光质调控植物开花时间和花性分化研究进展

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摘要: 光是植物生长发育的重要环境因素和调控信号。关于光周期调控植物开花的途径已经较为清晰, 但是光质调控植物花性分化的研究仍少见报道。本文对光质、光受体、植物激素、转录因子等对植物性别决定和开花的影响进行综述, 旨在揭示光质调控植物花性分化和开花的机制, 为该领域的探索提供参考。

关键词: 光质; 开花时间; 花性分化

植物开花时间和花性分化不仅取决于遗传因素, 还受环境因素的显著影响。植物生长发育受环境条件的影响中, 光是重要因素之一, 也是重要的调控信号。光照强度、光质和光周期影响和调控植物生长发育。目前, 光周期调控植物开花的途径已经较为清晰(Hemming等2008), 关于光质调控植物开花的时间还处于初步研究阶段, 光质对植物花性分化的影响更少见报道。本文概述光质、光受体、植物激素、转录因子影响植物性别决定和开花, 以及开花时间相关基因等方面最新研究进展。

1 光质对植物开花的影响

光质可以影响植物开花, 植物响应光环境主要通过不同光受体接受光和转导信号来完成。根据不同波长的光响应, 可以将光受体分成感受红光和远红光的光敏色素, 包括光敏色素A (phytochrome 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) (Gyula等2003; Franklin和Quail 2010); 感受蓝光和近紫外光的隐花色素, 有隐花色素1 (cryptochrome 1, CRY1)和隐花色素2 (CRY2) (Gyula等2003)。远红光、蓝光通过PHYA、CRY1和CRY2促进植物开花(Putterill等2004; Lin 2000), 红光通过PHYB、PHYD和PHYE抑制植物开花(Lin 2000); 但是CRY2促进植物开花, 不仅依赖蓝光, 也依赖红光(Lin 2000)。Fukuda等(2016)发现与白光相比, 蓝光处理的矮牵牛(*Petunia × hybrida)*较早出现花芽和提早开花, 而低光强红光处理下没有观察到花芽, 且在低光强红光照射期间切换高光强红光和蓝光也可以诱导花的发育, 表明蓝光对矮牵牛花芽的形成起着重要的信号作用, 而红光对矮牵牛花芽的形成取决于光照强度。Guo等(1998)发现无论是提供蓝光催

化剂还是缺少红光抑制剂, 野生型植物在蓝光下都提早开花, 而缺少蓝光CRY2催化剂时在红光下生长的野生型开花延迟, 且*cry2*突变体植物在蓝光下正常开花, 表明CRY2单独在蓝光下无法促进植物开花, 因此, PHYB和CRY2调节植物开花是一种相互拮抗的关系。还有研究发现, 光质可能也与植物性器官发育或花性分化有关。如在暗期中间, 用红光(red light, R)间断可以诱导光敏稻不育水稻(*Oryza sativa*)花粉高不育率, 而用红光/远红光(red light/far-red light, R/FR)间断暗期可使花粉育性恢复, 说明R/FR通过光敏色素参与调节光敏水稻的雄性器官发育和育性转变(Tong等1990)。这些研究表明光质可以调控植物开花时间, 并对植物花性分化有一定的影响。

2 光质与植物开花时间基因

FT (*flowering locus T*)是光周期途径植物开花时间决定的关键基因, 并且有研究认为*FT*基因的表达产物可能就是人们长期追寻的开花刺激物质——开花素(Abe等2005)。在模式植物拟南芥(*Arabidopsis thaliana*)中, CO (constans)/FT调节元件的表达变化是光周期诱导途径中最核心的环节, *FT*的mRNA从叶片转移到茎顶端分生组织(Lin等2007), 与bZIP锌指蛋白FD (flowering locus D)结合, 形成二聚体形式, 调控下游的花分生组织特征基因*AP1* (*apetala 1*)和*SOC1* (*suppressor of overexpression of constans 1*)的表达(Wigge等2005; Moon等2005), 再由他们调控其他的花器官特征基因如*AGL24* (*agamous-like 24*)等, 最终完成花器官发育(Yu等

2002; Abe等2005)。为了检验长距离运输的信使是FT mRNA还是FT蛋白, Lin等(2007)选择小西葫芦黄花叶病毒(*Zucchini yellow mosaic virus*, ZYMV)作为载体异位表达南瓜(*Cucurbita moschata*)的*FT*同源基因*CmFTL1*和*CmFTL2*。ZYMV病毒的基因组是RNA, 编码多聚蛋白, 由蛋白酶特异切割成不同的蛋白质产物, 表明整合在ZYMV病毒上的*Cm-FTL1*和*CmFTL2*可以越过mRNA直接产生蛋白。在非诱导日照条件下, 受该ZYMV重组病毒感染的南瓜植株提前开花, 感染开花的笋瓜(*C. maxima*)砧木可引起长日照接穗南瓜开花。对笋瓜砧木韧皮部汁液进行逆转录PCR (reverse transcription PCR, RT-PCR), 并没有检测到*CmFTL1*和*CmFTL2* mRNA的存在, 而质谱分析则显示接穗韧皮导管汁液存在来自砧木的CmFTL1和CmFTL2蛋白, 表明通过韧皮部汁液运输诱导长日照接穗南瓜开花的是南瓜砧木的CmFTL1和CmFTL2蛋白, 而不是*CmFTL1*和*CmFTL2* mRNA。由此可见, *FT*在从叶片到茎尖的成花信号传导中起重要作用, 并且作为长距离信使的是FT蛋白而不是mRNA。目前已在多种植物中分离出*FT*的同源基因, 并通过转基因证明*FT*基因的表达可促进植物提早开花(Hayama等2007), 如菊花(*Chrysanthemum morifolium*) (潘才博等2010)、水稻(Tamaki等2007)、猕猴桃(*Actinidia chinensis*) (Varkonyi-Gasic等2013)等。与*FT*基因功能相反, *TFL1* (*terminal flower 1*)会抑制植物开花, 二者相互拮抗, 同属于*PEBP*基因家族。有研究表明, *FT*与*TFL1*是促进还是抑制开花取决于其中一个关键的氨基酸, 即FT中的Tyr85或TFL1的His88 (Ahn等2006; Hanzawa等2005)。如张娟等(2013)在黄瓜(*Cucumis sativus*)上克隆出的同系物*CsFT*, 其第84位氨基酸为酪氨酸(Tyr), 因此, *CsFT*是黄瓜中*FT*的同源基因, 可促进黄瓜开花, 这与Sato (2009)在黄瓜上所克隆到的*FT*同系物一样。但是与拟南芥开花机制不同的是, *CsFT*基因在黄瓜的雌花和雄花中高度表达, 而在黄瓜叶子中几乎不表达, 由此推测它可能直接在茎顶端分生组织发挥作用(张娟等2013)。也有研究通过数量性状基因座测序(quantitative trait loci sequencing, QTL-seq)技术鉴别黄瓜早期开花的*FT*基因, 发现*Csa1G651710*是*FT*的同系物, 可作为黄瓜早期开花的候选基因(Lu等2014)。

*CO*基因早期激活的目标基因是*FT*, 由光周期诱导的*CO*直接转录激活*FT*的表达(Böhlenius等2006)。CO蛋白是一个转录因子, 它通过调控下游基因*FT*和*SOC1*的表达控制开花时间。*CO*调控*FT*的表达, 但是*SOC1*的表达量与*CO*活性强弱并不直接相关(Wigge等2005)。还有研究发现, 在35S::FT植株中*SOC1*的表达水平显著增加, 在*FT*突变中明显减少, *FT*、*SOC1*双突变会增加晚花表型, *SOC1*的表达水平不会因*FT*的突变而大大降低, 由此表明*SOC1*基因既受到*FT*基因调控, 又不会完全受控于*FT*, 同时, 也说明还有其他途径调控*SOC1*的表达(Moon等2005; Yoo等2005)。*AGL24* (*agamous-like 24*)是另一个开花信号整合子, 其功能与*SOC1*相似, 两者能够通过结合到对方的启动子上相互提高彼此的表达水平。*AGL24*与*SOC1*属于*MADS-box*基因, 能互作调节赤霉素(gibberellin, GA)开花途径, 这表明*AGL24*和*SOC1*之间能形成正反馈回路(Liu等2008; Michaels等2003)。

CO蛋白的稳定性既受到隐花色素CRY1、CRY2和光敏色素PHYA的正调控, 又受到PHYB的负调控(Valverde等2004)。蓝光通过*FKF1* (*f-box 1*)对*CO*的转录具有重要的作用(Imaizumi等2003)。Cerdan和Chory (2003)认为光质通过光敏色素PHYB、PHYD、PHYE调控*FT*, 光周期通过光敏色素调控*FT*, 而PHYB通过*PFT1* (*phytochrome and flowering time 1*)调控*FT*, 且途径不需要*CO*基因介导, 这表明光质调控成花是依赖于叶片感应的。也有研究发现, 蓝光通过诱导*FT*和*SOC1*的表达来促进拟南芥的开花(Hori等2011)。蓝光处理下, *SOC1*基因*FBP28*在矮牵牛中高度表达(Fukuda等2011)。*MED25*是*PFT1*的亚基核心模块之一, 它在茉莉酸信号和光质途径中PHYB的下游调控*FT*的表达以调控植物开花(Cerdan和Chory 2003; Elfving等2011; Wollenberg等2008)。

3 光受体与植物激素

光受体是接收光信号的载体, 在植物体内至少存在4类光受体: (1)光敏色素和隐花色素, 感受红光(620~700 nm)和远红光(700~800 nm); (2)隐花色素, 又称为蓝光受体, 感受蓝光(380~500 nm)和紫外线A (ultraviolet A, UV-A; 320~380 nm); (3)紫外线B (UV-B, 280~320 nm)受体, 感受UV-B区域的

光, 但是这类光受体尚未得到鉴定(Suesslin和Frohn-meyer 2003); (4)蓝绿光受体, 又称ZTLs (zeitlupes)家族光受体, 主要感受蓝绿光(450~520 nm) (Somers等2000)。许多实验证明光受体可以调控植物激素的合成。Yang等(1993)发现光敏色素能诱导赤霉素-3-羟基化酶编码基因的转录, 而此酶是催化产生活性赤霉素GA1和GA4的关键酶。红光通过光敏色素PHYA和PHYB诱导GA合成酶基因表达(Ait-Ali等1999)。Welle等(1995)试验证明红光瞬时处理下, 大豆(*Glycine max*)幼苗体内GA代谢酶基因*GA2ox*的表达量约增加5倍, 但是在*phyA*和*phyB*突变体中*GA2ox*基因的表达量无明显变化, 说明光敏色素介导红光诱导大豆幼苗中*GA2ox*基因表达, 降低有生物活性的GA积累。然而随照光时间延长, 有生物活性的GA含量下降而反馈促进*GA20ox*和*GA3ox*基因的表达, 又使幼苗体内有生物活性的GA含量恢复到正常水平。Bai等(2012)发现DELLA-BZR1-PIF4是一个核心转录部分; 植物通过GA、油菜素内酯(brassinosteroid, BR)和光信号相互作用介导生长调节, 如DELLAs抑制BR活性成分, 而GA诱导DELLA降解解除这种抑制。光敏色素互作因子(phytochrome interacting factor, PIF)在光敏色素介导的光信号传导途径中起着中枢作用。拟南芥种子受到光照后, PHYB Pfr结合PIF1/PIL5, 诱导PIF降解, 促进GA生物合成, 提高GA的含量, 也降低脱落酸(abscisic acid, ABA)生物合成基因的转录, 从而使ABA含量下降(Shen等2005), 所以PHYB介导的光信号负调控水稻ABA的积累(顾建伟2012), 而PHYA在远红光处理下正调节ABA信号(Mach 2014)。光敏色素互作因子*PIF3*可以直接激活*EIN3* (*ethylene-insensitive 3*) (Zhong等2012), *EIN3*是乙烯(ethylene, ETH)信号转导途径中的转录因子。生长素(auxin, IAA)被认为是光敏色素被激活后的一个传播因子, 参与信号传导(廖祥儒等2001)。在植物发育早期光敏色素和IAA信号之间有许多反应, 如依赖光促进IAA动态平衡(Kurepin等2012; Wu等2010)。此外, UV-B光受体UVR8 (UV resistance locus 8)可以抑制IAA合成和促进GA分解代谢(Hayes等2014)。茉莉酸(jasmonic acid, JA)信号途径的许多组件, 如*COI1*、*JAZ*、*MYC2*和*JAR1*影响光信号介导响应(Riemann等2008; Wang

等2011)。以上这些研究表明光信号通过光受体调控植物激素的合成和分解。

4 植物激素与花性分化

植物花性分化是一个很复杂的过程, 它与植物激素密切相关。研究证明, ETH对植物雌性发育尤为重要。如外源ETH或ETH释放物能增加瓜类作物雌花的发生(Yang等2015)。Li等(2009)发现*CsACS2*关键氨基酸突变后会导致黄瓜从两性花变成单性花。*CTR1*是ETH信号传导途径的一个负调控因子, 在没有ETH的情况下, 与ETH受体结合, 抑制ETH响应途径。ETH存在时, 会使受体钝化和阻遏负调节物*CTR1*, 然后通过其他下游组件, 包括*EIN2*和*EIN3*, 引发ETH响应途径(Wang等2002)。Manzano等(2013)以两个差异显著的西葫芦(*C. pepo*)雌雄同株自交系Bolognese (Bog; ETH敏感型, 早过渡雌花品种)、自交系Vegetable spaghetti (Veg; ETH非敏感型, 晚过渡雌花)为材料研究发现, 在植物发育的较早阶段, 当Bog已经产生雌花, 而Veg还没转型成雌花时, Bog的尖端产生较多的ETH, *CpACO1*的表达也较高; 而ETH受体和*CTR*类基因在Veg和Bog植物尖端的表达显示, 这些基因对雌花过渡起负调控作用。Bog较早转型成雌花不仅与茎尖较高的ETH产量有关, 也与ETH负调节物过早衰变有关。*AP3*属于MADS-box B类基因, 可以控制双子叶植物花瓣和雄蕊的发育(秦巧平等2006)。*AP3*启动子驱动黄瓜ETH信号转导途径的调控因子*CsE-TR1*下调, 拟南芥雄蕊停止发育并产生类似雌蕊的花(Duan等2008; Wang等2010)。有研究发现, IAA加强瓜类植物的雌性化(Ming等2011), 是因为IAA可以诱导*CsACS3*的表达(陈惠明等2005), 从而通过诱导ETH合成促进雌花发育(Takahashi和Jaffe 1984)。

GA作为一种内源生长调节剂, 对植物雄蕊发育发挥着重要的作用, 如外施GA可促进雄花产生, 外施抑制GA生物合成的化合物乙烯利、IAA等可以促进雌花形成。GA可以通过*GAMYB*的转录调节调控拟南芥和水稻雄蕊与花药的发育; 在黄瓜中*GAMYB*的同系物*CsGAMYB1*表达受外源GA3上调, 抑制*CsGAMYB1*的表达会使雌雄花节率下降, 而且这个过程不影响ETH的产生和*F*、*M*基因的表达, 表明*CsGAMYB1*可调控黄瓜性别表达, 而ETH

不参与此过程(Zhang等2014)。黄瓜GA信号转导因子*GID1* (*gibberellin-insensitive dwarf 1*)、*DELLA*和*GAMYB*的同系物在雄花发育中的表达高于GA合成基因，而*DELLA*的同系物*CsGAIP*是表达量最高的，并且主要在茎和雄花花芽中表达(Jin等2011)，张颜(2014)也有相似的研究结果。有研究表明，ABA与GA是相互拮抗的，如ABA抑制牵牛开花，而GA能够完全逆转ABA的抑制作用(Wijayanti等1997)。在短日照条件下，同时喷施外源*S-ABA*与GA的混合物能够诱导菠菜(*Spinacia oleracea*)开花，但是如果单独施加*S-ABA*或者GA几乎不能促进菠菜开花(Kamuro等2001)，因此，ABA与GA影响植物的相互作用因植物种类而异。此外，ABA有助于黄瓜雌花的发生(Rudich等1972)，江玲等(1998)发现ABA可显著促进四年生无花史的马尾松(*Pinus massoniana*)幼树雄球花的形成，表明ABA因植物的种类不同而起到促进雌花或雄花发育的作用。

JA和BR对植物雄蕊的发育也起着重要的作用(Acosta等2009; Hartwig等2011; Song等2013)。如拟南芥、番茄(*Solanum lycopersicum*)和玉米(*Zea mays*)等植物花的发育和不育性受JA影响(Wasternack和Hause 2013)；当BR合成或信号通路受阻断时，雄蕊发育缩短和花粉畸形发育导致雄性能育性降低(Ye等2010)。还有研究表明，喷施外源细胞分裂素(cytokinin, CTK)可使山葡萄(*Vitis amurensis*)基因型为雄性的花转变为表型雌性，开花结实(艾军等2002)。多胺也会影响黄瓜的花性分化(Papadopoulou和Grumet 2005)。内源IAA、尸胺、亚精胺的水平较高有利于雌花形成，反之，内源GA、腐胺水平较高有利于雄花形成(Wang等2005; 陈学好等2002)。在长日照处理下，光敏核不育水稻雄性不育；在短日照处理下，光敏核不育水稻表现可育；而在长日照处理下的叶片中发现GAs和IAA含量剧减，生殖器官中早期IAA亏缺，ABA含量降低，并伴随着抗逆性能的减弱及GA1、GA4的不足，共同导致了光敏稻的花药败育(Tong等1990)。由此可见，激素与植物性别决定密切相关，而光可能通过光受体调控植物激素的合成与分解，因而控制植物性别分化。

5　植物花性分化和开花相关的转录因子

植物MYB转录因子家族是功能多样、数量众多的转录因子之一，主要集中参与了细胞分化、细胞周期的调节、激素和环境因子应答，并对植物次生代谢以及叶片等器官形态建成具有重要的调节作用(刘守梅等2012)。但是也有不少研究证明MYB转录因子与植物花朵的发育有关。Mandaokar等(2006)在拟南芥中发现JA介导*MYB21*和*MYB24*两个调控因子响应雄蕊发育。*MYB21*和*MYB24*可以直接作用于茉莉酸ZIM蛋白，参与JA调控花药发育和花丝伸长(Song等2011)。*MYC5*诱导*MYB21*表达激活JA信号途径调控雄蕊发育(Figueroa和Browse 2015)。Reeves等(2012)也发现*MYB21*和*MYB24*可以促进花瓣和雄蕊的发育。所以，在JA信号途径调控花器官发育中MYB转录因子基因发挥着重要的作用(王俊斌等2009)。

植物中bHLH家族成员是数量众多的转录因子之一。目前，大部分研究表明，bHLH主要参与调控植物生长发育(Liu等2009; MacAlister等2007)、植物适应缺铁胁迫反应(Wang等2007; Yuan等2008)、植物适应其他非生物胁迫逆境反应(Jiang等2009; Kumar等2012; Li等2010; Meng等2009; Oh等2012)等过程。也有极少数研究表明bHLH转录因子与光信号转导、激素信号转导和开花有关。PIFs转录因子是一种光敏色素互作因子，属于bHLH家族，可以直接与光敏色素的活化形式相互作用开始光敏色素信号转导，如PIF3可以直接与PHYB结合，形成的复合物与光反应元件结合，诱导一系列的基因表达(Basu等2000)。Kumar等(2012)以拟南芥为研究材料发现*PIF4*可以活化*FT*基因，激活开花。*PIF5*可以直接调控*SOMNUS*基因的表达而间接调控与代谢相关基因的表达，从而影响拟南芥ABA和GA的含量(Kim等2008)。

WRKY转录因子参与植物多种代谢途径，如植物损伤(Skibbe等2008)、衰老(Guo等2004)、发育代谢(Devaiah等2007; Soler等2007)等过程，在生物胁迫及非生物胁迫方面发挥着非常重要的作用。但是，目前也有很多研究发现WRKY转录因子家族成员可以调控植物开花。如*WRKY25*通过直接或间接负调*AP1*调控植物提早开花(王芳秀等2011)。Luo等(2013)通过定量PCR (quantitative real time PCR, qPCR)和微阵列分析发现野生大豆中WRKY家族的成员*GsWRKY20*可能通过调控开花

相关基因*FLC (flowering locus C)*、*FT*、*SOC1*、*CO*以及花分生组织*AP1*、*AP3*、*AG (agamous)*等, 从而提早开花。也有研究证明WRKY转录因子是响应ABA信号途径的关键点(Jiang和Yu 2009; Ren等2010; Rushton等2012; Shang等2010), 它的家族成员涉及ABA信号和IAA运输途径(Song等2010)。

　　以上转录因子主要受环境信号调控, 而光属于环境信号之一。尤其是*bHLH*家族中的*PIFs*转录因子可以直接作用于光敏色素信号转导, *MYB*转录因子和*WRKY*转录因子又与植物激素、花性分化和开花具有密切关系。因此, 综上所述, 将光、光受体、激素、转录因子、开花时间、性别决定几大方面归纳为图1。
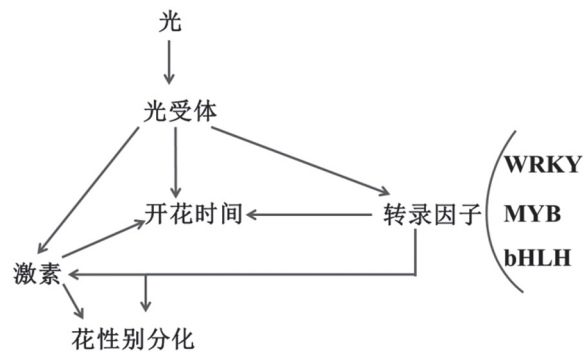

图1　光质调控植物花性分化和开花时间的可能机制
Fig.1　Possible mechanisms of light regulating flower sex differentiation and flowering time of plant

光受体: 光质信号的接受体; 开花时间: 可直接受光受体影响或间接受转录因子和激素的影响; 转录因子: 包括WRKY、MYB、bHLH三大转录因子, 直接受光受体影响, 作用于开花时间、花性别分化和激素; 激素: 植物内源激素, 直接受光受体影响或间接受转录因子影响, 作用于开花时间和花性别分化; 花性别分化: 光信号通过激素和转录因子间接影响。

6　展望

　　光是植物生长发育的重要环境因子, 地球上植物发育所需的光源主要来自于太阳辐射。光不仅作为触发信号影响着植物的光形态建成, 光质对植物的整个生长发育也具有重要的影响。近年来, 利用光质调控植株形态建成和生长发育成为研究的热点, 主要包括光质对植物生长发育、产量、品种等方面, 但是光质调控植物开花时间和植物花性分化还处于初步研究阶段。因此, 未来借鉴光周期调控模式植物拟南芥开花途径(Wigge

等2005), 各种植物激素调控途径, MYB、bHLH、WRKY转录因子调控植物开花及花性分化途径等的经验, 阐明光质调控植物花性分化、开花的过程和机理, 将是一条任重道远且意义重大的探索之路。

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Advances in regulation of light quality on flowering time and sex differentiation in plant

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Abstract: Light is an important environmental factor and regulatory signal which affects plant growth and development. The plant flowering regulation pathway by photoperiod is already clear, while the regulation of plant flowering and sex differentiation by light quality is little known. This paper focuses on the role of light quality, light receptor, phytohormone and transcription factor in plant sex differentiation.
Key words: light quality; flowering time; sex differentiation