

植物下胚轴向光弯曲机制研究进展

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摘要: 植物向光弯曲生长主要是由于其向光和背光面生长素的不对称分布引起。近年来研究发现, 在不同强度的蓝光单侧照射下, 植物可能存在不同的向光弯曲调节机制。目前, 关于向光素PHOT1介导弱蓝光引起的下胚轴弯曲研究较为详细, 即PHOT1感受蓝光后, 与其下游的信号蛋白NPH3、RPT2和PKS1相互作用, 调控生长素运输蛋白的活性及定位, 诱导生长素的不对称分布引起向光弯曲。PHOT1和PHOT2以功能冗余方式调节强蓝光引起的植物下胚轴向光弯曲, NPH3可能作为共享调节因子, 引发不同的信号转导通路实现功能互补。此外, 其他光受体、激素、蛋白激酶、蛋白磷酸酶以及Ca²⁺也参与了植物向光弯曲的调节。本文就近年来有关植物下胚轴向光弯曲信号组分及可能的网络关系进行总结, 并对该研究领域存在的问题及今后可能的研究方向进行展望。

关键词: 向光素; 向光弯曲; 信号转导

Research Advances in Plant Hypocotyl Phototropism

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Abstract: The bending of the seedling stem toward unilateral light is caused by asymmetrical auxin distribution between the shaded and illuminated sides of plant organs. In recent years, genetic analysis has shown that plant may have different mechanisms in response to different light intensities in phototropism. In weak blue light, blue light receptors phototropin1 (PHOT1) regulates phototropism by directly interacting with signaling proteins NPH3, RPT2 and PKS1, resulting in asymmetrical distribution of auxin. In strong blue light, PHOT1 and PHOT2 contribute redundantly to blue-light-induced phototropic curvature of hypocotyls. The NPH3 may act as a common factor in different signaling pathways to complement functions. In addition, other photoreceptors, such as hormones, protein phosphatase and Ca²⁺, are also involved in phototropic response. This paper summarized some signaling components and their possible relationship in phototropism, and the problems remained are discussed, finally the possible research directions in this field are proposed.

Key words: phototropin; phototropism; signal transduction

蓝光(320~500 nm)对植物的生长发育有着极其重要的作用。植物的向光反应、气孔开放、叶绿体迁移主要由蓝光诱导, 尤其是在提高弱光下植物的光合作用、降低强光对植物伤害等方面, 蓝光起重要的调节作用(Kagawa等2001; Kasahara等2002; Takemiya等2005)。尽管人们认识这些现象已近一个世纪, 但对其分子机制的研究还很有限。近年来, 随蓝光受体向光素的发现, 人们对向光反应的光受体以及光受体下游的信号传递途径等问题都做了较深入的研究, 为进一步探明向光反应信号转导的分子机制奠定了基础。本文就拟南芥向光素受体介导的下胚轴弯曲及信号转导研究进展进行综述。

1 向光素受体

目前发现拟南芥蓝光受体向光素有2个: 向光素1 (phototropin 1, PHOT1)和向光素2 (phototropin 2, PHOT2)。1995年, Liscum和Briggs (1995)通过单侧蓝光照射拟南芥下胚轴, 筛选出非向光弯曲突变体, 分离出了向光素蛋白PHOT1。随后, Huala等(1997)将PHOT1鉴定为一个有120 kDa的质膜蛋白。PHOT2是从突变拟南芥叶片中分离的向光素受体, 该突变体在强蓝光下丧失叶绿体避光反应,

收稿 2011-07-27 修定 2011-09-02

资助 国家自然科学基金(30871300)和河南省教育厅自然科学基金项目(2011B180007)。

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PHOT2也是一个115 kDa的质膜蛋白(Kagawa等2001),与PHOT1蛋白同源性达到54.6%,相似性67.4%。

拟南芥向光素蛋白包括两个部分,即N端的光感受区和C端的Ser/Thr蛋白激酶区(Christie 2007)(图1)。N端光感受区含有两个LOV (light, oxygen, voltage)区,分别命名为LOV1和LOV2。每个LOV区由大约110个氨基酸组成,属于PAS (per, arnt, sim)家族的成员(Taylor和Zhulin 1999)。每个LOV区都以非共价键的形式结合一分子的黄素单核苷酸(flavin mononucleotide, FMN) (Christie等1999),并参与蛋白互作和配体结合(Huala等1997)。蓝光激发引起一个可逆的光循环,FMN和LOV区内保守的半胱氨酸之间形成共价结合,共价结合物的形成诱导了蛋白构象的变化,激活C端激酶区,引起受体自磷酸化(Christie 2007)。PHOT1的C端与LOV2之间存在一个保守的 α 螺旋(命名为Ja)(图1),大约20个氨基酸,作为LOV2光激活激酶活性的耦合螺旋连接器发挥作用(Harper等2003)。黑暗条件下,定点突变Ja内的第608位异亮氨酸(isoleucine, Ile)为谷氨酸(glutamate, Glu),也会产生PHOT1激酶活性(Harper等2004; Jones等2007),由此证明了LOV2区是PHOT1激酶活性暗状态的抑制子(Kaiserli等2009)。C端的Ser/Thr蛋白激酶区属于AGC蛋白激酶家族(Bögge等2003)。自磷酸化作用是向光素信号转导的前提条件,近年来利用质谱(LC-MS/MS)分析方法,已经在PHOT1的N端、LOV1与LOV2之间的连接区、激酶区及C末端鉴定了多个磷酸化位点(Inoue等2008; Sullivan等2008)(图1箭头所示)。其中第851位的丝氨酸残基(Ser851)是向光素在蓝光下开启自磷酸化作用的一个重要位点

(Inoue等2008),介导许多生理反应。

PHOT1和PHOT2以光强依赖的方式调节植物许多生理反应。弱蓝光下,PHOT1和PHOT2以功能冗余的方式调节叶绿体聚光运动、气孔开放、叶片伸展及叶片定位(Christie 2007)。PHOT1单独介导下胚轴伸长抑制和强光下的mRNA降解(Folta和Spalding 2001; Folta和Kaufman 2003)。PHOT2单独介导黑暗、强光条件下的叶绿体运动及核定位(Sakai等2001; Tsuboi等2007)。虽然向光素蛋白是亲水性蛋白,与质膜结合,但蓝光下,拟南芥一部分PHOT1蛋白会迅速从质膜释放入胞质(Sakamoto和Briggs 2002; Wan等2008),PHOT2迁移至高尔基体(Kong等2006, 2007)。这种光诱导部分蛋白内移的基本机制和生物学重要性还不清楚,可能代表着向光素信号转导的一种模式。

蓝光诱导气孔开放是由于向光素激活了保卫细胞质膜上的 H^+ -ATPase,使 H^+ -ATPase C-末端的丝氨酸和苏氨酸发生磷酸化,磷酸化后的质膜 H^+ -ATPase与14-3-3蛋白特异结合,导致酶活性增强,向胞外泵出质子 H^+ 使质膜发生超极化,激活电压依赖的质膜 K^+ 离子通道及相关阴离子通道从而使离子内流,降低细胞水势,细胞发生吸水膨胀从而诱导气孔开放(Kinoshita和Shimazaki 1999)。

2 向光弯曲信号转导机制

植物向光性是植物对光所产生的最普遍反应,即在受单侧光照时植物体部分向光弯曲。向光运动使植物处于最适宜利用光能的位置。蓝光诱导生长素的不对称分布和信号跨组织转导引起了下胚轴向光弯曲(Esmon等2006; Holland等2009)。其中,生长素是向光反应的中心调节子(Holland等2009)。生长素的运输受生长素运输蛋白PIN (pin-

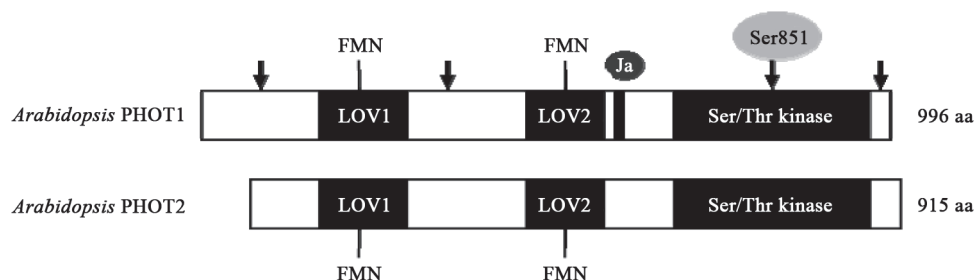


图1 拟南芥向光素受体的结构

Fig.1 Protein structures of the *Arabidopsis* phototropin

参考Briggs和Christie (2002)文献并作修改。

formed)、AUX1 (auxin-resistant 1)、PGP (p-glycoprotein)及生长素转录因子ARFs (auxin response factors)的调节(Friml等2002; Noh等2003; Tatematsu等2004; Stone等2007)。

2.1 向光素对生长素的调控

向光素PHOT1直接调节生长素输出载体PIN1的定位(Blakeslee等2004)。蓝光处理后, PIN1的迁移降低了生长素向基部运输, 滞留下来的生长素促进细胞伸展, 参与向光弯曲。PGP基因突变降低了极性运输, 增加了生长素的横向运输, 使向光性得到增强(Noh等2003)。NPH4 (nonphototropic hypocotyl 4)基因编码一个生长素转录因子ARF7, NPH4/ARF7转录因子可响应内源生长素浓度的变化(Harper等2000)。在缺乏蓝光刺激时, 下胚轴中的NPH4/ARF7以异聚体状态与Aux/IAA蛋白结合, 使转录失活。而受光刺激后, 背光面积的生长素诱导Aux/IAA蛋白降解, NPH4/ARF7同聚化, 转录激活诱导相关基因的表达, 引起下胚轴向光弯曲(Tatematsu等2004; Esmon等2005; Liscum和Reed 2002)。近来研究发现甘蓝(*Brassica oleracea* var. *capitata* L.)下胚轴向光刺激后有8个基因转录量不同程度的积累, 其中有几个是生长素响应启动元件(auxin-responsive promoter elements, AuxREs), 还有2个基因编码伸展性, 参与细胞壁延伸(Esmon等2006)。AUX1编码一个高亲和性生长素输入载体, 当缺乏NPH4/ARF7蛋白时, AUX1在拟南芥向光反应信号转导中才起重要作用(Stone等2007)。

2.2 PHOT1和PHOT2介导下胚轴向光弯曲机制差异

向光素PHOT1介导弱蓝光($0.01\sim 1\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)和强蓝光($>1\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)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等2001)。Cho等(2007)证明向光素LOV2区是介导向光反应所必须的。目前, 关于PHOT1介导弱蓝光引起的下胚轴弯曲机制研究较为明确, 即PHOT1感受弱蓝光后, 与其下游的信号蛋白NPH3 (nonphototropic hypocotyls 3)、RPT2 (root phototropism 2)和光敏色素PHYA (phytochrome A)底物PKS1 (phytochrome kinase substrate 1)发生生理互作(Motchoulski和Liscum 1999; Sakai等2000; Inada等2004; Lariguet等2006; Pedmale和Liscum 2007), 这些PHOT1互作蛋白以一定的方式

调控生长素输入载体PIN1和输出载体AUX1的活性及定位, 导致下胚轴向光和背光侧中生长素的不对称分布, NPH4/ARF7作为生长素转录激活因子直接调控引起向光弯曲的相关基因的表达, 诱导向光弯曲。遗传分析表明, 单侧弱蓝光下, 拟南芥*nph3*单突变、*pks1pks2pks4*三突变与*phot1*突变体表型相似, 下胚轴完全丧失了向光性(Motchoulski和Liscum 1999; Lariguet等2006); *rpt2*、*pks1*单突变体下胚轴弯曲度有所降低(Sakai等2000; Lariguet等2006)。生化试验证明, 蓝光诱导PHOT1刺激NPH3发生去磷酸化作用, 一定浓度的蛋白磷酸酶抑制剂处理黄化苗也抑制了向光弯曲(Pedmale和Liscum 2007), 进一步证明了转录后修饰是PHOT1介导的向光反应中一个重要的过程(Pedmale和Liscum 2007)。此外, 亚细胞定位分析证明PKS1、NPH3在下胚轴伸长区高度表达(Lariguet等2006)。这些研究为其正调节向光弯曲提供了一个有力的证据。

强蓝光下, PHOT1和PHOT2以功能冗余方式调节拟南芥下胚轴向光弯曲(Sakai等2001)。研究发现, NPH3和PHOT1、PHOT2体内互作(Carbonnel等2010), RPT2仅与PHOT1生理互作(Inada等2004), *RCN1* (root curling in naphthylphthalamic acid 1)基因编码蛋白磷酸酶2A (protein phosphatase 2A, PP2A)的A1亚基, 其与PHOT2蛋白特异互作, 负调节PHOT2介导的向光弯曲(Tseng和Briggs 2010)。单侧强蓝光照射下, *nph3*突变体下胚轴不发生向光弯曲(Inada等2004), *phot1 rpt2*双突变与*phot1*单突变体向光弯曲表型相似, 强蓝光下向光反应正常, 而*phot2 rpt2*双突变与*rpt2*单突变体表型相似, 下胚轴弯曲度明显下降(Inada等2004)。由此推断, NPH3是强光下PHOT1和PHOT2介导向光弯曲的共有信号, 而RPT2仅在PHOT1介导的信号途径中发挥作用。我们的研究也表明, 单侧强蓝光下, *phot1*突变体下胚轴弯曲度比*phot2*突变体更大, 可能PHOT1介导的信号通路负调节PHOT2介导的向光弯曲(未发表资料)。以上所述的研究结果表明, 作为功能冗余的PHOT1和PHOT2蛋白, 可能以NPH3为共同的支架, 采用不同的信号传递载体, 以调节不同强度的蓝光引起的拟南芥下胚轴向光反应。

2.3 钙在向光素介导生理反应中的作用

Ca²⁺是最重要的胞内信使,能应对一系列胞外信号,调控植物反应。Ca²⁺来源于胞外空间和胞内钙库的释放,胞内钙库的释放器官如内质网、液泡等(Stoelzle等2003; Harada等2003; Harada和Shimazaki 2007)。实验证明,向光素PHOT1和PHOT2介导蓝光刺激的胞质Ca²⁺增加,并且PHOT1和PHOT2可能采用不同的机制介导蓝光调节胞质Ca²⁺的变化(Stoelzle等2003; Harada和Shimazaki 2007)。Folta和Spalding (2001)证明蓝光诱导拟南芥黄化苗胞质Ca²⁺的增加。Shimazaki等(1999)利用药理学方法证明Ca²⁺参与了蓝光依赖的质子泵和表皮气孔的开放。Baum等(1999)报道Ca²⁺参与调节蓝光诱导的拟南芥下胚轴弯曲,然而Folta和Spalding (2001)研究发现抑制拟南芥下胚轴胞内Ca²⁺的升高,并不抑制向光弯曲。因此, Ca²⁺是否参与拟南芥下胚轴的向光弯曲反应还存有争议。鉴于单侧光可引起玉米、向日葵等胚芽鞘的向光侧与背光侧细胞内Ca²⁺不对称分布,推测Ca²⁺可能在蓝光下调节拟南芥下胚轴向光弯曲生长。

2.4 参与向光素介导的向光反应的其他调控成分

研究表明,拟南芥蓝光受体隐花色素(cryptochrome, CRY)和红光受体(phytochrome, PHY)也参与了向光素介导的向光反应。突变体 $cry1$ 和 $cry2$ 具有向光性反应,但是 $cry1cry2$ 双突变体的向光性反应微弱,相反,过量表达CRY的转基因植物的向光性反应增强,且对光高度敏感(Ahmad等1998; Ohgishi等2004)。红光受体光敏素 $phyA$ 突变体黄化苗脉冲弱蓝光后,弯曲度比野生型低(Lariguet等2006),并且在下胚轴的伸长区,PHYA阻止了蓝光诱导的PHOT1::GFP向胞质的迁移(Han等2008)。弱蓝光照射下,红光受体PHYB、PHYD与PHYA功能冗余方式调节下胚轴向光反应(Whippo和Hangarter 2004)。另外,强蓝光下,赤霉素(GA)作为隐花色素下游因子调控向光弯曲(Tsuchida-Mayama等2010)。乙烯和油菜素内酯(BR)通过诱导生长素相关基因的表达参与向光反应(Whippo和Hangarter 2005)。

3 小结与展望

近年来,随着分子遗传学的发展,通过对拟南芥突变体的分离和研究,人们对蓝光受体向光素

介导的下胚轴弯曲反应机制有了深入的了解,即蓝光处理后,向光素与其下游的信号分子RPT2、NPH3、PKS1和ARF7等作用,调控生长素在下胚轴的不对称分布,导致植物下胚轴向光弯曲反应。然而,鉴于目前研究技术和方法的限制,仍存在如下问题需进一步探讨:(1)强蓝光下,虽已证明NPH3和RCN1参与了PHOT2介导的下胚轴向光弯曲调节,但是由于PHOT1和PHOT2功能存在互补性,限制了人们对PHOT2下游信号分子及其转导途径研究;(2)蓝光引起向光素自磷酸化作用是其介导生理反应的前提,推测植物可能通过不同的激酶底物,以实现其对不同生理反应的差异调控,遗憾的是,与向光素作用的底物蛋白研究还很有限;(3)生长素的不对称分布决定了植物的向性运动,但是强蓝光下PHOT1和PHOT2对生长素运输分布的调节机制并不清楚;(4)尽管Ca²⁺参与向光素调节拟南芥的诸多生理反应,然而由于技术的限制,针对Ca²⁺是否参与拟南芥下胚轴的向光弯曲还存有争议;(5)拟南芥蓝光受体CRY、红光受体PHY以及一些激素如赤霉素、乙烯和油菜素内酯也参与调节拟南芥向光反应,然而这些光受体是如何以向光素为主体构成复杂的信号网络,以调控生长素及其他激素的运输,其机制尚需进一步研究。因此,综合利用细胞生物学、遗传学以及分子生物学等技术和手段,分离和鉴定植物向光弯曲反应信号途径的一些新的下游信号因子,构建PHOT1和PHOT2介导的信号转导网络,揭示二者在调节蓝光依赖的下胚轴弯曲的差异,将为人们深入认识和了解植物下胚轴向光弯曲反应机制提供新的途径。

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