，又存在功能冗余。PHYA是一类在光照下迅速分解的光不稳定型蛋白，参与幼苗的远红光感受及介导早期的红光反应; PHYB、PHYC、PHYD和PHYE属于光稳定型蛋白，在持续红光或白光下起主要作用(Tepperman et al., 2006; Kami et al., 2010)。*PHYA*可促进拟南芥开花(Johnson et al., 1994)。*PHYB*抑制开花(Guo et al., 1998)。*PHYC*在短日照(SD)下抑制开花，而在长日照下与*PHYA*共同促进开花(Monte et al., 2003)。*PHYD*和*PHYE*抑制开花，*PHYB*、*PHYD*和*PHYE*存在功能冗余(Devlin and Kay, 2000) (表1)。

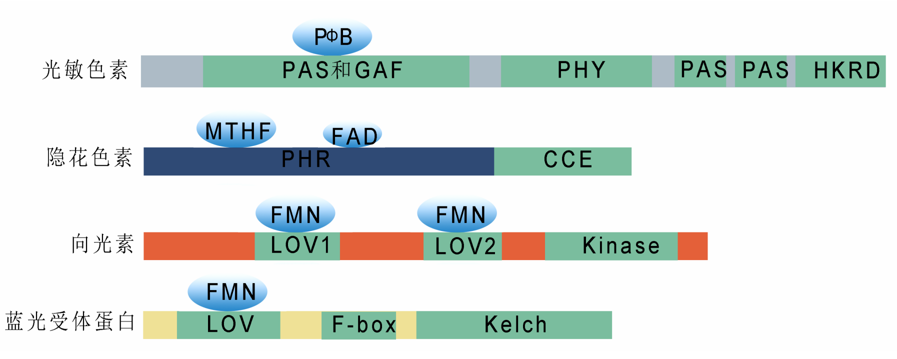

图1 植物光受体结构示意图

光敏色素N端为可共价结合生色团的光感受结构域，包括PAS、GAF和PHY等亚功能域; C端为光调节结构域，主要参与光敏色素二聚体的形成及下游的信号转导过程，包括PAS和HKRD两个亚功能域。隐花色素N端为非共价结合生色团黄素(FAD)和叶酸(MTHF)的光裂解酶相关PHR结构域，C端是对蛋白互作和信号转导十分重要的CCE结构域。向光素通过2个N端的LOV结构域(LOV1和LOV2)结合生色团黄素单核苷酸FMN来感知光照信号，并通过LOV结构域与辅因子结合或与其它蛋白发生互作。蓝光受体蛋白ZTLs含有3个重要的功能保守结构域: N端的LOV结构域、中间的F-box基序和C端的Kelch重复序列。ZTLs以LOV结构域结合生色团黄素单核苷酸FMN, Kelch结构域则与蛋白质的相互作用相关。

Figure 1 Schematic structural diagrams of plant photoreceptors

The N-terminus of phytochromes is a photosensory region (containing PAS, GAF, and PHY), which covalently binds chromophores. The C-terminal light regulatory domains, including PAS and HKRD, are involved in phytochrome dimer formation and downstream signaling transduction. The N-terminus of cryptochromes is a PHR domain, which non-covalently binds FAD and MTHF, and the C-terminal CCE domain is important for protein-protein interactions and signaling transduction. The two N-terminal LOV domains (LOV1 and LOV2) of phototropins bind FMN to perceive light signals and are required for interaction with other proteins. ZTL proteins contain three important functional conserved domains: the N-terminal LOV domain, the intermediate F-box motif, and the C-terminal Kelch repeat region. The LOV domain binds to FMN, and the Kelch domain mediates protein-protein interactions.

拟南芥隐花色素基因家族由3个成员组成: *CRY1*、*CRY2*和*CRY3*。*CRY1*和*CRY2*与植物昼夜节律钟相关，参与调控幼苗去黄化和成花诱导过程(Chaves et al., 2011)。*CRY1*和*CRY2*在拟南芥中均可促进开花(Koornneef et al., 1991; Ahmad and Cashmore, 1993; Guo et al., 1998) (表1)。*CRY3*属于cry-DASH (*Drosophila*、*Arabidopsis*、*Synechocystis*及*Homo*)分支，从进化上看CRY3是介于隐花色素和光裂解酶之间的中间体(Brudler et al., 2003), 其功能有待进一步研究。

作为昼夜节律钟的重要组成因子, ZTLs参与植物昼夜节律信号的输入，调控下游的成花诱导和花器官形成基因的表达(Baudry et al., 2010)。FKF1是一种E3泛素化连接酶，通过调控蛋白稳定性，影响下游基因的转录(Imaizumi et al., 2005)。*FKF1*对开花具有促进作用(Imaizumi et al., 2005), ZTL和LKP2对开花具有抑制作用，LKP2和ZTL均可以与FKF1互作进而抑制其蛋白积累(Somers et al., 2000; Más et al., 2003; Takase et al., 2011)。ZTL可以在体外与PHYB和CRY1相互作用，可能具有将信号输入到昼夜节律钟的功能(Jarillo et al., 2001) (表1)。

向光素是植物中与细胞质膜相关的蓝光受体，参与调控植物的向光性生长、光诱导的气孔开放和叶绿体运动及下胚轴伸长等生物学过程(Briggs and Christie, 2002; Celaya and Liscum, 2005) (表1)。

UVR8是拟南芥中吸收紫外线UV-B的植物特有的色素蛋白，在没有UV-B的情况下，UVR8形成对称的同源二聚体，其表面上的色氨酸残基可行使生色团功能。在UV-B辐射下，细胞质中的UVR8发生单体化并迁移入细胞核内积累，维持核内UV-B的信号转导(Rizzini et al., 2011; Christie et al., 2012; Wu et al., 2012; Qian et al., 2016)。目前，已陆续鉴定出多个与UVR8相互作用的蛋白，包括COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1)、WRKY36、BES1

表1 拟南芥光受体类型及生理功能

Table 1 Photoreceptors and their physiological functions in *Arabidopsis thaliana*

光受体	基因	生理功能	主要参考文献
光敏色素	*PHYA*	促进开花，幼苗去黄化，种子萌发，避阴反应	Johnson et al., 1994; Schäfer and Bowler, 2002; Tepperman et al., 2006; Heschel et al., 2007
	PHYB	抑制开花，幼苗去黄化，种子萌发，气孔发育，避阴反应	Guo et al., 1998; Schäfer and Bowler, 2002; Heschel et al., 2007; Wang et al., 2010; Kami et al., 2010
	PHYC	短日照下抑制开花，长日照下促进开花	Monte et al., 2003
	PHYD	抑制开花，种子萌发，避阴反应	Devlin and Kay, 2000; Schäfer and Bowler, 2002; Heschel et al., 2007
	PHYE	抑制开花，种子萌发，避阴反应	Devlin and Kay, 2000; Schäfer and Bowler, 2002; Heschel et al., 2007
隐花色素	*CRY1*	促进开花，气孔发育，幼苗去黄化	Ahmad and Cashmore, 1993; Mao et al., 2005
	CRY2	促进开花，幼苗去黄化，昼夜节律调控	Koornneef et al., 1991; Guo et al., 1998
向光素	*PHOT1*	向光性，光诱导的气孔开放和叶绿体运动，抑制下胚轴伸长	Briggs and Christie, 2002; Celaya and Liscum, 2005
	PHOT2	向光性，光诱导的气孔开放和叶绿体运动，抑制下胚轴伸长	Briggs and Christie, 2002; Celaya and Liscum, 2005
ZTLs	*FKF1*	促进开花，昼夜节律信号输入	Imaizumi et al., 2005; Baudry et al., 2010
	ZTL	长日照下抑制开花，昼夜节律信号输入	Somers et al., 2000; Baudry et al., 2010
	LKP2	抑制开花	Takase et al., 2011
紫外受体	*UVR8*	抑制下胚轴伸长，光形态建成，抑制开花	Favory et al., 2009; Gruber et al., 2010; Yang et al., 2018; Liang et al., 2018

(BRI1-EMS-SUPPRESSOR 1)和BIM1 (BES1-INTERACTING MYC-LIKE 1)等，其在植物体内的生理功能主要包括抑制下胚轴伸长、调控光形态建成及开花等(Favory et al., 2009; Gruber et al., 2010; Yang et al., 2018; Liang et al., 2018; Dotto et al., 2018) (表1)。

2 光受体在光周期成花途径中的调控作用

在许多植物中，光周期是影响开花的重要环境因子，光周期途径是调控植物开花的途径之一(Johansson and Staiger, 2015)。拟南芥是一种典型的长日照植物，长日照促进其开花，短日照则抑制其开花。*CO*的转录及转录后水平调控和*FT*的转录水平调控是关键调控节点，而这种机制受到上游光受体输入信号的影响。

2.1 光受体对*CO*转录水平的调控

隐花色素、光敏色素和FKF1/ZTL/LKP2均参与*CO*基因转录水平的调控。*CO*的转录主要受到CDF1 (CYCLING ODF FACTOR 1)和FKF1-GI (GIGANTEA)复合体的调控(Imaizumi et al., 2005; Fornara et al., 2009)。CDFs家族是一类转录因子，早晨CDF1可直接抑制*CO*的转录(Sawa et al., 2007)。FKF1是一种E3泛素化连接酶，GI是植物特有的核蛋白(Mizoguchi et al., 2005)。FKF1和GI呈现出振荡表达，以蓝光依赖的形式相互作用形成FKF1-GI复合体，该复合体使转录抑制因子CDF1在下午发生降解，进而激活*CO*的转录(Sawa et al., 2007; Fornara et al., 2009)。除FKF1外，ZTL和LKP2也均能与GI形成蛋白复合体，进而作用于相同的靶蛋白(如CDF1) (图2)。然而，与FKF1不同，过表达*ZTL*和*LKP2*的转基因植株在长日照条件下强烈抑制*CO*的表达而表现出晚花表型(Schultz et al., 2001; Somers et al., 2004)，这是由于LKP2和/或ZTL会影响光照初期FKF1蛋白的积累(Takase et al., 2011)。

CRY2在*CO*的转录调控中行使重要功能。光通过诱导CRY2形成同源二聚体的方式来激活CRY2，而BIC1 (BLUE-LIGHTINHIBITOR OF CRYPTOCHROMES 1)可与CRY2直接互作阻断CRY2的二聚化反应和后续的信号转导过程(Wang et al., 2016)。COP1

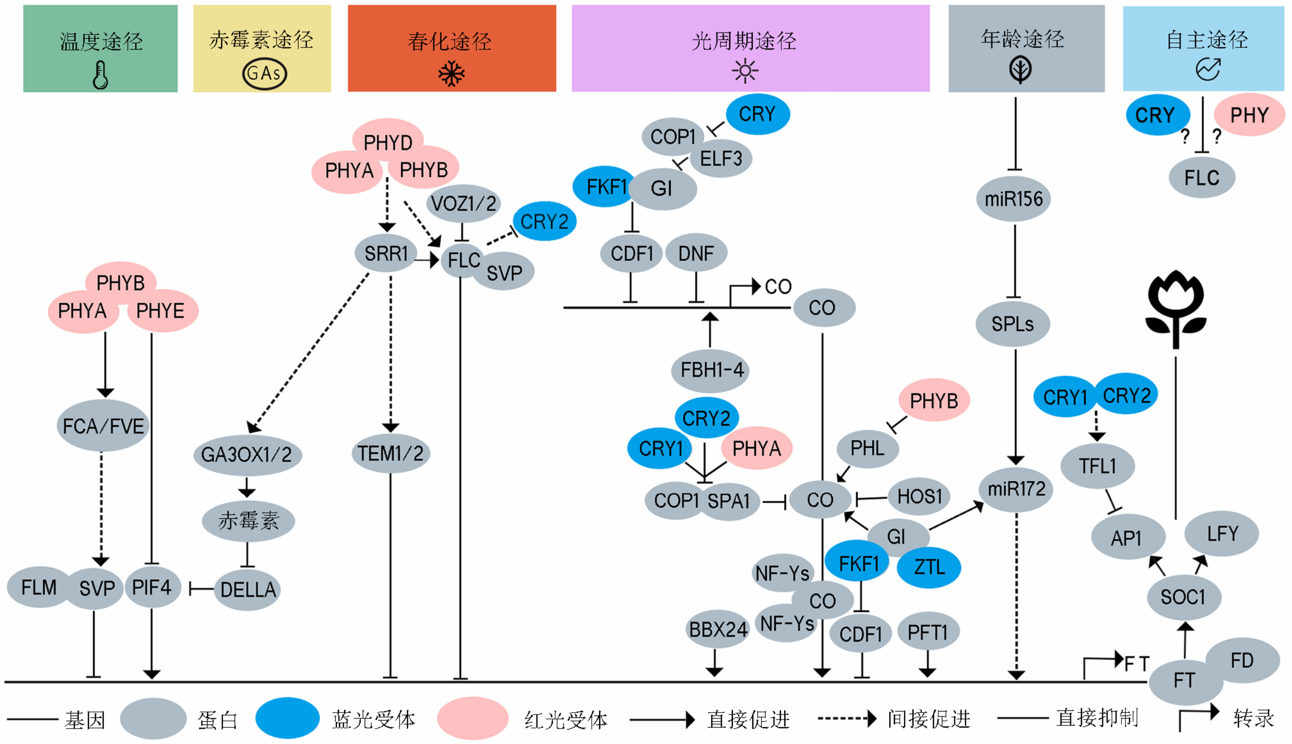

图2 光受体介导环境信号调控拟南芥开花示意图

植物中已探明至少有6种开花调控途径: 光周期途径、春化途径、温度途径、自主途径、赤霉素途径和年龄途径。在叶片中, 光敏色素、隐花色素和ZTL/FKF1/LKP2等光受体介导光信号并将信号传递给昼夜节律钟, 经过多种开花途径的信号整合, 最终直接或间接调控*CO*、*FT*和*FLC*的表达和蛋白稳定性。温度途径中光敏色素通过FCA/FVE间接调控*FLM*、*SVP*和*PIF4*进而调控*FT*的转录; 赤霉素途径和春化途径由*SRR1*进行信号整合, 通过GA生物合成途径*GA3OX1/2*以及DELLA蛋白调控*FT*的转录, 春化途径通过VOZ1/2和光敏色素调控*FLC*、*SVP*和*TEM1/2*进而调控*FT*的表达; 自主途径通过抑制开花阻遏物和春化途径关键基因*FLC*促进开花; 光受体在光周期途径中发挥重要作用, GI、CDF1、DNF、FBH1-4、COP1、SPA1、HOS1和NF-Ys等蛋白直接或间接与光受体互作, 对*CO*转录、转录后水平以及*FT*的转录水平等关键调控节点进行调控。年龄途径通过*miR156*/*172*和*SPLs*调控*FT*的表达。不同的开花途径之间存在信号整合机制, 最终开花信号被整合到*FT*、*SOC1*和*LFY*, 激活*AP1*和*LFY*, 进而完成开花起始。实线箭头表示直接促进, 虚线箭头表示间接促进, 钝化线表示直接抑制, 红色表示红光/远红光受体, 蓝色表示蓝光受体, 灰色表示信号蛋白。

Figure 2 A schematic diagram of flowering time regulation by photoreceptor-mediated environmental signaling in Arabidopsis

Six flowering regulatory pathways have been identified in plants, including photoperiodic pathway, vernalization pathway, temperature pathway, autonomous pathway, gibberellin pathway, and age pathway. Phytochromes, cryptochromes, and ZTL/FKF1/LKP2 perceive light signals in leaves, and transmit the signals to the circadian clock. After signaling integration through multiple flowering pathways, the photoreceptors eventually directly or indirectly regulate *CO*, *FT* and *FLC* expression and protein stability. In the ambient temperature pathway, the phytochromes indirectly regulate the transcription of *FT* by *FLM*, *SVP* and *PIF4* through FCA/FVE. *SRR1* integrates signals from the gibberellin pathway and vernalization pathway and regulate *FT* transcription through *GA3OX1/2* and DELLA proteins in the GA pathway. In the vernalization pathway, VOZ1/2 and phytochromes regulates *FT* expression through *FLC*, *SVP*, and *TEM1/2*. The autonomous pathway promotes flowering by repressing *FLC*. Photoreceptors play an important role in the photoperiodic pathway. GI, CDF1, DNF, FBH1-4, COP1, SPA1, HOS1, and NF-Ys directly or indirectly interact with photoreceptors to regulate *CO* transcription, CO stability, and *FT* transcription. The age pathway regulates *FT* expression through miR156/172 and *SPLs*. There are signal integration mechanisms between different flowering pathways. The signals are integrated into *FT*, *SOC1,* and *LFY*, leading to the activation of *AP1* and *LFY* and eventually the initiation of flowering. Solid arrows indicate direct promotion; dotted arrows indicate indirect promotion; blunted lines indicate direct inhibition; red ovals indicate red/far-red light photoreceptors; blue ovals indicate blue light photoreceptors, and gray ovals indicates signaling intermediate proteins.

是含有Ring结构域的E3泛素化连接酶，ELF3 (EARLY FLOWERING 3)是无保守结构域的植物特异性蛋白，也是植物昼夜节律晚间复合体的组成部分(Bendix et al., 2015)。黑暗状态下，COP1与ELF3形成COP1/ELF3复合体并降解GI蛋白，蓝光激活的CRY2能够抑制COP1/ELF3复合体的活性，促进GI蛋白的积累，形成FKF1-GI复合体(Yu et al., 2008) (图2)。

此外，人们还鉴定出其它*CO*转录的调节因子。ELF4 (EARLY FLOWERING 4)可在夜间限制GI蛋白结合*CO*启动子的能力，进而影响其转录(Kim et al., 2013)。E3泛素化连接酶DNF (DAY NEUTRAL FLOWERING)在短日照下抑制*CO*的表达，在维持*CO*的低水平表达中起重要作用(Morris et al., 2010)。FLOWERING BHLH蛋白FBH1、FBH2、FBH3和FBH4以及中介体复合物PFT1 (PHYTOCHROME AND FLOWERING TIME)/MED25可促进*CO*的表达(Iñigo et al., 2012; Ito et al., 2012b)。此外，MSI1 (MULTICOPY SUPPRESSOR OF IRA 1)可结合组蛋白，在光周期途径中对于*CO*的转录激活是必需的(Steinbach and Hennig, 2014)。

2.2 光受体对CO蛋白稳定性的调控

除*CO*的转录水平调控外，隐花色素、光敏色素和FKF1可以调控CO蛋白的稳定性。在长日照条件下，CO蛋白在早晨丰度很低，而在下午出现积累(Song et al., 2012)。COP1-SPA1 (SUPPRESSOR OF PHYTOCHROME A)泛素连接酶复合体参与CO蛋白丰度的动态调节，可在夜间降解CO蛋白(Laubinger et al., 2006; Jang et al., 2008)。光活化的CRY降低了COP1-SPA1复合物的活性，但CRY1和CRY2对COP1-SPA1复合体活性的抑制机制不同。CRY1与SPA1的C端结合阻止SPA1-COP1复合体的形成(Liu et al., 2011)，而CRY2通过结合SPA1的N端进而促进SPA1与COP1的结合，但抑制SPA1-COP1复合体的活性，促进CO蛋白的积累(Zuo et al., 2011)。此外，光敏色素PHYA可稳定CO蛋白进而促进开花；而PHYB促进CO的降解从而抑制开花。与CRY2机制类似，PHYA也能够抑制COP1-SPA1复合体的形成(Valverde et al., 2004; Sheerin et al., 2015)。PHYB则在早晨以独立于COP1的途径降解CO蛋白(Jang et al., 2008)。还有研究表明，PHL (PHYTOCHROME-DEPENDENT LATE-FLOWERING)参与PHYB依赖的开花调控过程，PHL有可能通过形成PHYB-PHL-CO复合体从而拮抗PHYB对CO的抑制作用(Endo et al., 2013)。除了COP1，另一种E3泛素连接酶HOS1 (HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE1)也参与CO蛋白的去稳定性过程(Lazaro et al., 2012) (图2)。

此外，FKF1能够通过LOV结构域与CO互作从而稳定CO蛋白活性，蓝光能增强它们之间的相互作用(Song et al., 2012)。有研究推测，UVR8可能与光敏色素和/或隐花色素共同竞争COP1 (Favory et al., 2009)。自然状态下的UVR8二聚体在UV-B辐射下解聚成单体，快速在细胞核中积累，其单体直接与COP1结合，推测二者结合进而释放HY5 (ELONGATED HYPOCOTYL 5)转录因子，打开了UV-B信号通路(Rizzini et al., 2011; Jenkins, 2014)。COP1和HY5均是光信号转导的重要下游信号分子，这暗示UV-B信号与可见光信号可能存在相互干扰机制。但是目前UVR8/COP1作用如何影响COP1对下游响应基因的激活并不清楚。

2.3 光受体对*FT*转录水平的调控

*FT*的表达丰度决定了开花时间。CO是*FT*基因主要的转录激活因子之一，CO可以通过其CCT结构域结合*FT*启动子中2个CO应答元件(CO-responsive elements, CORE)，并可能通过富含谷氨酸的区域激活*FT*的转录(Tiwari et al., 2010)。NF-YA、NF-YB和NF-YC形成NF-Y (NUCLEAR FACTOR Y)复合物，结合在*FT*启动子上的CCAAT-box可进一步增强CO介导的*FT*转录激活(Cai et al., 2007; Kumimoto et al., 2008; Cao et al., 2014)。此外，光周期途径B-box家族成员STO (SALT TOLERANT)或BBX24可激活*FT*的表达(Li et al., 2014)，BBX19则被确定为长日照下开花的负调节因子(Wang et al., 2014)。隐花色素、光敏色素以及FKF1等光受体都参与*FT*的转录调控。在蓝光下转录因子CIB1 (CRYPTOCHROME INTERACTING BASIC HELIX-LOOP-HELIX1)与CRY2互作形成CRY2-CIB1复合物并结合*FT*启动子E-box元件(CANNTG)，进而激活*FT*的转录(Liu et al., 2008)。此外，ZTL和LKP2 (不包括FKF1)是CIB1蛋白

积累所必需的(Liu et al., 2013)。CO的转录抑制因子CDF蛋白也可与*FT*启动子结合抑制其转录(Song et al., 2012), 而FKF1-GI复合体可以移除*FT*转录起始位点附近的CDF1, 从而促进*FT*的表达(Song et al., 2012)。GI是PHYB信号转导的重要组分, 可直接激活*FT*的转录(Huq et al., 2000; Sawa and Kay, 2011)。PHYB与GI之间的相互作用已经在体内和酵母双杂交分析中得到证实, 这暗示红光参与*FT*的表达调控(Yeom et al., 2014)。此外, 在红光下PHYB也可与PFT1互作抑制其活性, 进而抑制*FT*的表达(图2)。

3 光受体在其它成花途径中的调控作用

3.1 光受体与春化途径

某些植物需要经历一段低温才能克服开花障碍的现象被称为春化, 春化作用是植物适应温带气候, 防止冬季开花并在春季有利条件下开花的重要保障(Kim et al., 2009)。转录因子FRI (FRIGIDA)和FLC (FLOWERING LOCUS C)在其中发挥重要作用。开花抑制因子FLC与SVP (SHORT VEGETATIVE PHASE)形成蛋白复合体, 进而抑制*SOC1*、*FT*和*FD*的转录(Amasino, 2010) (图2)。持续低温会下调*FLC*的表达及蛋白积累(Helliwell et al., 2006)。拟南芥在营养生长阶段响应低温, 通过一类B3转录因子VAL1 (VERNALIZATION 1)或VAL2等沉默*FLC*的表达, 形成“低温记忆”(Yuan et al., 2016b)。而在开花后的胚胎发育早期, *FLC*会被1个种子特有的“先驱”转录因子LEC1 (LEAFY COTYLEDON 1)重新激活(Tao et al., 2017; 许淑娟和种康, 2018)。此外, *FLC*也被自主途径的内源性调节因子下调表达, 包括染色质修饰因子FVE以及RNA结合蛋白FCA、FPA和FLK (Rataj and Simpson, 2014)。已证明FLC和自主途径中的几个组分影响植物昼夜节律振荡周期(Salathia et al., 2006)。

有研究表明, 光敏色素介导的光信号可以被整合到春化途径中, 参与调控*FLC*的转录(Strasser et al., 2009)。PHYB的互作蛋白VOZ1 (VASCULAR PLANT ONE-ZINC FINGER 1)和VOZ2可抑制*FLC*的表达, 从而促进开花, *voz1*/*voz2*双突变体表现晚花表型(Yasui et al., 2012; Yasui and Kohchi, 2014)。

3.2 光受体与温度途径

适当提高植物营养生长阶段的环境温度可促进开花, 而低温则会抑制开花(Samach and Wigge, 2005)。高温不仅会导致提早开花, 而且还会导致下胚轴和叶柄变长(Balasubramanian et al., 2006)。SVP通过抑制*FT*的转录在开花的温度途径中起重要作用(Lee et al., 2007)。另一类MADS-box蛋白FLM (FLOWERING LOCUS M)可在低温下形成SVP-FLM-β阻遏物, 抑制*FT*的转录; 而在高温下形成的SVP-FLM-δ复合物没有结合DNA的能力, 从而促进开花(Posé et al., 2013)。此外, *SVP*的表达呈现昼夜节律性振荡, 表明温度途径与昼夜节律钟之间存在整合机制(Fujiwara et al., 2008)。拟南芥*phyB*突变体在其最适温度(22°C)下开花提前, 而在16°C该突变体与WT具有相似的开花时间。在*phyA*/*phyB*/*phyD*三重突变背景下, *phyE*的功能突变表现显著的早花表型, 表明16°C时*PHYE*在开花调控中起主要作用(Halliday et al., 2003); *cry1*、*cry2*和*phyA*/*cry2*双突变体在16°C时开花显著推迟, 表明隐花色素和光敏色素也在温度途径中发挥调控开花的功能(Blázquez et al., 2003)。TFL1 (TERMINAL FLOWER 1)和FT二者同属磷脂酰乙醇胺结合蛋白家族(phosphatidylethanola-minebinding protein, PEBP), 尽管其氨基酸序列同源性高达60%, 但*TFL1*抑制开花, 而*FT*促进开花(Coelho et al., 2014)。*tfl1*突变可消除*crys*突变体中的温度反应, 昼夜节律组分*elf3*的突变可以抑制*phyB*突变体的温度反应, 表明至少存在2条路径可以将光信号整合到温度途径中(Strasser et al., 2009)。bHLH类转录因子PIF4 (PHYTOCHROME-INTERACTING FACTOR 4)是连接光受体和环境温度信号转导的重要因子, 通过与*FT*启动子结合介导高温开花, 过表达*PIF4*的株系表现出早花表型(Kumar et al., 2012), 而PIF4蛋白积累受到PHYB的负调控(de Lucas et al., 2008) (图2)。

3.3 光受体与赤霉素途径

赤霉素(gibberellins, GA)可通过降解转录抑制因子DELLA蛋白促进植物开花(Galvão et al., 2012)。GA生物合成途径受阻则会抑制高温下提早开花(Balasubramanian et al., 2006)。转录因子TEM (TEM-

RANILLO)可能具有整合光周期信号和GA途径的功能(Osnato et al., 2012)。TEM1和TEM2可抑制GA生物合成途径中*GA3OX1* (*GA3OXIDASE 1*)和*GA3OX2*基因的表达，过表达*TEM*基因的植物具有类似GA缺失型突变体的表型(Osnato et al., 2012)。此外，TEM1和TEM2也是*FT*的直接抑制因子，二者可与CO竞争结合*FT*启动子，*CO*和*TEM*之间相对蛋白量的高低决定了*FT*的转录水平(Castillejo and Pelaz, 2008)。此外，SRR1 (SENSITIVITY TO RED LIGHT REDUCED)蛋白在调节昼夜节律钟和PHYB介导的信号转导中发挥重要作用(Staiger et al., 2003)。*srr1*突变体和*phyB*突变体表现出许多相似的表型，表明*SRR1*是进行正常的*PHYB*信号转导所必需的。SRR1通过激活CDF1、TEM1、TEM2和FLC等*FT*转录抑制因子的表达，从而抑制拟南芥在短日照条件下开花(Johansson and Staiger, 2014) (图2)。此外，PIF4也可以进行光信号和GA信号的整合(de Lucas and Prat, 2014)。GA信号途径中关键的DELLA蛋白是PIF4的转录抑制因子，DELLA蛋白在长日照条件下以独立于CO和GI的方式调控*FT*的表达。GA含量增加可降低DELLA蛋白的稳定性，进而使PIF4在细胞核中积累(de Lucas et al., 2008)。

3.4 光受体与年龄途径

植物必须完成一定程度的营养生长才能进入生殖生长。miR156和miR172在拟南芥开花的年龄途径中发挥重要作用。成花抑制因子miR156的表达在幼龄期高于成年期，而成花促进因子miR172的表达在幼龄期低于成年期(Wu et al., 2009)。miR156是植物进化上最为保守的miRNA之一，其靶基因是SPLs (SQUAMOSA PROMOTER BINDING LIKEs)转录因子家族基因(Reinhart et al., 2002)。拟南芥基因组中有11个由miR156靶向的*SPL*基因，可以分为*SPL3* (*SPL3*、*SPL4*和*SPL5*)和*SPL9* (*SPL2*、*SPL6*、*SPL9*、*SPL10*、*SPL11*、*SPL13*、*SPL13-like*及*SPL15*)两组(Xing et al., 2010)。SPL9直接结合miR172启动子促进其表达(Wu et al., 2009)。miR172可调节AP2-like转录因子家族基因的转录，包括*AP2*、*SMZ* (*SCHLAFMUTZE*)、*SNZ* (*SCHNARCHZAPFEN*)、*TOE1* (*TARGET OFEAT 1*)、*TOE2*和*TOE3*等*FT*基因的转录抑制因子基因(Chen, 2004; Wu et al., 2009)。年龄途径和光周期途径的整合发生在2个层面上。首先，通过光周期途径中的GI参与miR172丰度的调控(图2)。其次，miR156的靶基因*SPL*在光周期途径的下游起作用，当拟南芥从短日照变为长日照时，*SPL*被快速诱导转录，这一过程可能由2个MADS-box基因*SOC1*和*FUL* (*FRUITFULL*)介导(Wang, 2014)。此外，UV-B可通过调控拟南芥体内miR156水平从而调控开花，UVR8在其中发挥关键作用(Dotto et al., 2018)。

4 总结与展望

在过去的几十年中，高等植物开花的调控网络一直是植物学研究的前沿和热点。目前，不同光受体的分子结构和生理功能已逐渐得到解析，发现了一大批与光受体互作的信号蛋白，人们对光周期途径、温度途径及GA途径的信号转导及整合机制也有了一定的认识(图2)，但是还存在一些问题有待深入研究。例如: (1)植物内源性昼夜节律钟的组分ELF3和GI被整合到光周期途径，而温度和激素等外界信号与昼夜节律钟的关系尚未阐明; (2) 有研究表明低氮会激活*CRY1*的表达，而蓝光信号可以逆转高氮引起的开花延迟(Yuan et al., 2016a)，这为研究氮和磷等营养信号与开花机制的关系提供了思路; (3) 关键信号蛋白的亚细胞定位、磷酸化和泛素化的作用机制有待探究; (4) 除了年龄途径的miR156和miR172，其它的表观遗传调控，如DNA甲基化和组蛋白修饰等在开花调控中的作用尚待揭示; (5) 自主途径通过抑制开花阻遏物和春化途径关键基因*FLC*而促进开花(Yan et al., 2010)，在春化途径中光敏色素参与*FLC*的转录调控，但是自主途径中FLC是否受到光受体的调控尚不清楚。此外，光受体在水稻(*Oryza sativa*)等重要农作物和园艺作物中的功能研究也取得了一定进展(Takano et al., 2005; Yang et al., 2017)，但下游关键调控因子的功能鉴定及其调控机制亟待研究。功能基因组学时代的到来以及转录组学、蛋白质组学、代谢组学和表型组学等组学技术的进步也可能为破解高等植物成花之谜带来全新的视角。

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Advances in Photoreceptor-mediated Signaling Transduction in Flowering Time Regulation

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Abstract Light is an important environmental factor that affects plant growth and development. Flowering is the most important event in higher plants. Plants perceive accurately changes in the surrounding light environments by photoreceptors, thus activating a series of signaling transduction processes and initiating flowering. Here, we summarized the current understanding of the structural characteristics and physiological functions of various photoreceptors in higher plants. We reviewed the molecular mechanisms of phytochromes, cryptochromes, and FKF1/ZTL/LKP2 in mediating signaling transduction and flowering time, including transcriptional and post-transcriptional regulation of *CO* and *FT*. Finally, we described the advances in photoreceptor-mediated-integration of light, temperature, and gibberellin signals in regulating flowering. Future directions in this area were also proposed.

Key words photoreceptor, flowering, phytochrome, cryptochrome

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