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PIF4转录因子调控植物热形态建成研究进展

赵小刚, 隋心意, 温祥珍*
山西农业大学园艺学院, 山西晋中030801
*通信作者(330821473@qq.com)

摘要: 热形态建成是植物在长期进化中产生的适应性性状。叶柄和节间伸长、叶片偏上生长有助于增强蒸腾作用, 提高植物对高温的适应性。研究表明, 光敏色素互作因子PIF4通过整合光照、昼夜节律和激素信号调控植物热形态建成。本文从这三方面介绍了近年来国内外对于PIF4在热形态建成方面的研究进展, 旨在为后续工作提供一些提供参考。此外, 本文也提出了本领域需要进一步研究的科学问题, 试图为解释PIF4调控热形态建成的分子机理提供新的研究信息。

关键词: 热形态建成; PIF4; 光照; 昼夜节律, 激素

Research progress of PIF4 transcription factors participating in plant thermomorphogenesis

ZHAO Xiaogang, SUI Xinyi, WEN Xiangzhen*
College of Horticulture, Shanxi Agricultural University, Jinzhong, Shanxi 030801, China
*Corresponding author (330821473@qq.com)

Abstract: Thermomorphogenesis is an adaptive trait produced by plants during long term evolution. Elongation of petioles and internodes and upward growth of leaves can enhance transpiration and improve the adaptability of plants to high ambient temperature. Phytochrome interacting factor 4 (PIF4) regulates plant thermomorphogenesis by integrating light, circadian rhythm and hormone signals. This article introduced research progress of PIF4 in thermomorphogenesis from three aspects, in order to provide reference for cultivate heat resistant varieties by molecular method. In addition, we proposed some scientific issues required for further investigations in this field to provide a research clue for understanding the molecular mechanisms of thermomorphogenesis regulated by PIF4.

Key words: thermomorphogenesis; PIF4; light; circadian rhythm; hormone

热形态建成(thermomorphogenesis)是指植物响应环境高温而产生的形态学变化(Erwin等1989; Quint等2016), 包括叶柄(petiole)、节间(internode)和下胚轴(hypocotyl)伸长(Gray等1998; van Zanten等2009), 偏上生长(hyponasty) (Koini等2009), 开花期提前(early flowering)等。叶柄、下胚轴伸长和偏上生长可以使叶片和土壤、叶片和叶片相互分离, 确保在水分充足的条件下实现最佳蒸腾(Gray等1998), 有助于植物在高温条件下生存(Crawford等2012)。但热形态建成会强制改变植物的碳源分配(Fukai和Silsbury 1976), 影响作物品质和产量(Lobell和Gourdji 2012; Bita和Gerats 2013), 并且松散的形态结构也使得植株倒伏风险增加(Berry等2004; Jung和Müller 2009)。Koini等(2009)研究表明, 光敏色素互作因子4 (PHYTOCHROME INTERACTING FAC-

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TOR 4, PIF4)是植物热形态建成的核心转录因子, 该基因通过接受外部光照信号来调控其内部昼夜节律、激素信号, 从而促进植株热形态建成。本文以拟南芥(*Arabidopsis thaliana*)热形态建成的分子机制为例, 对PIF4调控热形态建成的几个方面进行综述, 期望为后续研究和耐热新品种培育提供借鉴。

1 PIF4的结构及功能

PIF4属于螺旋-环-螺旋(basic Helix-Loop-Helix, bHLH)第15亚家族, 是重要的植物光形态建成抑制因子, 主要与PHYB结合介导光信号转导(Koini等2009)。免疫共沉淀分析(co-immunoprecipitation, CoIP)表明PIF4 N端的APB (ACTIVE PHYTOCHROME B BINDING DOMAIN)结合基序是PIF4与PHYB特异性结合不可缺少的功能结构域(Huq和Quail 2002)。缺失APB结构域的PIF4蛋白在红光条件下的稳定性增加, 说明PIF4与PHYB蛋白的相互作用对于红光诱导的PIF4蛋白降解是必须的(Shen等2007; Lorrain等2008)。PIF4 C端的bHLH功能结构域含有DNA结合域和HLH结构域。大部分bHLH家族蛋白的DNA结合域通过与靶基因启动子区的顺式调控元件E-box (5′-CANNTG-3′)相结合, 在转录水平上调控靶基因表达。染色体免疫共沉淀测序(chromatin immunoprecipitation followed by sequencing, ChIP-seq)和凝胶电泳迁移分析(electrophoresis mobility shift assay, EMSA)发现, G-box基序高度富含PIF4的目标启动子, 表明PIF4在体外与G-box基序结合(Huq和Quail 2002; Oh等2012)。

研究表明, 将野生型拟南芥转移到高温环境后不久, *PIF4*的转录显著增加, 并触发热形态建成, 而*pif4*突变体在高温条件下不表现出热形态建成的表型(Koini等2009; Sun等2012), 初步确定PIF4参与热形态建成。近10年的研究进一步表明, PIF4是热形态建成中的分子中心枢纽, 通过整合光信号、昼夜节律和激素信号调控热形态建成(Nomoto等2012; Jin和Zhu 2019; Qiu 2020)。

2 光信号调控PIF4介导的热形态建成

光信号是调控植物生长发育的重要环境因素之一, 不仅为其整个生长发育过程的光合作用提供能量, 而且参与调控植物体内众多的信号转导途径, 如光形态建成、庇荫反应、开花和衰老等过程。植物通过光受体来感知环境中光信号的存在、缺失、波长、强度、方向以及持续周期的变化, 并转换为内源信号调整自身的生长和发育。

模式植物拟南芥的光受体(photoreceptor)主要包括: (1)吸收红光/远红光(600~750 nm)的光敏色素(PHYTOCHROME, PHY) (Chen和Chory 2011); (2)吸收蓝光(320~500 nm)的向光素(PHOTOTROPIN, PHOT) (Christie 2007)、隐花色素(CRYPTOCHROME, CRY)和ZTL/FKF1/LKP2 (ZEITLUPE/FLAVIN BINDING KELCH REPEAT F-BOX1/LOV KELCH PROTEIN2)基因家族(Suetsugu和Wada 2013); (3)吸收紫外光UV-B (280~320 nm)的紫外光受体(UVB-resistance locus 8, UVR8) (Rizzini等2011)。这些光受体家族既相互独立, 又存在功能冗余, 共同调控植物的生长发育进程。长期以来, 人们认为光受体主要在光形态建成中发挥功能。但最近的研究表明, 光受体可能是植物感受环境高温的传感器。那么, 植物光受体如何调控PIF4介导的热形态建成? 下文主要针对这个问题进行综述。

2.1 光敏色素PHYB促进热形态建成

光敏色素是研究最为广泛的一类光受体, 主要参与植物对红光和远红光的调控。拟南芥光敏色素基因家族有PHYA、PHYB、PHYC、PHYD和PHYE共5个成员。PHYA是一类在光照下迅速分解的光不稳定型蛋白, 在远红光下起主要作用(Nagatani等1993), 主要参与植物由暗形态建成转变为光形态建成的调控(Bae和Choi 2008)。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等2010)。PHYB主要参与光形态建成、避荫反应和开花等生长发育过程(Guo等1998)。PHYC、PHYD、PHYE与PHYB共同参与避荫反应和光形态建成(Franklin等2003)。

光敏色素的功能与其蛋白活性密切相关。光敏色素存在不具有生物活性的红光吸收型Pr (phytochrome R-absorbing form, λ_{max}=660 nm)和具有生物活性的远红光吸收型Pfr (phytochrome FR-absorbing isomer, λ_{max}=730 nm) 2种类型。一般来说, 照射红光, Pr转变为Pfr, 并从细胞质转移到细胞核, 并降解光敏色素相互作用因子(PHYTOCHROME INTERACTING FACTORS, PIFs), 从而促进光形态建成; 照射

远红光, Pfr转变为Pr, 并从细胞核转移到细胞质, 植物光形态建成抑制因子表达量增加, 从而促进暗形态建成(Huq和Quail 2002)。但是在高温条件下, 光敏色素会发生“热逆转”, 即在高温条件下, 光敏色素在光下也以不具有生物活性的Pr型存在(Klose等2015; Burgie等2017), 这种转换对调节植物形态建成具有重要作用(Wada等2005)。

以PHYB为例。常温条件下, 黑暗中, PHYB以不具有生物活性的Pr型定位于细胞质中, 与此同时, PIF4蛋白在细胞核中大量积累, 抑制光形态建成相关基因表达, 进而抑制光形态建成; 照光后, PHYB由无生物活性的Pr型转变为有生物活性的Pfr型, 从细胞质转移到细胞核, 并与细胞核内的PIF4蛋白相互作用, 进而引起PIF4蛋白被磷酸化、泛素化及降解, 光形态建成相关基因得以表达, 进而促进光形态建成(Huq和Quail 2002)。另外, 照光后, 有生物活性的Pfr型的PHYB与HFR1结合, 并与光敏色素A抑制因子SUPPRESSOR OF PHYA (SPA)形成PHYB-COP1-SPA蛋白复合体, 限制COP1对TAA1的降解, 进而促进光形态建成(Yang等2005; Chang等2011)。

高温条件下, 红光/远红光通过PHYB调节PIF4蛋白的丰度来促进热形态建成。在高温、光照条件下, PHYB转化为不具有生物活性的Pr型, 具有生物活性的Pfr型PHYB数量减少, PIF4蛋白在光照条件下的丰度提高, 并结合到生长素生物合成途径的关键酶基因*YUCCA8* (*YUC8*)、*TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1* (*TAA1*)和*CYTOCHROME P450 FAMILY 79B2* (*CYP79B2*)的启动子上, 通过调节这些基因的表达促进生长素生物合成, 进而促进热形态建成(Sun等2012)。此外, PHYB信号转导中的转录激活因子HEMERA (HMR)与PIF4相互作用, 从而促进热形态建成(Qiu 2020)。但是PHYB突变体仍然具有对高温的响应能力, 所以PHYB不是光敏色素家族中唯一的热敏传感器(Casal和Balasubramanian 2019)。另外, 有研究发现PHOTOPERIODIC CONTROL OF HYPOCOTYL1 (PCH1)和PCHL通过与具有生理活性的Pfr型PHYB互作降低其热逆转速率, 进而减缓热形态建成(Enderle等2017)。

2.2 隐花色素CRY1抑制热形态建成

隐花色素是一类似光裂解酶(photolyase)的蓝光/紫外光A受体, 最早在拟南芥中通过遗传筛选蓝光不敏感突变体时被发现(Ahmad和Cashmore 1993)。拟南芥隐花色素基因家族有CRY1、CRY2和CRY3共3个成员。其中CRY1主要调控光形态建成(Ahmad和Cashmore 1993), CRY2主要调控光周期开花(Liu等2018), CRY3不具有光受体活性, 但能以光依赖的方式修复UV对DNA的损伤(Jansen等1998)。

照光后, CRYs形成同源二聚体或发生寡聚化, 进而行使功能。CRYs的功能由N端的PHOTOLYASE HOMOLOGOUS REGION (PHR)结构域和C端的CRYPTOCHROME C-TERMINAL DOMAIN (CCE)结构域决定。其中PHR结构域主要调控CRYs同源二聚体的形成; CCE结构域主要调控蛋白互作和光信号转导(Busza等2004; Banerjee等2007)。照光后, CRYs通过构象变化形成具有活性的同源二聚体, 并通过与下游蛋白互作进行光信号转导(Shao等2020)。另外有研究发现, 照光后, CRY2的黄素腺嘌呤二核苷酸(FAD)结合口袋的体积变大, 促进CRY2蛋白的寡聚化, 进而调控植物对光信号的响应(Ma等2020)。

以CRY1为例: 常温条件下, 黑暗中, SPA与COP1形成SPA-COP1蛋白复合体, COP1活性被激活, 泛素化并降解光形态建成正调节因子ELONGATED HYPOCOTYL5 (HY5), 植物光形态建成受到抑制; 照光后, 被光激活的CRY1与SPA结合形成CRY1-SPA复合体, 进而抑制SPA-COP1蛋白复合体形成, HY5蛋白积累量增多, 促进植物光形态建成(Liu等2011; Lian等2011)。照光后CRY1与生长素调控基因*AUXIN/INDOLE-3-ACETIC ACID* (*AUX/IAA*)发生相互作用, 从而抑制生长素受体TRANSPORT INHIBITOR RESPONSE1 (TIR1)与AUX/IAA的结合, 导致生长素诱导的AUX/IAA蛋白降解被抑制, 进而促进光形态建成(Xu等2018)。

高温条件下, 蓝光通过CRY1调节PIF4的转录活性来抑制热形态建成。CRY1和PIF4形成复合体并结合到PIF4下游靶基因的启动子上, 抑制PIF4下游靶基因的表达(Ma等2016)。另外, CRY1通过抑制COP1的活性来稳定温度响应负调节因子HFR1, HFR1通过与PIF4形成非DNA结合的异二聚体来抑制PIF4与靶基因结合(Hornitschek等2009; Foreman等2011)。此外, Gangappa和Kumar (2017)发现, 高温条件下, HY5通过与PIF4竞争结合*YUC8*、*TAA1*

等下游基因的启动子, 进而抑制热形态建成。

2.3 UVR8抑制热形态建成

紫外光受体UVR8是吸收紫外线UV-B的色素蛋白, 主要参与抑制下胚轴伸长、促进黄酮和花青素积累(Fasano等2014)、调节生物节律和气孔运动(Fehér等2011; Tossi等2014)以及提高光合速率(Davey等2012)等生物学过程。

UVR8的功能与其蛋白的存在状态密切相关。在没有UV-B的情况下, 两分子的UVR8蛋白通过稳定的电荷作用形成完全对称的同源二聚体; 照光后, UVR8蛋白从二聚体变为单体, 并与COP1相互作用从而起始UV-B信号通路, 引起转录调节和下游应答(Rizzini等2011)。

常温条件下, UVR8主要通过UVR8-COP1-HY5途径调控光形态建成。但与在可见光条件下不同, COP1在紫外光下主要发挥正调控因子的作用。Oravecz等(2006)发现, 在紫外光条件下, 与COP1互作不会导致UVR8蛋白活性降低或降解。据此推测UVR8可能是导致COP1功能变化的主要原因。照射紫外光后, UVR8和COP1形成稳定的UVR8-COP1蛋白复合体(Favory等2009; Cloix等2012), 并通过泛素化WD重复蛋白REPRESSOR OF UV-B PHOTOMORPHOGENESIS1 (RUP1)和RUP2稳定HY5蛋白(Ren等2019)进而促进光形态建成。暗中, UVR8蛋白由单体转化为二聚体, COP1通过泛素化途径降解HY5, 进而抑制光形态建成。此外, UVR8还通过与BR途径的正调控因子BRI1-EMS-SUPPRESSOR1 (BES1)/BES1-INTERACTING MYC-LIKE1 (BIM1)形成蛋白复合体, 进而抑制光形态建成(Liang等2018)。

高温条件下, 紫外光UV-B通过调节PIF4的转录来减弱热形态建成。UVR8不和PIF4相互作用, 而是以COP1依赖的方式调节PIF4的转录活性。在高温条件下, UV-B以依赖UVR8-COP1的方式减少PIF4转录(Hayes等2014)。另外, UVR8通过隔离COP1抑制HFR1降解, 高度积累的HFR1与PIF4形成二聚体, 限制PIF4对热敏基因的转录活性(Hayes等2016), 进而抑制热形态建成。

综上所述, 高温条件下, PHYB、CRY1和UVR8通过调节PIF4的转录或PIF4蛋白的水平来调节热形态建成。但是其他光受体是否参与了热形态建成? 调控植物光形态建成的其他基因是否参与了PIF4介导的热形态建成? 目前还不清楚。

3 生物钟调控PIF4介导的热形态建成

生物钟(circadian clock)是植物为适应昼夜变化、温度变化和季节交替而产生的信号系统, 它可以使植物预计外界环境波动, 协调重要的生理活动和发育过程。从概念上来说, 生物钟主要由输入途径(input pathway)、核心振荡器(central oscillator)和输出途径(output pathway) 3个部分组成(Barak等2000; Murtas和Millar 2000)。其中输入途径主要负责将光照和温度等环境信号传输到核心振荡器; 核心振荡器, 即生物钟的核心, 主要负责调控并产生近似24 h的昼夜节律; 输出途径主要负责接收核心振荡器产生的信号, 把生物钟与下胚轴伸长、叶片运动、气孔开闭和开花等生物过程相偶联。生物钟的这三个部分之间相互联系, 相互应答, 共同调控植物的生长发育(Pruneda-Paz和Kay 2010)。

Nozue等(2007)发现拟南芥*elf3*突变体*PIF4*的节律性表达和PIF4蛋白的丰度发生紊乱, 进而导致在常温下生长的拟南芥表现出与热形态建成类似的表型。那么, 生物钟怎样调控PIF4介导的热形态建成? 下文主要针对这个问题进行综述。

3.1 核心振荡器

核心振荡器由3个紧密关联的负反馈环组成。其中MYB类转录因子LATE-ELONGATED HYPOCOTYL (LHY)、CIRCADIAN CLOCK ASSOCIATED1 (CCA1)与伪应答调节因子TIMING OF CAB EXPRESSION1 (TOC1/PRR1)形成中心循环(core loop), PSEUDO RESPONSE REGULATOR5 (PRR5)、PRR7、PRR9与LHY、CCA1形成早晨循环(morning loop), EARLY FLOWERING3 (ELF3)、ELF4、LUX ARRHYTHMO (LUX)与LHY、CCA1形成傍晚循环(evening loop) (Shim和Imaizumi 2015)。从午夜到清晨, *LHY*和*CCA1*的表达量逐渐增加, 并依次促进*PRR9*和*PRR7*表达, 同时抑制*ELF3*、*ELF4*和*LUX*表达(Farré等2005); 从清晨到傍晚*PRR9*、*PRR7*和*PRR5*表达量逐渐增加, 并抑制*LHY*和*CCA1*表达(Nakamichi等2005); 从傍晚到午夜, *ELF3*、*ELF4*、*LUX*和*TOC1*表达量逐渐增加, 抑制*PRR9*、*PRR7*和*PRR5*表达; *TOC1*在午夜表达会抑制*CCA1*

表达(Gendron等2012)。此外, 位于输出途径的GI-GANTEA (GI)和ZTL参与傍晚循环, 并通过与中心循环的TOC1相互作用维持昼夜节律的稳定性(Kim等2007)。这样, 中心循环、早晨循环和傍晚循环共同组成了植物的生物钟系统, 并通过反馈调节将这个系统维持在一种相对平衡的状态, 以保证植物更好地适应环境变化。

3.2 EC调控PIF4在夜间的表达

Nozue等(2007)发现, PIF4在夜间的表达主要受由ELF3、ELF4和LUX组成的“晚间复合体” (evening complex, EC)调控。另外有研究表明, ELF3可以与PIF4通过蛋白-蛋白互作的方式调节植物生长(Nomoto等2012)。常温条件下, 从清晨到傍晚, EC蛋白的丰度逐渐增加, EC与*PIF4*的启动子结合并抑制其表达; 当EC蛋白的丰度在傍晚达到高峰时, *PIF4*的表达量最低(Covington等2001; Niwa等2009)。从午夜到中午, *PIF4*的表达量逐渐增加, 中午达到高峰(Proveniers和van Zanten 2013)。但是照光后, PIF4被PHYB和蛋白激酶BRASSINOSTEROID INSENSITIVE2 (BIN2)介导的信号转导迅速磷酸化和泛素化(Bernardo-García等2014), 因此PIF4蛋白的丰度从午夜到清晨逐渐提高, 从清晨到中午逐渐降低。PIF4蛋白这种在暗中积累、光下降解的模式有助于协调暗形态建成和光形态建成, 促进植物正常生长发育。

高温条件下, EC和ELF3结合*PIF4*启动子的能力减弱, 同时, 光信号调控因子DE-ETIOLATED1 (DET1)和COP1促进*PIF4*的表达并提高PIF4蛋白稳定性, 进而促进拟南芥热形态建成(Box等2015; Gangappa和Kumar 2017)。但究竟是哪种信号转导限制EC、ELF3和*PIF4*的启动子结合, 目前还没有明确的研究结果。Ding等(2018)发现, 温度升高时, BBX18、BBX23通过和ELF3互作抑制其在夜间的表达, 进而促进热形态建成。有两项研究表明, ELF3的变异解释了拟南芥株系中由温度诱导的PIF4表达和下胚轴伸长的大部分自然变异, 这个研究结果进一步说明了高温信息主要通过ELF3直接传送到PIF4 (Park等2017)。随后Jung等(2020)进一步发现ELF3主要通过PRION-LIKE DOMAIN (PrD)介导的相变感受环境温度变化。但是在长日照条件下生长的拟南芥*elf3*突变体仍然能表现出热形态建成表型, 因此可能存在特异性机制调节长日照条件下的热形态建成(Qiu 2020)。

3.3 GI调控PIF4在白天的表达

研究发现, GI通过抑制PIF4在白天的表达来维持生物钟核心基因在白天表达的稳定性, 进而限制热形态建成(Gould等2006)。在光照条件下, GI通过与DELLA蛋白互作增强其稳定性, 并直接影响DELLA蛋白的积累和响应赤霉素(gibberellins, GAs)的敏感性, 进而限制热形态建成(Nohales和Kay 2019)。长日照条件下GI蛋白的丰度远高于短日照条件下GI蛋白的丰度, 因此GI主要抑制长日照条件下的热形态建成(Qiu 2020)。

综上所述, 高温条件下, 生物钟通过调节PIF4的转录或PIF4蛋白的水平来调节热形态建成。但是目前对生物钟调控热形态建成的研究主要集中在EC蛋白复合体和GI基因这两方面, 生物钟的其他基因是否参与了PIF4调控的热形态建成? 不同光周期条件下PIF4调控热形态建成的机理是否相同? 目前还没有明确的研究结果。

4 PIF4通过调控激素合成介导热形态建成

激素的生物合成和信号转导基因是PIF4的主要靶基因, 这将PIF4与激素联系起来。研究发现, 生长素(auxin)、GAs和油菜素内酯(brassinosteroids, BRs)在热形态建成中起主要作用。那么, PIF4如何通过调控激素合成介导热形态建成? 下文主要针对这个问题进行综述。

4.1 生长素

生长素和生长素信号在PIF4介导的热形态建成中发挥重要作用(Franklin等2011; Sun等2012)。高温条件下, *PIF4*结合到*TAA1*、*YUC8*和*CYP79B*的启动子上, 刺激生长素的生物合成(Mashiguchi等2011; Stepanova等2011; Won等2011)。生长素生物合成激活生长素受体(TRANSPORT INHIBITOR RESPONSE1/AUXIN-RELATED F-BOX, TIR/AFBs)家族的F-box蛋白和AUX/IAA、生长素响应因子AUXIN RESPONSE FACTORS (ARFs)介导的转录级联(Chapman和Estelle 2009)。生长素-$SCF^{TIR/AFB}$复合物泛素化并靶向降解AUX/IAA, 减轻其对ARFs的抑制并启动生长素转录反应(Leyser 2010)。生长素的生物合成诱导*SMALL AUXIN UP RNA 19*~

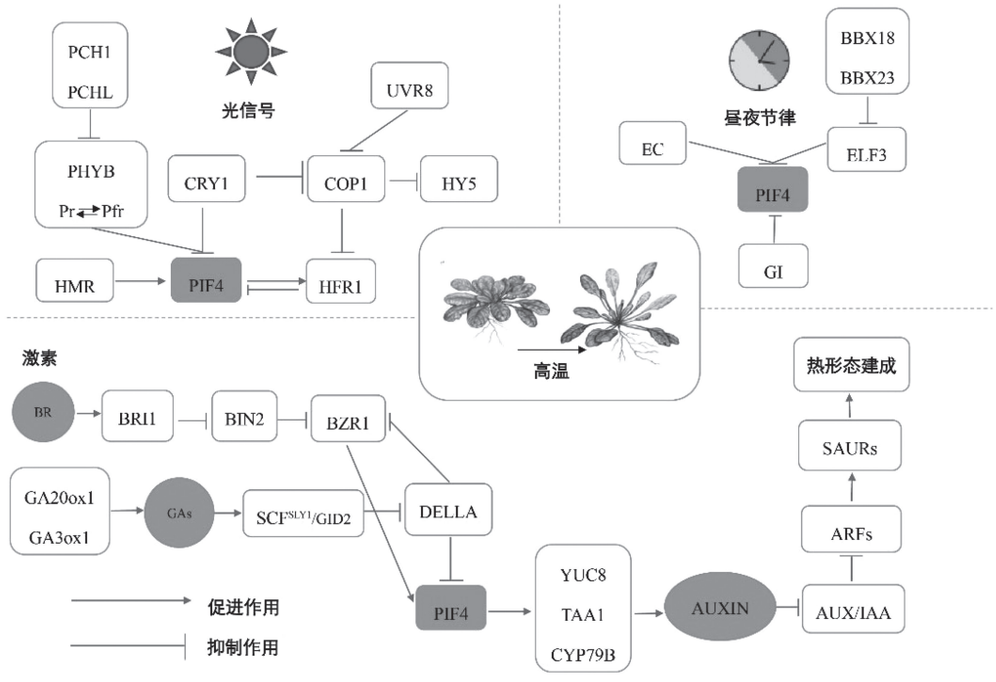

图1 PIF4调控热形态建成模式

Fig. 1 The model of PIF4 regulating thermomorphogenesis

24 (*SAUR19~24*), *SAUR61~68*上调表达(Stavang等2009; Franklin等2011), 这些基因通过增加细胞质膜的氢离子的浓度促进热形态建成(Chae等2012; Spartz等2012)。

4.2 赤霉素

高温促进GAs生物合成基因表达量增加和抑制生长的DELLA蛋白降解, 进而促进热形态建成。拟南芥DELLA蛋白是由5个部分功能冗余的基因*GA INSENSITIVE* (*GAI*)、*REPRESSOR OF ga1*-3 (*RGA*)和*RGA-LIKE1~3* (*RGL1~3*)编码的一个抑制因子家族。常温条件下, 这些基因结合*PIF4*的DNA识别域, 抑制其转录活性(Feng等2008, Gallego-Bartolomé等2010)。高温条件下, 拟南芥幼苗中GAs生物合成基因*GA20ox1*和*GA3ox1*的表达上调, GAs合成增加(Stavang等2009)。GA受体基因*GIBBERELLIN INSENSITIVE DWARF1* (*GID1*)对GA的感知促进了GA-GID1复合体与DELLA相互作用, 有利于E3连接酶复合体SCF^{SLY1}/GID2识别这些抑制因子, 促进DELLA蛋白泛素化及26S蛋白酶体介导的降解, 释放PIF4, 激活细胞伸长基因(Willige等2007; Gao等2011; Sun等2012)。但是拟南芥*DELLA*蛋白五突变体幼苗仍然表现出微弱的下胚轴伸长反应, 因此GAs途径并不足以诱导热形态建成(Koini等2009; Stavang等2009)。

4.3 油菜素内酯

BR信号和GAs信号协同促进热形态建成。常温条件下, DELLA蛋白与BR信号调节基因*BRASSINAZOLE RESISTANT1* (*BZR1*)的启动子区结合, 抑制其转录活性; 高温条件下, GAs的含量增加, DELLA蛋白被降解并释放BZR1, 激活BR信号转导(Bai等2012)。膜受体激酶BRASSINOSTEROID INSENSITIVE1 (BRI1)对BR的感知启动信号级联, 激活BES1和BZR1 (Kim和Wang 2010; Clouse 2011)。BZR1和PIF4通过DNA结合域形成PIF4-BZR复合体, 并且和AUXIN RESPONSE FACTOR6 (ARF6)互作, 协同促进热形态建成(Bai等2012; Oh等2012)。

综上所述, 高温条件下, PIF4通过调控激素合成介导热形态建成。但是目前的研究主要集中于这三种激素单独促进热形态建成这一方面, 研究这三种激素如何协同调控热形态建成将促进我们对

这一现象更深入的理解。

5 结语

近年来, 随着对PIF4研究的不断深入, PIF4在调节热形态建成中的枢纽功能逐渐清晰起来。但仍有一些重要的科学问题需要进一步研究。如: (1) 光照、昼夜节律和高温如何协同调节PIF4介导的热形态建成? (2) PIF4如何协调热形态建成和光形态建成的关系, 以促进植物高温环境的适应性? (3) PIF4在园艺植物中是否具有热形态建成的功能? 这些都将成为下一步的研究重点。相信随着对PIF4调控热形态建成功能研究的不断深入, 能够对培育耐高温新品种和促进经济作物高产栽培方面提供重要的理论依据。

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