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·专题论坛·

向光素调节植物向光性及其与光敏色素/隐花色素的相互关系

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摘要 蓝光受体向光素(PHOT1/PHOT2)调节蓝光诱导的植物运动反应，包括植物向光性、叶绿体运动、气孔运动和叶片伸展等。其中，向光素介导的植物向光性能够促使植物弯向光源，确保其以最佳取向捕获光源，优化光合作用。光敏色素和隐花色素作为光受体也参与植物的向光性调节。该文综述了向光素介导的拟南芥(*Arabidopsis thaliana*)下胚轴向光弯曲信号转导及其与光敏色素、隐花色素协同作用的分子机制，以期为改造植物光捕获能力及提高光利用效率提供理论基础。

关键词 向光素，向光性，光敏色素，隐花色素，信号转导

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植物营固生生长，因此环境适应性的生长和发育对其生存来说非常重要。光照不仅是植物生长所需要的能量来源，也是一种重要的环境信号。植物通过感受入射光的方向、波长和强度来调整相关生理反应(Hohm et al., 2013)。其中，向光性是受光调节的最重要的反应之一，向光性使植物弯向入射光以获得供其生长的最适光照(Whippo and Hangarter, 2006)。植物的向光性生长，在苔藓、蕨类和被子植物中普遍存在(Suetsugu and Wada, 2007; Briggs, 2014)。开花植物中，尽管红光也增强植物的向光性，但向光性生长主要由蓝光诱导(Hohm et al., 2013)。拟南芥(*Arabidopsis thaliana*)下胚轴的向光性生长主要受向光素(PHOT1与PHOT2)、光敏色素A(phyA)、隐花色素1(cry1)和隐花色素2(cry2)五种光受体调节(Sakai et al., 2012; Goyal et al., 2013)。其中，位于细胞质膜内侧的PHOT1和PHOT2，直接或间接调节生长素载体的活性与极性分布，促使生长素的不对称分布和向光性反应的发生(Sakai et al., 2001; Stone et al., 2005; Christie, 2007)。位于细胞核的光敏色素A(phyA)、隐花色素1(cry1)和隐花色素2(cry2)(Stone et al., 2005; Liu et al., 2011)，则是通过调节相关基因的转录，间接调节植物下胚轴的向光性和根的向重力性反应(Lascève et al., 1999; Lariguet and Fankhauser, 2004; Ohgishi et al., 2004; Iino, 2006; Kang et al., 2008; Nagashima et al., 2008a)。Nagashima等(2008b)报道激活光敏色素和隐花色素，抑制生长素载体*ABCB19*(ATP-BINDING CASSETTE SUB-FAMILY B-TYPE 19)的表达，可增强植物的向光性反应。目前的研究结果表明，光敏色素和隐花色素可在基因表达、蛋白修饰和生长素运输等多个水平参与调节向光素介导的植物向光性反应(钱善勤等，2004; Sakai et al., 2012; Liscum et al., 2014)。本文重点阐述了向光素介导拟南芥下胚轴向光弯曲的信号转导及其与光敏色素和隐花色素协同作用的分子机制。

1 植物对蓝光的感受和信号转导

1.1 蓝光受体向光素

蓝光受体向光素(PHOT1和PHOT2)调节拟南芥的运动反应，如向光性、叶绿体的避光和聚光运动、气孔开放以及子叶伸展等(Christie, 2007)。向光素主要由N-端的2个与FMN结合的光感受结构域的重复保守序列LOV1(light, oxygen, voltage1)、LOV2和C-端的丝氨酸/苏氨酸蛋白激酶区组成(Huala et al., 1997; Christie et al., 1999; Briggs and Christie, 2002)。PHOT1和PHOT2虽没有跨膜结构域，但暗处理可使其分布于细胞质膜内侧(Sakamoto and Briggs, 2002; Kong et al., 2006)。蓝光照射下，位于质膜内侧的

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PHOT1蛋白部分被释放到细胞质中(Sakamoto and Briggs, 2002; Wan et al., 2008), 部分PHOT2蛋白则与高尔基体偶联(Kong et al., 2006)。表达分析结果显示, *PHOT1*在拟南芥整株幼苗中均有表达, 尤其在茎顶端弯钩处和黄化幼苗的根伸长区表达最为丰富(Sakamoto and Briggs, 2002)。*PHOT2*主要在拟南芥子叶和茎顶端弯钩处表达, 而在根中表达较少(Kagawa et al., 2001; Kong et al., 2006)。*PHOT1*和*PHOT2*的表达模式, 解释了强蓝光下*PHOT1*基因突变拟南芥依然表现下胚轴向光性正常而根的负向光性缺失现象, 即PHOT1和PHOT2以功能冗余的方式调节拟南芥下胚轴的向光弯曲反应, 而PHOT1单独调节拟南芥根的负向光性生长。

向光素的激活依赖于蓝光诱导的自体磷酸化, 特别是分子内LOV2和激酶结构域活性环上第851位丝氨酸的自磷酸化(Salomon et al., 2003; Sullivan et al., 2008; Okajima et al., 2011)。拟南芥第851位丝氨酸被丙氨酸取代, 可造成PHOT1介导的向光性反应缺失(Sullivan et al., 2008)。Inoue等(2008)研究发现, 种子植物、蕨类、苔藓和绿藻中PHOT1和PHOT2的Ser851都很保守, 表明植物向光素的Ser851的磷酸化在向光素介导的反应中普遍存在。此外, 早期报道单侧蓝光照射可诱导燕麦(*Avena sativa*)胚芽鞘中PHOT1的自磷酸化呈梯度分布, 向光侧的磷酸化水平高于背光侧(Salomon et al., 1997a, 1997b), 该结果似乎说明单侧蓝光照射引起植物向光侧和背光侧向光素的活性差异, 导致植物器官向光弯曲生长。

1.2 向光素介导下胚轴向光弯曲的下游信号组分

植物向光性生长主要受蓝光受体向光素(PHOT1和PHOT2)的调节。PHOT1介导弱蓝光(0.01–1 μmol·m^{-2}·s^{-1})和强蓝光(>1 μmol·m^{-2}·s^{-1})诱导的下胚轴向光弯曲。而PHOT2仅在强蓝光下起作用, 且与PHOT1功能冗余(Sakai et al., 2001; Briggs and Christie, 2002)。蓝光引起PHOT1或PHOT2自体磷酸化是开启植物蓝光反应的普遍步骤(Inoue et al., 2008)。由此推测植物可能通过不同组织或细胞表达不同的向光素激酶底物, 以实现向光素对不同生理反应的调控。目前, 除了向光素受体本身外, 只鉴定到2个向光素激酶的底物, 即生长素运输载体ABCB19和光敏色素作用激酶底物PKS4(PHYTOCHROME KINASE SUBSTRATE 4)(Christie et al., 2011; Demarsy et al., 2012)。有研究表明蓝光激活向光素, 使其磷酸化ABCB19和PKS4, 进而抑制它们的活性, 可增强拟南芥下胚轴的向光弯曲(Christie et al., 2011; Demarsy et al., 2012)。该结果表明ABCB19和PKS4负调节蓝光诱导的向光弯曲反应。蛋白互作分析发现NPH3(NONPHOTOTROPIC HYPOCOTYL 3)、RPT2(ROOT PHOTOTROPISM 2)和PKS1(PHYTOCHROME KINASE SUBSTRATE 1)均可与PHOT1相互作用, 调节生长素在拟南芥下胚轴向光侧和背光侧的不对称分布, 使植物发生向光弯曲(Motchoulski and Liscum, 1999; Harper et al., 2000; Inada et al., 2004; Lariguet et al., 2006; Kaiserli et al., 2009)。目前, 虽已证明NPH3和RPT2也参与调节PHOT2介导的强蓝光诱导的下胚轴向光弯曲反应(Sakai et al., 2000; Inada et al., 2004; Sakai, 2005), 然而, RPT2并不与PHOT2体内互作调节下胚轴的向光弯曲(Inada et al., 2004; Lariguet et al., 2006)。Tseng和Briggs(2010)研究发现, 与PHOT2蛋白特异互作的RCN1(ROOTS CURL in NPA1), 负调节PHOT2介导的下胚轴向光弯曲, 并不调节PHOT1介导的蓝光反应。综上所述, 尽管PHOT1和PHOT2介导蓝光诱导的拟南芥下胚轴向光弯曲的信号转导部分组分已得到鉴定, 但该过程的详细机制仍不清楚。

1.2.1 **NPH3**

拟南芥*NPH3*基因突变, 可导致其缺失所有强度蓝光诱导的下胚轴向光弯曲反应, 表明NPH3既调节PHOT1介导的弱蓝光诱导拟南芥下胚轴的向光弯曲, 又调节PHOT1和PHOT2介导的强蓝光反应(Liscum and Briggs, 1996; Motchoulski and Liscum, 1999; Roberts et al., 2011)。*NPH3*基因编码的蛋白, 含有蛋白-蛋白相互作用结构域BTB/POZ(Broad-complex, tramtrack and bric-a-brac/Pox virus and zinc finger)和位于蛋白N与C末端的螺旋-螺旋结构域(Motchoulski and Liscum, 1999)。NPH3蛋白通过其C末端定位于细胞质膜, 在体外体内均可与PHOT1和PHOT2发生相互作用(Motchoulski and Liscum, 1999; Inada et al., 2004; Lariguet et al., 2006; de Carbonnel et al., 2010)。水稻(*Oryza sativa*)中NPH3的同源蛋白CPT1(coleoptile phototropism1), 通过

调节生长素在胚芽鞘的重新分布进而介导其向光反应(Haga et al., 2005), 再次证明NPH3在植物向光性反应中的功能。有研究表明, 蓝光照射可诱导拟南芥NPH3蛋白发生PHOT1依赖的去磷酸化反应(Pedmale and Liscum, 2007)。鉴于强蓝光下*phot1*突变体下胚轴向光弯曲, 而NPH3蛋白并未发生去磷酸化, 说明PHOT2调节拟南芥下胚轴向光性不需要NPH3的去磷酸化(Tsuchida-Mayama et al., 2008)。目前, 关于PHOT1调节NPH3去磷酸化的生物学意义尚不清楚。

1.2.2 **RPT2**

*RPT2*基因与*NPH3*序列同源, 其编码蛋白含有BTB/POZ和位于N与C末端的螺旋-螺旋结构域(Sakai et al., 2000)。*RPT2*基因突变可导致拟南芥缺失根的负向光性生长, 但仍表现出中等强度的下胚轴向光弯曲反应(Sakai et al., 2000; Inada et al., 2004)。RPT2蛋白定位于细胞质膜, 在体内可与PHOT1和NPH3形成复合物(Inada et al., 2004)。弱蓝光可诱导*rpt2*突变体下胚轴向光弯曲, 但是下胚轴的向光弯曲度随着光强度的增强逐渐减弱, 表明*RPT2*基因赋予了拟南芥适应向光弯曲反应增强的功能(Sakai et al., 2000; Inada et al., 2004)。遗传分析结果显示, 在下胚轴响应强蓝光反应时, 有RPT2存在, PHOT1起正向作用; RPT2不存在, PHOT1则起负作用。这种负作用导致*rpt2*单突变体缺失中强度蓝光诱导的下胚轴向光弯曲表型, 而*phot1rpt2*双突变体表现下胚轴向光弯曲表型(Liscum, 2002; Inada et al., 2004)。

1.2.3 **EHB1**

最近, Knauer等(2011)通过酵母三杂, 成功筛选到1个可以与PHOT1和NPH3复合体结合的蛋白EHB1 (ENHANCED BENDING 1), 其分子量为25 kDa, N末端含有与Ca^{2+}结合的结构域(C2/CaLB), C端含有与ZAC ARF-GAP(ATP酶激活的ADP核糖基化因子)蛋白相似的基序结构。当受到单侧蓝光或重力刺激时, *ehb1*突变体下胚轴弯曲度增强, 表明该蛋白是向光性和向重力性反应的负调控因子(Knauer et al., 2011)。此外, 有研究表明, EHB1有可能是向光素或生长素驱动Ca^{2+}内流进入囊泡运输途径的信号转导子(Harada and Shimazaki, 2007)。

1.2.4 **PKS家族**

PKS家族的PKS1、PKS2和PKS4蛋白属于一个小的蛋白家族, 该家族蛋白作为光敏色素激酶的底物, 是拟南芥光敏色素信号转导途径的重要组成成分(Fankhauser et al., 1999; Lariguet et al., 2006)。已有研究表明, PKS1、PKS2和PKS4参与调节向光素PHOT1介导的蓝光反应, 如拟南芥下胚轴向光弯曲、根负向光性生长以及叶片的伸展和定位等(Lariguet et al., 2006; Boccalandro et al., 2008; de Carbonnel et al., 2010)。PKS1和PKS4在组织表达方面非常相似, 在下胚轴伸长区和根中高表达(Lariguet et al., 2003; Schepens et al., 2008)。光处理可瞬时精确地诱导*PKS1*基因的表达(Lariguet et al., 2003), 抑制*PKS4*基因的表达(Schepens et al., 2008)。光敏色素A调节光诱导的*PKS1*基因的表达, 正调节拟南芥根的负向光性反应(Boccalandro et al., 2008)。Lariguet等(2006)报道, PKS1可以与NPH3和PHOT1在体内相互作用, 调节拟南芥的向光性反应。*PKS1*、*PKS2*和*PKS4*单基因突变没有表型, 双突变体下胚轴向光弯曲度明显降低, 三突变体则完全缺失下胚轴向光性, 表明它们在下胚轴向光弯曲方面存在功能冗余(Lariguet et al., 2006; Zhao et al., 2013)。Demarsy等(2012)研究证实PKS4可被PHOT1磷酸化。黑暗条件下, PKS4以单体形式(PKS4D)存在, 蓝光照射几秒后, 发生依赖于PHOT1的磷酸化反应, 导致其出现第2种形式PKS4L, 负调控植物的向光性。de Carbonnel等(2010)研究证明, PKSs蛋白可能参与调节光依赖的生长素运输。

1.2.5 **蛋白磷酸酶2A(PP2A)**

Tseng和Briggs(2010)研究发现*RCN1*(root curling in n-naphthylphthalamic acid1)编码Ser/Thr蛋白磷酸酶2A(PP2A)的A1亚基, RCN1与PHOT2蛋白特异互作, 负调节PHOT2介导的拟南芥下胚轴向光弯曲, 而并不调节PHOT1介导的反应。Briggs和Christie (2002)研究发现, *phot1-5rcn1-1*双突变体中PP2A的活性降低, 蓝光诱导的拟南芥下胚轴向光弯曲和气孔开放明显增强, 暗示PP2A参与调节PHOT2介导的蓝光信号转导。当用PP2A抑制剂处理时, *phot1-5*突变

体在下胚轴向光弯曲和气孔开放反应中，表现出与*phot1-5rcn1-1*相似的表型。免疫学分析显示，在抑制PP2A活性时，由蓝光照射转入黑暗，PHOT2在体内的去磷酸化水平明显降低，这暗示被磷酸化的PHOT2蛋白可能是PP2A的底物，因而降低PP2A活性会增强PHOT2蛋白的活性，但不影响PHOT1蛋白的去磷酸化及其介导的拟南芥下胚轴向光弯曲和气孔开放反应(Tseng and Briggs, 2010)。

1.3 生长素分布与向光素介导的下胚轴向光弯曲

生长素的不对称分布决定植物的向性生长(Tanaka et al., 2006)。向光素介导的信号转导，调节单侧蓝光处理引起的生长素不对称分布(Haga et al., 2005)。研究表明很多向光弯曲突变体表现出生长素相关信号途径缺陷表型(Sakai et al., 2012)，该结果支持了Cholodny-Went理论，即生长素的不对称分布决定植物的向性反应(Went and Thimann, 1937)。生长素的运输和不对称分布依赖于生长素的运输载体(Briggs, 1963; Liscum, 2002; Holland et al., 2009)。目前，植物中有3种生长素运输载体家族已被鉴定，包括生长素外流载体PINs家族、内流载体(AUX1)及类似家族(LAX)和ABCB运输载体(Blakeslee et al., 2005; Whippo and Hangarter, 2006; Robert and Friml, 2009; Zažímalová et al., 2010)。

1.3.1 生长素外流载体PINs蛋白

拟南芥中PINs家族共有8个成员，其中PIN1、PIN2、PIN3、PIN4和PIN7有长的亲水环，呈现极性膜定位，可将生长素从细胞质运输到胞外基质(Zažímalová et al., 2010)。与具长亲水环的PINs不同，PIN6的亲水环比较短，PIN5和PIN8几乎没有亲水环。这些短亲水环的PINs定位于内质网，可能介导生长素从细胞基质流向内质网腔(Mravec et al., 2009)。研究发现，在向光性反应中，细胞与细胞之间生长素的运输似乎比细胞内部生长素的平衡调控更重要。利用生长素报告基因*DR5rev*:GFP观察生长素分布时，发现*PIN3*基因突变，拟南芥黄化幼苗下胚轴照光侧和背光侧表皮DR5活性不对称分布程度降低，表现中等强度的向光弯曲而非缺失(Friml et al., 2002; Ding et al., 2011)。这表明PIN3参与调节生长素极性运输介导的植物向光性，也暗示除了PIN3外还有其它成员参与生长素的不对称分布调控。Ding等(2011)检测*pin3pin7*和*pin2pin3-pin7*突变体黄化幼苗向光弯曲反应时，发现*PIN3*基因突变背景下，*PIN7*基因突变可导致拟南芥下胚轴向光弯曲程度稍微减弱，*PIN2*基因的再突变对拟南芥下胚轴向光性没有影响。Christie等(2011)发现去黄化和暗适应的*pin1*、*pin2*和*pin4*突变体向光弯曲类似于野生型，而*pin7*突变体的弯曲度较野生型小。上述结果表明，拟南芥下胚轴向光反应可能主要受PIN3和PIN7调节。免疫定位实验显示，蓝光处理可诱导PIN1在拟南芥下胚轴背光侧和向光侧呈梯度分布(Blakeslee et al., 2004)，说明PIN1在向光弯曲反应中起一定的作用。然而截至目前尚无遗传学证据表明PIN1对植物向光弯曲反应有贡献。进一步检查*pin*多突变体(如*pin1 pin3 pin4 pin7*四突变体)的向光性反应，将有望揭示PINs蛋白之间的功能冗余。

1.3.2 生长素内流载体AUX1及LAX

生长素内流载体AUX1/LAX与生长素质子同向转移通透酶有关。目前，发现拟南芥基因组中有4种生长素内流载体基因，即*AUX1*、*LAX1*、*LAX2*和LAX3(Titapiwatanakun and Murphy, 2009; Zažímalová et al., 2010)。*AUX1*基因突变，拟南芥下胚轴向光弯曲正常，而根的向光弯曲反应增强(Okada and Shimura, 1992; Watahiki et al., 1999)。遗传学研究表明，去黄化或暗适应的*aux1lax2lax3*三突变体幼苗下胚轴向光弯曲反应减弱(Christie et al., 2011)。此外，有报道显示*AUX1*基因突变可增强*nph4*/*msg1*突变体的下胚轴向光弯曲表型(Watahiki et al., 1999; Stone et al., 2008)。然而目前关于向光素是否控制生长素输入载体AUX1/LAX的活性并无报道。

1.3.3 生长素转运蛋白ABCB19

ABCB转运蛋白含有2个在真核和原核中均相当保守的ABC结构域(Martinoia et al., 2002)。拟南芥基因组编码22种ABCB蛋白，虽然大多数ABCB转运蛋白的功能未知，但是其中ABCB1、ABCB4和ABCB19三种蛋白被证明是生长素转运蛋白(Titapiwatanakun and Murphy, 2009)。ABCB1和ABCB19表现生长素外流活性，ABCB4则兼具生长素内流和外流活性。*ABCB19*基因突变，拟南芥下胚轴向光弯曲度增强，暗示ABCB19是下胚轴向光弯曲的负调控因子(Noh et

al., 2003)。*abcb19*突变体黄化幼苗，其体内生长素向基部运输严重缺失(Noh et al., 2001)，说明ABCB19是生长素从茎端向根部运输所必需的。Christie等(2011)报道用蓝光处理，PHOT1可直接磷酸化ABCB19，进而抑制ABCB19的生长素运输活性。用红光或蓝光照射4小时后可减少下胚轴ABCB19蛋白的含量，抑制生长素向基部的运输(Nagashima et al., 2008a)。可见，红光或蓝光诱导ABCB19蛋白含量的降低及PHOT1对ABCB19活性的抑制，协同作用抑制生长素向基部的运输，增强拟南芥下胚轴的向光弯曲。

ABCB19作为生长素外流载体，除自身调节生长素外流外，也可与PIN1蛋白结合，稳定PIN1的膜定位，调节PIN1的运输活性(Blakeslee et al., 2007; Titapiwatanakun et al., 2009)。此外，酵母中ABCB19表现出与PIN2的结合活性，皮层细胞中*ABCB19*与*PIN3*和*PIN4*共表达，这些结果说明ABCB19可能控制包括PIN1、PIN2、PIN3以及PIN4在内的PINs的运输活性(Titapiwatanakun and Murphy, 2009)。ABCB19蛋白可与生长素外流载体抑制剂NPA(N-1-萘基邻胺甲酰苯甲酸)结合(Noh et al., 2001)，NPA抑制拟南芥下胚轴向光性和向重力性反应需要ABCB19的参与，但其对下胚轴生长的抑制并不需要ABCB19(Nagashima et al., 2008b)。生长素报告基因*DR5rev*:GUS的GUS染色分析显示，NPA对下胚轴向性生长的抑制主要是抑制ABCB19依赖的生长素不对称分布。NPA发挥抑制作用主要是通过抑制生长素外流载体PINs的活性来实现，这些载体通过ABCB19调节生长素的不对称分布(Titapiwatanakun et al., 2009)。

2 向光素与光敏色素/隐花色素调节植物向光性的信号交叉

尽管被子植物的向光性主要由蓝光受体向光素(PHOT1和PHOT2)介导，然而强蓝光照射后，*phot1phot2*双突变体表现出轻微的向光弯曲(Sakai et al., 2001)，*phot1phot2cry1cry2*四突变体缺失所有强度蓝光诱导的下胚轴向光弯曲(Ohgishi et al., 2004)，而*phyAcry1cry2*三突变体和*phyAphyBcry1cry2*四突变体表现严重的向光性缺失(Tsuchida-Mayama et al., 2010)。这些结果表明除向光素PHOT1和PHOT2外，光敏色素与隐花色素也参与调节植物的向光性反应。Han等(2008)研究发现蓝光处理前2小时，红光预处理会抑制光敏色素A调节的PHOT1向胞质释放。尽管在一些物种中存在光敏色素与向光素的嵌合体(Phy-phot, neochromes)(Marcotte et al., 1999; Suetsugu et al., 2005)，且在苔藓和拟南芥中，活化的光敏色素可与质膜定位的向光素相互作用(Jaedicke et al., 2012)，然而目前关于光敏色素如何调控PHOT1的细胞膜定位并不清楚。

2.1 光敏色素及隐花色素通过调节基因表达和蛋白修饰介导植物的向光性

在拟南芥黄化幼苗中，光敏色素和隐花色素分别介导红光和蓝光诱导的*RPT2*基因表达(Sakai et al., 2000; Tsuchida-Mayama et al., 2010)。*phyAcry1cry2*三突变体表型类似于*rpt2*突变体，表现强蓝光诱导的拟南芥下胚轴向光弯曲缺失，而组成型表达*RPT2*基因可部分恢复*phyAcry1cry2*三突变植株的向光性(Tsuchida-Mayama et al., 2010)。该结果表明光敏色素及隐花色素通过调节*RPT2*基因的表达，调节植物的向光性生长。红光激活光敏色素，抑制蓝光诱导的PHOT1向细胞质迁移(Rösler et al., 2007; Han et al., 2008; Rösler, 2010)，暗示光敏色素调节植物的向光性反应，可能依赖于其在细胞质中的定位。为了证实光敏色素A在细胞质还是细胞核中起作用，Kami等(2012)以光敏色素A核输入受损的双突变体(*fhy1fhl*)和光敏色素A核定位复合体phyA-NLS-GFP为材料，分析了拟南芥下胚轴向光弯曲反应，结果发现双突变体(*fhy1fhl*)向光弯曲明显慢于野生型，而phyA-NLS-GFP下胚轴向光弯曲快于野生型。这些结果证实光敏色素A参与调节植物的向光性生长，可能主要依赖于其在细胞核中的定位，调控相关基因(如*RPT2*和*PKS1*等)的转录。

PKS4磷酸化研究为光敏色素通过另一种途径调节植物向光性生长提供了证据。蓝光活化PHOT1，进而磷酸化PKS4形成PKS4L(PKS4L是PKS4受光特异诱导的磷酸化状态)，而PKS4L可被TYPE2磷酸酶迅速去磷酸化，该过程可被光敏色素加强(Demarsy et al., 2012)。PKS4L抑制向光性，光敏色素增强PKS4L的去磷酸化，可能是其增强植物向光性生长的另一种

途径(Demarsy et al., 2012)。然而, 光敏色素是直接调控细胞质中PKS4L的去磷酸化, 还是通过其它组分间接调节PKS4的磷酸化状态, 目前尚不清楚。此外, 有报道称光敏色素也能调控PKS1的磷酸化(Fankhauser et al., 1999; Han et al., 2008)。然而关于光敏色素调节PKS1的磷酸化后如何参与调节向光弯曲并不清楚。

2.2 光敏色素和隐花色素通过调控生长素的运输来调节植物的向光性

光敏色素A、光敏色素B以及隐花色素的激活, 可明显抑制生长素外流载体*ABCB19*的表达(Blakeslee et al., 2007; Nagashima et al., 2008a), 进而抑制拟南芥和番茄(*Lycopersicon esculintum*)黄化幼苗下胚轴生长素向基部的运输, 增强植物的向光性(Noh et al., 2003; Nagashima et al., 2008b; Liu et al., 2011)。此外, ABCB19的活性也可被PHOT1介导的磷酸化所抑制, 这为光受体协同作用调节植物向光性提供了有力的证据(Christie et al., 2011)。研究还发现光敏色素也调节其它生长素运输载体, 如*PIN1*(PIN-FORMED-1)、*PIN3*、*PIN7*和*PID*(PINOID)的表达(Devlin et al., 2003; Blakeslee et al., 2007; Ding et al., 2011; Sakai et al., 2012)。尽管目前的研究已经在某种程度上阐述了光敏色素增加植物向光性的机制, 然而光敏色素和隐花色素通过调节生长素运输载体来调节向光性的假设仍需进一步探究。

2.3 光敏色素和隐花色素抑制负向重力性而促进植物的向光性

虽然光在决定植物下胚轴生长方向上起关键性作用, 但光下生长的植物幼苗必须同时整合光和重力来引导其生长, 因而调控向地性反应的因子可能间接调控向光性(Hangarter, 1997; Iino, 2006)。在光照条件下, 光敏色素和隐花色素都能抑制拟南芥黄化苗的负向重力性, 促进其向光性(Hangarter, 1997; Sakai et al., 2001; Lariguet and Fankhauser, 2004; Ohgishi et al., 2004; Iino, 2006)。事实上, *phot1*突变体下胚轴在弱蓝光下表现负向重力性, 而在黑暗环境下表现向重力性。前者可以通过光敏色素A或隐花色素基因的突变而恢复, 表明光敏色素和隐花色素抑制了光照条件下下胚轴的负向重力性(Lariguet and Fankhauser, 2004; Ohgishi et al., 2004)。最近的研究表明, 光敏色素A和光敏色素B抑制下胚轴的负向重力性, 主要是红光或远红光处理后下胚轴中对重力敏感的内胚层淀粉体转化为有叶绿体或白色体特征的其它质体, 使下胚轴失去了对重力的敏感性所致(Vitha et al., 2000; Kim et al., 2011)。

3 研究展望

单侧蓝光诱导的向光弯曲可以优化植物茎叶的最佳生长取向, 捕获合适的光源, 引起了植物生物学家的广泛关注。自蓝光受体向光素(PHOT1和PHOT2)被发现以来, 人们对植物向光弯曲反应的分子机制研究已取得显著进展。PHOT1可调节较宽范围蓝光引起的拟南芥下胚轴向光弯曲, 而PHOT2仅介导强蓝光诱导的下胚轴向光弯曲, PHOT1和PHOT2在调节下胚轴向光弯曲方面既体现功能冗余性又表现其作用的特异性。然而, PHOT1和PHOT2是如何进行特异性调控的尚不清楚。何种因素决定一个生理反应是由PHOT1或PHOT2单独调节还是共同调节? 如何调控可使PHOT1和PHOT2只在一个信号途径中起作用, 而不参与其它信号途径? 翻译后修饰可否能赋予PHOT1和PHOT2之间的特异性反应? 另外, 生长素运输载体蛋白PINs和AUX1等基因的多突变体表现出明显的向光性表型缺陷, 那么向光素是否调节生长素的侧向运输以及如何调控? 对这些问题的深入研究将有助于最终阐明向光素信号转导途径和植物应答光刺激的复杂机制。此外, 关于隐花色素和光敏色素是否参与假定的下胚轴顶端感受光区域或者在伸长区导致不对称生长也不清楚。这些信息对于阐明光受体在分子水平上的信号级联作用也极为重要。最后, 植物如何通过整合向重力性和向光性信号, 进而控制下胚轴的生长方向也需进一步探讨。

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Specificity and Crosstalk of Phototropin with Cryptochrome and Phytochrome in Regulating Hypocotyl Phototropism

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Abstract Blue light (BL) is a key factor controlling plant growth and morphogenesis. BL receptors phototropin1 (PHOT1) and phototropin2 (PHOT2) mediate BL-induced plant movements such as phototropism, chloroplast relocation and stomatal opening responses. Phototropism allows plants to bend toward light by perceiving the direction, wavelength and intensity of incident light so that they can obtain optimum light. Phytochrome and cryptochrome are also involved in asymmetric regulation of hypocotyl growth, causing plant phototropic growth. In this review, we discuss the signaling for phototropins and focus on the crosstalk with phytochrome and cryptochrome signaling in regulating phototropism. Fundamental progress in understanding the role of phototropins and phytochrome or cryptochrome in phototropism will continue to provide a rational basis for biotechnological improvements in developing light-trapping plants with improved light-use efficiency.

Key words phototropin, phototropism, phytochrome, cryptochrome, signaling

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