

光敏色素作用因子PIFs在植物生长发育中的研究进展

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摘要 植物光敏色素作用因子(phytochrome interacting factors, PIFs)属于碱性-螺旋-环-螺旋(basic helix-loop-helix, bHLH)转录因子家族, 在植物生长发育中起到“枢纽”作用, 参与调控光形态建成、暗形态建成、非生物胁迫、生物钟、开花、种子萌发、避荫反应等过程。该文主要介绍PIFs转录因子参与调控植物生长发育最新研究进展, 并对PIFs转录因子的研究现状进行总结与展望, 为进一步探讨PIFs转录因子的功能及机制提供参考。

关键词 光敏色素作用因子; 植物生长发育; 转录因子; 信号转导

Research Advances of PIFs in Plant Growth and Development

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Abstract The plant phytochrome interacting factors (PIFs) belong to the family of basic helix-loop-helix (bHLH) transcription factors, which play a “hub” role in plant growth and development. PIFs are involved in the regulation of photomorphogenesis, skotomorphogenesis, abiotic stress, circadian clock, flowering, seed germination, and shade avoidance syndrome. This review mainly introduces the latest research progress of PIFs transcription factors involved in the regulation of plant growth and development. This review summarizes and prospects the research status of PIFs transcription factors, which provides a reference for further exploring the function and mechanism of PIFs transcription factors.

Keywords PIFs; plant growth and development; transcription factors; signal transduction

光是重要的环境信号, 调控植物生长发育的多个方面, 光敏色素(phytochrome, phy)是红光和远红光的光受体, 是一种可溶性色素蛋白, 光敏色素家族成员包括光敏色素A(phyA)、光敏色素B(phyB)、光敏色素C(phyC)、光敏色素D(phyD)和光敏色素E(phyE)^[1-2]。光敏色素具有红光吸收型(Pr)和远红光吸收型(Pfr), 研究发现, Pr在体内最先合成, 在红光条件下可以由Pr转换成Pfr, 在黑暗中Pfr可缓慢地逆转为Pr^[3]。光敏色素作用因子(phytochrome interacting factors, PIFs)与光敏色素Pfr相互作用, 属于转录

因子bHLH家族中第15亚家族^[4]。PIF3是最先发现能够与PhyB和PhyA相互作用的转录因子^[5], 目前为止, 拟南芥(*Arabidopsis thaliana*)中发现PIFs家族有7个成员(PIF1, PIF3~PIF8); 水稻(*Oryza sativa*)中有6个成员(OsPIL11-OsPIL16); 玉米(*Zea mays*)中有7个成员(ZmPIF1-ZmPIF7)^[6-7]。植物PIFs转录因子有1个保守的N末端APB结构域(active phytochrome B-binding motif)和1个bHLH结构域(basic helix-loop-helix motif), 部分PIFs含有1个APA结构域(active phytochrome A-binding motif)^[8]。近几年随着对PIFs研究的不断

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深入,发现PIFs转录因子不仅在光信号中具有重要作用,在植物生长发育的多个方面都起到关键信号节点作用。PIFs参与了光、温度和防御等外部环境信号以及生物钟、激素、糖代谢等内部环境信号,集成复杂的调控网络调节植物的抗逆、生物钟、开花、种子萌发和避荫反应等过程^[9-12]。

1 PIFs促进光形态建成、抑制暗形态建成

拟南芥幼苗是研究光形态建成的经典模式植物,在黑暗中生长的幼苗经历了黄化过程,其特征是下胚轴伸长、子叶闭合、顶端弯钩;相比之下,正常光条件下幼苗表现为下胚轴缩短及子叶张开^[13-14]。PIFs作为光形态建成的负调控蛋白,与光敏色素直接相互作用,在光形态建成中具有重要作用^[15-16]。研究发现,拟南芥PIF3突变体*pi3*表现出在红光下子叶面积增加,下胚轴变短的表型,表明PIF3负调控光形态建成^[17];拟南芥PIF4也能负调控植物光形态建成^[18]。另外拟南芥光敏色素相互作用因子PIF7与PIF3和PIF4一起通过调节phyB水平,参与调控幼苗去黄化,正调控红光响应^[19]。光照条件下光敏色素进入细胞核,促使PIFs降解或抑制PIFs结合DNA,促进光形态建成^[20-22]。PIFs的降解需要HMR(HEMERA)的参与,HMR是phyB的互作蛋白,光条件下phyB与HMR相互作用促进HMR的积累,降解PIFs,促进光形态建成^[23]。研究发现,DELLA蛋白能与PIFs直接相互作用,抑制PIFs响应光和赤霉素(GA)信号,抑制下胚轴伸长^[24-25];DELLA蛋白也能通过26S蛋白酶体促进PIFs的降解^[26],表明DELLA蛋白可以通过降解PIFs,抑制PIFs活性促进植物光形态建成。在PIFs参与的光形态建成机制中,泛素E3连接酶是降解PIF1和PIF3的主要酶,其中BTB(bric-a-brack)型泛素E3连接酶和BTB的同源蛋白LRB(LIGHT-RESPONSE BTB)共同结合phyB-PIF3复合体并且诱导PIF3的降解,促进植物光形态建成^[27]。在光照条件下,光敏色素降解PIF3,促进TCP家族转录因子TCP4结合下游生长素应答基因*SAUR14/16/50*的启动子,抑制*SAUR14/16/50*基因的表达,促使子叶展开;在黑暗条件下,PIF3积累与TCP4竞争性结合*SAUR14/16/50*基因的启动子,提高*SAUR14/16/50*基因的表达,促使子叶闭合^[28](图1)。

光诱导PIFs降解促进光形态建成,PIFs在黑暗中稳定存在促进暗形态建成,PIFs的平衡对于暗形态建

成到光形态建成具有重要作用。拟南芥PIFs转录因子的四突变体*pi4q*(PIF1、PIF3、PIF4、PIF5)表现出光形态建成的表型,表明PIFs在调节植物暗形态建成中具有重要作用^[29]。许多蛋白(如DET1和SPA)在黑暗中维持PIFs的稳定性以促进暗形态建成,而其他蛋白(如BIN2、COP1、HFR1和DELLA)促进黑暗中PIFs的降解^[30]。黑暗中光形态抑制蛋白DET1与PIFs相互作用,能够维持PIFs的稳定,从而起到稳定暗形态建成的作用^[31]。BZR1是油菜素内酯(BR)信号转导途径中关键转录因子,有研究显示,BZR1在体外或体内能够与PIF4特异性互作,形成异源二聚体共同调控多个基因表达,促进植物生长^[33]。BIN2(brassinosteroid-insensitive)是GSK3类激酶,是BR信号通路的负调控因子,能够磷酸化拟南芥转录因子PIF3和PIF4,黑暗中促进PIF3和PIF4的降解^[32-33];而COP1/SPA1复合物中的SPA1可以与PIF3相互作用,与BIN2竞争性结合PIF3,从而阻止BIN2在黑暗中磷酸化降解PIF3^[33],因此BIN2促进PIFs的降解,而COP1/SPA1复合体在黑暗中稳定PIFs促进植物暗形态建成。此外,光照条件下,PIFs也能够促进COP1-SPA复合物对光敏色素的泛素化降解,通过26S蛋白酶体降解光敏色素负反馈调控红光和远红光信号^[34-35]。HFR1是光敏色素介导的光信号传导途径的调控因子,研究发现,HFR1对于从暗形态建成到光形态建成的快速转变非常重要,PIF1和HFR1在体内通过26S蛋白酶体途径相互降解,PIFs和HFR1之间的协同降解机制,是拟南芥光形态发育的基础^[36](图1)。

2 PIFs参与植物非生物胁迫

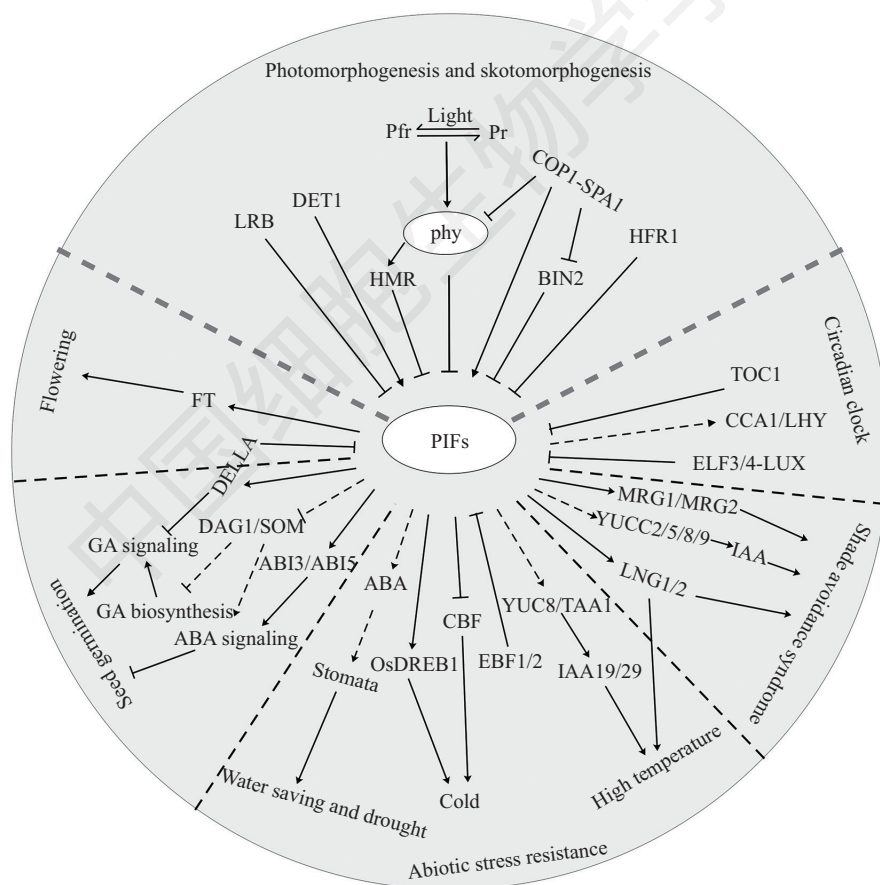
2.1 PIFs参与植物高温响应

植物生长过程中受到环境、温度等诸多因素的影响,PIFs不仅参与植物的光形态建成,而且通过植物激素共同调节植物对非生物胁迫的抗性^[37]。温度是影响植物分布和季节响应的主要环境因素,拟南芥PIF4已被报道参与植物高温响应^[38-39],高温能够促进PIF4的表达,随着温度的升高PIF4的表达也随之上升^[40]。与黑暗生长条件类似,在高温条件下光敏色素由活性的Pfr形式转变为非活性Pr形式即“热逆转”,“热逆转”可以维持PIF4的稳定^[41-42]。PIF4的上游抑制蛋白phyB和CRY1(cryptochrome 1)在高温环境下都能转变为非活性状态,失去了降解PIF4的能力,维持PIF4的稳定^[22,30]。植物响应高温的表型和

避荫反应的表型极为类似, 共同特点是通过牺牲叶片的生长促进叶柄迅速伸长^[43-44]。研究发现, PIF4在响应高温环境时, 能够激活生长素生物合成基因 *YUC8*、*TAA1* 促进生长素应答基因 *IAA19*、*IAA29* 的表达, 调节植物下胚轴和叶柄伸长^[37]。此外, 研究发现, 在高温条件下PIF4能够促进两种同源基因 *LNG1* (*LONGIFOLIA1*) 和 *LNG2* (*LONGIFOLIA2*) 的表达。LNG蛋白存在于在细胞质和细胞核中, 调节拟南芥的叶片形态, 对细胞伸长具有促进作用; 在拟南芥中 *LNG1* 和 *LNG2* 双突变体 *lng1/lng2* 表现为叶柄和叶片变短^[45], 因此高温导致的叶柄伸长也可能通过PIF4促进 *LNG1* 和 *LNG2* 基因实现。最新研究发现, 在高温条件下 *phyB* 促进HMR的积累, HMR直接与PIF4相互作用, 共同促进高温响应基因的表达^[46](图1)。

2.2 PIFs参与植物低温响应

PIFs不仅在植物高温胁迫中发挥重要作用, 也参与植物的低温胁迫。在低温条件下拟南芥PIF3的突变体表现出明显的抗冻性, 而PIF3过表达植株表现出明显的低温敏感表型。两个F-box蛋白EBF1和EBF2是植物低温胁迫响应路径的调控因子, EBF1和EBF2能够通过26S蛋白酶体直接靶向降解PIF3^[47]; 低温能够促使EBF1和EBF2蛋白降解, 从而使PIF3蛋白更加稳定, PIF3能够直接结合在 *CBFs* 的启动子区, 抑制 *CBFs* 及其下游低温响应基因表达^[47]。此外, 拟南芥PIF4和PIF7也能通过光周期依赖方式下调 *CBF* 基因的表达来降低植物抵抗低温的能力^[48]。水稻PIFs转录因子 *OsPIL16* 能够被低温诱导表达, *OsPIL16* 能正向调控 *OsDREB1* 的表达, 并且增强水稻



PIFs在植物生长发育过程中调控光暗形态建成、植物非生物胁迫、生物钟、开花、种子萌发、避荫反应等过程。——▶: 促进; ——|: 抑制; - - - - -▶: 间接促进; - - - - -|: 间接抑制。

PIFs regulate photomorphogenesis, skotomorphogenesis, plant abiotic stress resistance, circadian clock, flowering, seed germination, and shade avoidance syndrome during plant growth and development. ——▶: induction; ——|: repressive; - - - - -▶: indirectly induced; - - - - -|: indirectly repressed.

图1 PIFs主要参与的植物生长发育过程

Fig.1 The major processes of phytochrome interacting factors (PIFs) involved in plant growth and development

细胞膜完整性,降低细胞内丙二醛浓度,提高水稻对低温胁迫的耐受能力^[49](图1)。

2.3 PIFs参与植物干旱胁迫响应

早期研究发现,在拟南芥中*phyB*突变体气孔密度低于野生型对照,且*phyB*能够调节气孔开闭^[50]。*phyB*和COP1双突变体*phyB/cop1*的气孔开闭程度低于COP1单突变体的气孔开闭;拟南芥PIF3和PIF4双突变体*pif3/pif4*的气孔开闭程度大于野生型,表明*phyB*可能通过PIFs调节气孔开闭^[50]。脱落酸(ABA)的积累可以促进气孔关闭、减少蒸腾散失,帮助植物在干旱胁迫下存活^[51],*phyB*通过增强对ABA的敏感性能够提高拟南芥抗旱性^[52]。本实验室进一步研究发现,玉米PIFs转录因子基因*ZmPIF1*和*ZmPIF3*能够通过ABA信号路径,调节气孔开闭,降低转基因水稻的蒸腾速率,提高转基因水稻的节水抗旱性^[53-55](图1)。

3 PIFs参与调控生物钟

光是调节植物生物钟的重要因素,光被生物体内一系列光受体所感知,从而使植物适应不断变化的环境条件,研究发现,PIFs也参与生物钟的调节^[56]。CCA1/LHY属于MYB家族转录因子,是生物钟的核心组件,PIFs能够结合CCA1/LHY启动子的G-box区域,参与生物钟的调节^[56]。进一步研究发现,糖类能增强PIFs结合CCA1/LHY启动子的能力,影响生物钟^[57]。拟南芥中TOC1与PIF3直接相互作用,抑制生物钟的中心组件CCA1/LHY的表达;研究发现,在短日照条件下TOC1能够抑制PIF3转录活性促进植物生长,表明TOC1和PIF3共同调节生物钟相关基因表达^[58]。此外,还有研究报道,生物钟调节蛋白TOC1与拟南芥PIF4直接相互作用抑制PIF4的表达,同时调控昼夜节律和高温响应^[59]。最近研究发现,受昼夜节律调控表达的ELF3、ELF4和LUX蛋白可以形成复合物ELF3-ELF4-LUX,抑制PIF4和PIF5的转录;同时ELF3也可以单独与PIF4结合,阻止PIF4激活下游调控基因,影响植物昼夜节律^[60-61](图1)。

4 PIFs参与调控开花

植物开花由光和温度等环境信号控制,PIFs能够通过感知季节带来的昼夜长短和温度变化调节植物的生物节律,调控植物开花。拟南芥PIF4突变体*pif4*在高温条件下出现晚开花的表型,进一步研究发现,温度升高促进PIF4的表达,PIF4通过结合开花相

关的正调控因子*FT*(FLOWERING LOCUS T)基因的启动子,调节*FT*基因的表达促进开花^[62]。有研究显示,在拟南芥中DELLA蛋白通过阻止PIF4与DNA结合能力,抑制PIF4的活性,从而调节植物开花时间,在缺乏DELLA蛋白时植物会表现出提前开花的表型^[63]。植物激素GA降解DELLA蛋白,在*FT*诱导开花中具有重要作用;在GA缺乏的植株中,DELLA蛋白积累,PIF4的活性被抑制,抑制*FT*相关基因的表达,导致开花延迟^[64](图1)。

5 PIFs参与调控种子萌发

植物种子萌发受到诸多激素调控,其中GA和ABA是最主要的两种植物激素,而PIFs参与了GA和ABA信号转导途径,在调控种子萌发中具有重要作用^[65]。拟南芥PIF1通过GA信号路径抑制黑暗中种子萌发,PIF1能够与两个DELLA蛋白基因*RGAI*和*GAI*的启动子结合,激活*RGAI*和*GAI*的表达,抑制黑暗中种子萌发^[65];而光诱导PIF1降解,产生大量的*DAG1*(*DOF AFFECTING GERMINATION 1*)和*SOM*(*SOMNUS*),*DAG1*和*SOM*的表达调节GA生物合成基因*GA3ox1*和*GA3ox2*的表达,促进GA生物合成,促进种子萌发^[66]。此外在黑暗中,PIF1通过与ABA信号通路基因*ABI3*(*ABA-INSENSITIVE3*)和*ABI5*(*ABA-INSENSITIVE5*)的启动子结合,激活ABA信号转导,抑制GA信号,从而抑制种子萌发。PIF1与*ABI3*发生相互作用也能抑制*SOM*的表达,*SOM*通过抑制GA生物合成路径的相关基因也能产生抑制种子萌发的效果^[66](图1)。

6 PIFs参与调控避荫反应

植物周围的光质在很大程度上取决于其邻近植物的密度,植物能够感知不同的光照来应对光的变化,其表现出下胚轴伸长、节间伸长和提前开花等特征,即避荫反应(shade avoidance syndrome, SAS)。植物通过不同的光受体识别避荫信号,介导避荫反应,在R/FR比例降低的条件下,*phyB*的活性降低,PIFs激活生长素合成基因的转录,引起避荫反应。有研究表明,在低R/FR条件下,*phyB*由活性的Pif转变成无活性的Pr,维持拟南芥PIF4和PIF5的稳定,进而促进叶柄伸长基因*LNG1*和*LNG2*的表达,表明PIF4和PIF5在植物避荫反应中具有重要作用^[67]。也有研究发现,PIF4和PIF5在隐花色素的下游响应

蓝光介导的拟南芥下胚轴伸长, 响应植物的避荫信号^[68]。拟南芥PIF7也参与避荫反应, 通过诱导生长素合成基因*YUCC2/5/8/9*的表达, 调节叶片中IAA的含量促进植物组织伸长^[69]。最近的研究发现, PIF7能够结合组蛋白MRG1/MRG2, 利用组蛋白乙酰化酶诱导组蛋白乙酰化, 通过表观遗传调控植物的避荫反应^[70]。

7 PIFs研究的目的及意义

PIFs参与植物整个生长发育进程, 在光形态建成、暗形态建成、植物抗逆、生物钟、花期调节以及种子萌发等生物进程中都具有重要作用(图1)。然而到目前为止对于PIFs的研究大部分集中在双子叶模式植物拟南芥中, 其他植物中PIFs的研究还比较少。随着近几年对PIFs研究越来越深入, PIFs在作物生长发育中的研究被逐渐报道, 但其分子机制研究还不够深入, 作物中PIFs的研究仍然包含很多有待解决的问题。通过PIFs在作物生长发育过程中的深入研究, 有助于进一步完善PIFs在植物生长发育的调控网络, 为PIFs的遗传育种应用做准备。

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