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拟南芥 ZTL/FKF1/LKP2 蛋白家族功能研究进展

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摘要:植物通过各类受体来感知外界环境的改变从而调节自身的生长和发育情况。在拟南芥中,植物主要通过隐花色素 (Cryptochromes) 和向光素 (Phototropins) 感知蓝光。同时 ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-box1 (FKF1) 和 LOV KELCH PROTEIN2 (LKP2) 蛋白家族也作为蓝光受体参与调控植物生长发育过程。因其特殊的蛋白结构组成,在植物的光周期开花、节律性和光形态建成等方面发挥了重要的调控作用。近来,ZTL/FKF1/LKP2 蛋白家族被发现参与植物逆境胁迫响应。本文归纳了 ZTL/FKF1/LKP2 的生物学功能研究进展,并对其作用机制进行了总结与讨论。

关键词:ZTL;FKF1;LKP2;光周期开花;生物钟;拟南芥

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Progress of function studies of ZTL/FKF1/LKP2 proteins family in *Arabidopsis*

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Abstract:Plants use a variety of receptors to sense changes in the external environment to regulate their growth and development. In *Arabidopsis*, plants primarily perceive blue light through cryptochromes and phototropins. ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX1 (FKF1), and LOV KELCH PROTEIN2 (LKP2) proteins family also function as a blue light receptor to involve in various developmental processes. Due to its special protein structure, it plays an important regulatory role in plant photoperiodic flowering, rhythm, and photomorphogenesis. Recently, the ZTL/FKF1/LKP2 protein family was found to be involved in plant stress response. This paper reviews the research progress of the biological functions of ZTL/FKF1/LKP2, and summarizes and discusses its mechanism.

Keywords:ZTL; FKF1; LKP2; Photoperiodic flowering; Circadian clock; *Arabidopsis*

植物的生长受到多种环境因素的影响,如温度、湿度、光照等。光不仅是能量来源,也作为周围环境的一部分影响植物的生长发育。植物能够通过各类光受体敏锐地感知光质和光强的变化,进而适应环境的变化。植物体内有一类红光/远红光受体:光敏色素^[1] (Phytochromes) 和两类蓝光受体:隐花色素^[2] 和向光素^[3]。在拟南芥中,主要含有两种同源

的隐花色素,CRY1 和 CRY2。CRY1 主要参与蓝光对下胚轴伸长的抑制作用^[4],CRY2 则主要参与调控植物的开花时间^[5]。拟南芥的向光素也有两种,即 phot1 和 phot2,主要参与控制植物的向光性^[3]。F-box 蛋白家族成员 ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX1 (FKF1) 和 LOV KELCH PROTEIN2 (LKP2) 含有与向光素高度类似

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的 LOV (Light, Oxygen, or Voltage) 结构域^[6], 能够吸收蓝光, 被证明作为蓝光受体在植物体内发挥作用^[7-9]。本文对 ZTL/FKF1/LKP2 蛋白家族的生物学功能研究进展进行综述, 探讨其作用机制。

1 ZTL/FKF1/LKP2 蛋白家族的结构

ZTL/FKF1/LKP2 蛋白家族包含了三个功能结构域: LOV (Light, Oxygen, or Voltage)、F-box 和 Kelch repeats (见图 1)^[10]。LOV 结构域是一个小的光感原件, 属于 PAS 结构域大家族中的一员^[11]。ZTL/FKF1/LKP2 家族成员的 LOV 结构域通过结合黄素单核苷酸 (其作为发色团) 而参与蓝光感知。F-box 结构域通过与 ASK 蛋白家族成员结合参与形

SKP1/CUL1/F-box (SCF) 泛素连接酶复合体^[12]。kelch 重复结构域由 kelch 基序的 5~7 个串联重复组成, 并形成 β -螺旋桨结构, 是典型的蛋白互作结构域^[13]。F-box 蛋白在 SCF 复合体中通过其 kelch 结构域参与识别和结合靶蛋白, 促进靶蛋白被泛素化降解^[14]。ZTL/FKF1/LKP2 蛋白家族在植物体内通常通过其 F-box 结构域和 kelch 结构域, 行使 SCF 泛素连接酶的功能^[15-16]。因此, 这三个功能结构域赋予 ZTL/FKF1/LKP2 即能作为蓝光受体在植物体内参与光信号传导, 也具有 F-box 蛋白的功能。ZTL/FKF1/LKP2 通常介导靶蛋白以蓝光依赖的方式通过泛素蛋白酶体途径降解, 进而调控植物的生长发育。

	LOV	F-box	Kelch repeat		
ZTL	32	161	195	241 292	564
FKF1	35	158	196	242 293	579
LKP2	44	168	211	257 304	571

图 1 ZTL/FKF1/LKP2 的蛋白结构

Fig.1 Protein structures of ZTL/FKF1/LKP2

2 ZTL/FKF1/LKP2 蛋白家族的功能

ZTL/FKF1/LKP2 蛋白家族虽然在氨基酸序列上具有很高的相似性 (70%~80%)^[7-9], 但三者并没有表现出很明显的功能重叠, 在植物体内的功能差异较大。例如; ZTL 在生物钟的调控中更为关键; FKF1 则在光周期开花调控中的作用更为显著^[7-8]; LKP2 在生物钟调控中也扮演着重要的角色^[17]。因为这些相似与差异, 三者的作用机制也更为复杂。

2.1 ZTL/FKF1/LKP2 蛋白家族参与调控生物钟

植物生物钟振荡受到多种转录因子和蛋白的调控, 包括 *TIMING OF CAB EXPRESSION1* (*TOC1*, 也叫做 *PRR1*)、*CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*) 和 *LATE ELONGATED HYPOCOTYL* (*LHY*)。这些转录因子和蛋白构成多个负反馈循环, 组成中心振荡器, 共同维持生物钟的正常运行^[18-19]。例如; *TOC1* 在夜晚表达, 能够在黎明通过直接调节转录因子 *CCA1 HIKING EXPEDITION* (*CHE*) 的活性, 使 *CCA1* 和 *LHY* 的表达增加, 而 *CCA1* 和 *LHY* 则负调节 *TOC1* 的表达, 从而形成负反馈循环共同调控

生物钟振荡^[20-22]。在拟南芥中, ZTL/FKF1/LKP2 蛋白家族主要通过调节生物钟蛋白的稳定性, 参与调控生物钟振荡。ZTL 的 LOV 结构域能够特异的结合 *TOC1* 和 *PSEUDO RESPONSE REGULATOR 5* (*PRR5*), 进而促进这些蛋白通过泛素蛋白酶体途径降解 (见图 2)^[23]。*TOC1* 和 *PRR5* 蛋白在 *ztl* 突变体中积累, 在 ZTL 过表达株系中则减少^[24]。在白天, 蓝光诱导 ZTL 与 *GIGANTEA* (*GI*) 结合, 从而保护 *TOC1* 和 *PRR5* 免于被 ZTL 降解 (见图 2)^[25]。虽然 LKP2 和 FKF1 都能够与 *TOC1* 和 *PRR5* 结合, 但是其作用较 ZTL 弱^[23]。最近研究发现, ZTL 与 *CHE* 直接相互作用, 介导 *CHE* 的泛素化降解 (见图 2)。在黑暗中, *CHE* 蛋白降解, 而在 *ztl* 突变植物中降解速度变慢^[14]。此外, ZTL 也可通过感知蓝光强度的变化来调控植物的生物钟振荡^[26]。

Somers 等^[8]2000 年报道, 长日照 (LD) 条件下, *ztl* 突变体表现出明显的长周期表型, 而 *fkf1* 突变体则没有明显的生物钟周期缺陷^[23]。*lkp2* 功能缺失突变体的生物节律与野生型也基本一致^[27]。与 *ztl* 单突变体相比, *lkp2 ztl* 双突变体的周期节律并没有明显变化, 而 *fkf1 ztl* 则表现出较长的周期^[28]。在红

光或蓝光下,将 ZTL 的 LOV 或 LOV-F-box 结构域过表达导致昼夜节律延长^[25]。LKP2 的 LOV 或 LOV-F-box 结构域过表达植株则表现出更短的周期^[17]。

ZTL LOV 和 LKP2 LOV 对生物钟调控的不同作用可能是由于它们的相互作用蛋白不同,或者对相互作用蛋白的亲合力不同有关,还有待进一步研究。

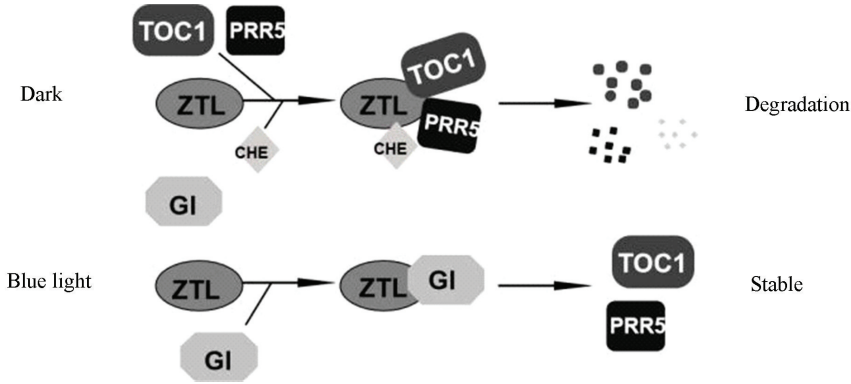


图 2 ZTL/FKF1/LKP2 光介导调控生物钟蛋白的稳定性

Fig.2 ZTL/FKF1/LKP2 mediate light regulation of circadian clock proteins stability

2.2 ZTL/FKF1/LKP2 蛋白家族在光周期开花途径中的功能

植物开花时间受到多种内外源因素精确调控,形成了光周期、自主开花、赤霉素和春化多种开花途径^[29]。拟南芥是长日照植物,长日照诱导其开花,短日照则抑制其开花。锌指型转录因子 *CONSTANS* (*CO*)对 *FLOWERING LOCUS T* (*FT*) 基因表达量的调控,在拟南芥光周期开花途径中至关重要^[30]。长日照下,*CO* 直接结合 *FT* 的启动子,促进 *FT* 的表达,进而促进开花^[31]。ZTL、FKF1 和 LKP2 通过直接调控 *CO* 蛋白的稳定性,或者调控 *CO* 基因的转录水平,进而调控光周期开花。ZTL 在长日照中介导 *CO* 蛋白在早上降解^[32];FKF1 则在长日照中通过其 LOV 结构域与 *CO* 蛋白结合,维持 *CO* 蛋白在傍晚

的稳定性,进而促进 *FT* 的表达(见图 3)^[33]。FKF1/ZTL/LKP2 还协同介导转录因子 *CYCLING DOF FACTOR 1* (*CDF1*) 和 *CDF2* 蛋白降解,解除 *CDF1* 和 *CDF2* 对 *CO* 转录的抑制作用,诱导 *CO* 转录表达,从而促进开花(见图 3)^[34-36]。此外,光依赖的 *FKF1-CONSTITUTIVE PHOTOMORPHOGENIC1* (*COP1*)相互作用,通过抑制 E3 泛素连接酶 *COP1* 的活性,解除 *COP1* 对 *CO* 蛋白的降解,进而促进 *FT* 的表达和开花(见图 3)^[37-38]。最近研究发现,FKF1 与赤霉素信号途径关键负调节子 *DELLA* 蛋白互动,部分通过促进 *DELLA* 蛋白降解进而促进植物开花(结果未发表)。此外,*ztl* 突变还导致花开放、香味散发、花梗运动的节律发生改变^[39]。

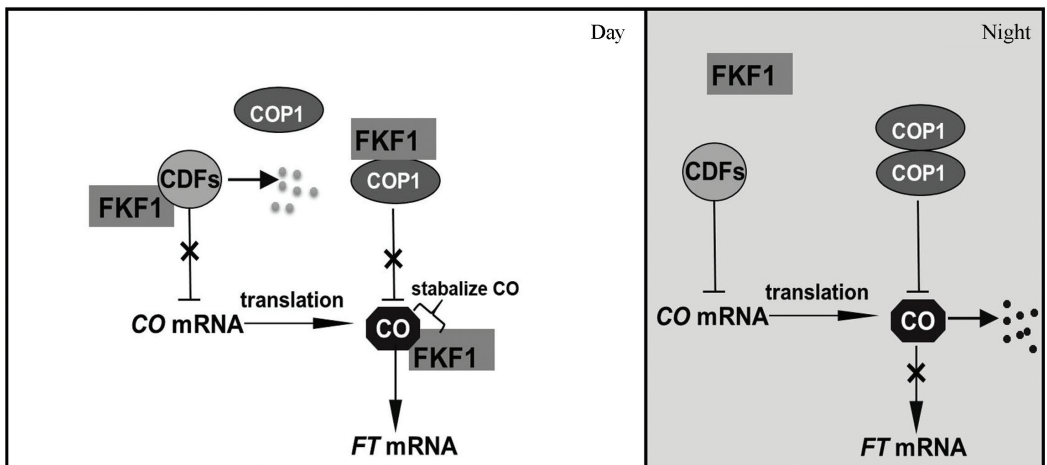


图 3 FKF1 在光周期开花途径中的功能

Fig.3 Function of FKF1 in the control of photoperiodic flowering

在光周期开花信号通路中,虽然 ZTL/FKF1/LKP2 有多个相同的靶蛋白,但其中起主导作用的是 FKF1。长日照下, *fkf1* 突变体表现出明显的晚花表型^[36]。短日照下, *ztl* 突变体表现微弱的早花表型;在短日照和长日照下, *lkp2* 突变体无明显开花表型, *lkp2 ztl* 双突变则表现出比 *ztl* 单突变体更明显的早花表型,且这种早花表型依赖于 FKF1^[24]。相反,过表达 ZTL 或者 LKP2 下调了 *CO* 和 *FT* 的表达,导致植物在长日照下开花延迟,这种晚花表型也依赖于 FKF1^[24]。ZTL 和 LKP2 主要通过调控 FKF1 蛋白定位和蛋白水平,进而调控植物光周期开花^[24,40]。

2.3 ZTL/FKF1/LKP2 蛋白家族的其它功能

ZTL/FKF1/LKP2 除了影响植物光周期开花以及生物钟节律外,在植物光形态建成、逆境胁迫响应中也起重要调控作用。LKP2 促进白光下拟南芥幼苗下胚轴伸长。LKP2 过表达导致拟南芥幼苗中生长素 IAA 水平升高,PHYTOCHROME-INTERACTING FACTOR4 (PIF4) 和 PIF5 的表达水平上调,进而使下胚轴伸长^[41]。ZTL 也促进白光下拟南芥幼苗下胚轴伸长,并且在高温诱导的下胚轴伸长中起正调控作用^[42]。*fkf1* 突变体在红光和蓝光下则表现出短下胚轴的表型,因此 FKF1 在光形态建成中可能起负调控作用^[7]。Gil 等^[43] 2017 年研究发现 ZTL 能够与 Heat shock protein 90 (HSP90) 互作,介导响应高温而形成的蛋白聚集体的泛素化降解,控制蛋白的质量,从而稳定生物钟并增强植物的耐热性。此外,LKP2 在植物干旱胁迫响应中起正调控作用,LKP2 过表达使植物气孔孔径变小,干旱胁迫响应基因表达量上升,耐旱性增强^[44]。

3 展 望

近年来,关于 ZTL/FKF1/LKP2 的研究更多的关注于其在植物生物钟和光周期开花途径中的功能及其调控机制。ZTL/FKF1/LKP2 也参与调控植物其它生物学过程,包括光形态建成和逆境胁迫响应,但其作用机制尚不完全明确。已有的基因芯片结果显示,LKP2 过表达引起了众多信号通路基因的改变,尤其是生长素信号通路相关基因表达发生明显改变^[44]。目前,有研究报道,蓝光受体 CRY1 和红光/远红光受体 PHYB /PHYA 能够与 AUX/IAA 蛋白互作来影响生长素的信号转导,调控植物的生长发育^[45-46]。同时,CRY1 能够通过调节油菜素内酯 (BR) 的合成^[47] 与信号转导^[48-49] 来影响植物的光形态建成。最新研究表明,紫外光 UV-B 与 BR 信号协同调控下胚轴伸长^[50]。因此,ZTL/FKF1/LKP2

也可能在光信号通路与激素信号通路的交叉会话中发挥作用,这为我们今后的研究提供新的思路。

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