

综述 Reviews

光照对植物花色苷生物合成的调控及机制

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摘要: 花色苷是决定高等植物花、果实、叶片和种皮颜色的主要色素, 其生物合成与积累过程受自身遗传背景和环境因子共同调控。光照是影响植物花色苷生物合成的主要环境因子之一, 不同光质和强度的光对花色苷合成的影响存在一定差异, 其中光质起更为关键的作用。本文重点从光受体、光信号转导及其与转录因子和结构基因互作的角度对光照调控花色苷合成的整个过程进行了总结, 并对今后的研究方向进行了展望, 以期能为园艺植物新品种选育和栽培设施的改进提供参考。

关键词: 光照; 花色苷; 光受体; 转录因子

花色苷属于酚类化合物中的类黄酮类, 存在于植物表皮细胞的液泡中, 随细胞液酸碱度的改变呈现橙色、红色及蓝色(Otaga等2005)。目前, 已知天然存在的花色苷达250多种, 其中常见的花色苷有6种, 分别为天竺葵色素(pelargonidin)、矢车菊色素(cyanidin)、飞燕草色素(delphinidin)、芍药色素(peonidin)、牵牛花色苷(petunidin)和锦葵色素(malvidin) (由春香等2013)。花色苷不仅赋予了植物丰富的色彩, 还具有预防心脑血管疾病、改善血糖平衡等生物学功能(Sun等2013)。对于植物自身而言, 植物细胞内花色苷等次生代谢产物不仅可以保护植物免受紫外线伤害(Jaakola 2013), 还有助于吸引昆虫传粉和借助动物传播种子(刘晓芬等2013; Grotewold 2006)。

花色苷生物合成和调控是自身遗传背景和外界环境因子通过复杂的调控网络共同作用完成的(Jaakola 2013; Wang等2016)。编码基因决定了花色苷合成的种类和时期, 而光照等环境因子则影响了花色苷生物合成时间、速率和积累量(胡可等2010)。光照是影响植物花色苷合成最重要的环境因子, 可以通过信号转导途径调控花色苷生物合成相关转录因子和结构基因的表达来影响花色苷的合成和积累(唐杏姣和戴思兰2011; Jaakola 2013)。本文总结了近年来国内外光调控植物花色苷合成与积累方面的最新研究进展, 并对今后的研究方向进行了展望, 以期能为植物花色苷代谢机制的阐明、园艺植物的新品种选育及栽培措施改进提供依据和理论支持。

1 植物花色苷生物合成

植物花色苷代谢途径的研究已较为透彻, 在拟南芥(*Arabidopsis thaliana*)、矮牵牛(*Petunia hybrida*)和玉米(*Zea mays*)等模式植物及葡萄(*Vitis vinifera*) (Kobayashi等2004)、苹果(*Malus pumila*) (Li等2012)、杨梅(*Myrica rubra*) (Niu等2010)、橙(*Citrus sinensis*) (Butelli等2012)、荔枝(*Litchi chinensis*) (Wei等2011; Lai等2014)和油桃(*Prunus persica*) (Ravaglia等2013)等果树作物中至少有18个基因参与了花色苷的生物合成和调控, 其中包括15个结构基因和3个调控基因家族(由春香等2013; Nesi等2000)。花色苷通过莽草酸途径形成, 由苯丙氨酸解氨酶(phenylalanine ammonia-lyase, PAL)、查尔酮合成酶(chalcone synthase, CHS)、查尔酮异构酶(chalcone isomerase, CHI)、黄烷酮-3-羟化酶(flavanone 3-hydroxylase, F3H)、类黄酮-3'-羟化酶(flavonoid 3'-hydroxylase, F3'H)、类黄酮-3',5'-羟化酶(flavonoid 3',5'-hydroxylase, F3'5'H)、二氢黄酮醇还原酶(dihydroflavonol 4-reductase, DFR)和尿苷二磷酸-葡萄糖:类黄酮-3-O-葡萄糖基转移酶(uridine diphosphate-glucose:flavonoid 3-O-glucosyltransferase, UFGT)等一系列结构基因编码的酶催化完成, 而结构基因受MYB、bHLH (basic helix-loop-helix, 碱

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性螺旋-环-螺旋)和WD40这三类转录因子组成的MBW (MYB-bHLH-WD40)转录复合体的协同调控(刘晓芬等2013; Nesi等2000) (图1)。

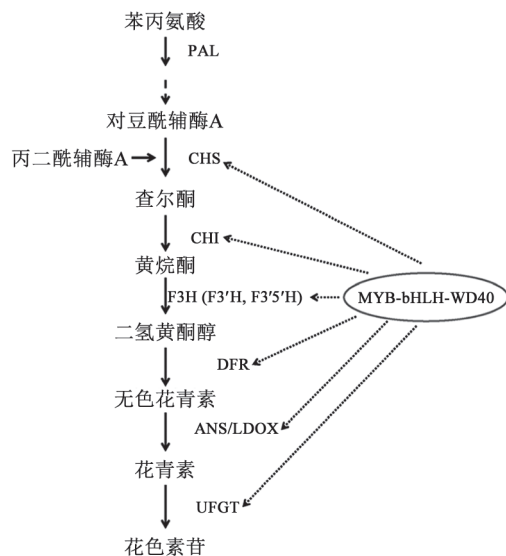


图1 植物花色苷生物合成与转录调控

Fig.1 Anthocyanin biosynthesis pathway and transcriptional regulation in plant

PAL: 苯丙氨酸解氨酶; CHS: 查尔酮合成酶; CHI: 查尔酮异构酶; F3H: 黄烷酮-3-羟化酶; F3'H: 类黄酮-3'-羟化酶; F3'5'H: 类黄酮-3',5'-羟化酶; DFR: 二氢黄酮醇还原酶; ANS: 花色苷合成酶; LDOX: 无色花色苷加氧酶; UFGT: 尿苷二磷酸-葡萄糖:类黄酮-3-O-葡萄糖基转移酶; MYB-bHLH-WD40: 转录复合体。参考刘晓芬等(2013)、Nesi等(2000)、Zoratti等(2014)并略有修改。

2 光对花色苷合成的影响

光照(光质、光照强度、光照时间)是影响果实花色苷合成最重要的环境因子之一。光照可从两方面影响花色苷的合成:一方面光照可通过影响光合作用促进糖、苯丙氨酸等花色苷前体物质的合成,另一方面其通过一定的机制增强花色苷生物合成途径相关酶的活性直接调控花色苷的合成(王惠聪等2004)。花色苷的合成与否及其合成量与不同光质、光照强度、光照时间有密切关系(Jaakola 2013)。在光诱导花色苷合成过程中,不同物种在不同光强和光质条件下,相关基因的表达模式存在较大差异(胡可等2010; Albert等2009)。

2.1 光质对花色苷合成的影响

光质差异是影响花色苷合成和积累的关键

因素(Weiss 2000)。生长在不同光照条件下,植物的花、叶和果实颜色存在明显差异(唐杏姣和戴思兰2011)。不同波长的光都能不同程度影响拟南芥幼苗花色苷合成,其中中波紫外线(ultraviolet B, UV-B)、蓝光的诱导效应最为明显,白光、远红(far-red, FR)光次之,红光最弱(陈大清2002; 唐杏姣和戴思兰2011)。在番茄(*Solanum lycopersicum*)中,红光处理下其果实番茄红素增加最为明显,蓝光处理下花色苷的含量显著增加(陈强2009)。光质可以影响茶树(*Camellia sinensis*)芽叶花色苷关键酶基因的表达,UV的效果最为明显,其可以上调CHS、CHI、F3H、DFR、ANS、ANR (anthocyanin reductase, 花色苷还原酶基因)等基因的表达;蓝紫光可以诱导CHS、F3H和DFR的表达,ANS受红光和橙光调控,CHI、ANR对蓝光和红光的调控响应不敏感(李智2014)。白光可以显著增加草莓(*Fragaria ananassa*)果实花色苷的含量和相关酶的活性;与白光相比,红光和黄光的效果更显著,而绿光和蓝光的效果不如白光(Miao等2016)。在葡萄中,蓝光和红光晚上照射,可能通过影响*VvNCED1*、*VIMYBA1-2*、*VIMYBA2*等基因的表达而影响脱落酸(abscisic acid, ABA)和花色苷的合成(Rodyoung等2016)。

不同光质对烟草(*Nicotiana tabacum*)叶片类黄酮含量影响的研究结果表明:类黄酮的含量与FR (716~810 nm)和近红外(near-infrared, NIR, 810~2200 nm)光呈显著正相关,而与UV-A (350~400 nm)的比例和红光/远红光的比值(R/FR)呈负相关;而类黄酮糖苷的含量与UV-A和R/FR呈正相关,与FR和NIR呈负相关。这表明高比例的FR和NIR可以激活类黄酮甲基转移酶的活性,而抑制了类黄酮糖基转移酶的活性,高比例的UV-A和高R/FR比值则起相反的作用(Fu等2016)。

与其他波长的光相比,蓝光和UV更易促进植物花色苷的合成,其中UV-A和UV-B均可以显著促进其合成(高飞等2014)。UV-A和UV-B可通过诱导CHS、ANS、UFGT等关键酶基因的表达促进植物花色苷的积累(Ubi等2006; Zhang等2012)。与黑暗培养及其他光质处理相比,UV-A通过提高PAL、UFGT等酶的活性,上调MYB75等转录因子及CRY1、CRY2、UVR8等光受体基因的表达,诱

导大豆(*Glycine max*)芽苗菜下胚轴中花色素苷的积累(戚楠楠等2015)。在不同连续光照时间(3、12、24、36 h)下,UV-A处理的萝卜(*Raphanus sativus*)芽苗菜下胚轴花色素苷含量均显著高于白光处理(张晓燕等2016)。

2.2 光照强度对花色素苷合成的影响

光照强度主要通过影响叶片和果实中花色素苷的含量及比例来实现对花色素苷合成的调控(姜卫兵等2005)。多数植物花色素苷的积累与光照强度呈正相关,强光可以诱导花色素苷合成结构基因和调控基因的表达,使花色素苷积累量增加,而遮光和弱光抑制相关基因的表达,从而抑制花色素苷的合成(Albert等2009; Matus等2009)。紫叶小檗(*Berberis thunbergii*)叶片颜色随光照强度的降低而变浅(高飞等2014)。紫叶加拿大紫荆(*Cercis canadensis*)叶色在不同光照强度环境下存在显著差异,强光环境下的叶片呈紫红色,中等光强条件下的叶片呈暗紫红色,弱光环境下的叶片都接近绿色(杨玲2007)。光照强度是影响茶树芽叶花色素苷关键酶基因表达的重要因素,光强降低,茶树花色素苷代谢关键酶基因的表达下降,花色素苷积累量降低(李智2014)。此外,强光下植物体内花色素苷的合成也是植物适应环境、自我保护的重要机制(Hughes 2005; Zeng等2010)。

套袋等栽培技术可以有效调控苹果(赵宗方等1992; 丁文展等2015)、葡萄(Matus等2009; Guan等2016)、桃(*Amygdalus persica*) (柳蕴芬等2010)、荔枝(Wei等2011; Zhang等2016)、梨(*Pyrus sorotina*) (孙永旺2015)等果实着色。在苹果中,花色素苷含量与光照强度呈极显著的线性相关(赵宗方等1992)。完全遮光处理下,荔枝果实UFGT等花色素苷合成酶的活性受到抑制,导致花色素苷合成受阻,恢复光照后,UFGT活性和表达量迅速增加,花色素苷快速积累(王惠聪等2004; Zhang等2016)。套袋处理时,梨果实中花色素苷、叶绿素和类胡萝卜素含量都很低,摘袋72 h后花色素苷开始积累,至240 h时达到较高水平,说明套袋通过改变花色素苷/(叶绿素+类胡萝卜素)比值而改变红色砂梨的着色(孙永旺2015)。在葡萄的研究中,遮光处理可以通过改变花色素苷合成和转运相关基因的表达来降低花色素苷的含量,ABA和糖分在此过程中扮演重要角色(Guan等2016)。

2.3 光照时间对花色素苷合成的影响

光照时间长短对植物花色素苷的积累也有一定的影响。长日照能够促进越橘(*Vaccinium myrtillus*) (Lätti等2008)花色素苷的积累。与每天8 h光照条件相比,16 h光照条件下生长30 d的甘薯(*Ipomoea batatas*)叶片类黄酮合成途径中结构基因的表达量更高,并积累相对更多的花色素苷和黄酮醇(Carvalho等2010)。在短日照(10 h)处理下的扭叶松(*Pinus contorta*)幼苗,其花色素苷的积累显著低于长日照(14~15.5 h)处理下的含量,而花色素苷、原花青素和黄烷-3-醇在不同光照时长处理之间的差异较小(Camm等1993)。UV-A连续处理24和36 h,萝卜芽苗菜下胚轴花色素苷含量显著高于UV-A处理3和12 h时,表明相对较长时间的UV-A更有利于花色素苷的合成(张晓燕等2016)。短日照条件下,四季海棠(*Begonia semperflorens*)种子积累更多的碳水化合物和ABA,从而促进花色素苷的合成;低碳水化合物含量和高赤霉素(gibberellin, GA)含量抑制了DFR和UFGT的活性,从而阻碍了花色素苷的合成(Zhang等2016)。

3 光对花色素苷合成的调控机制

光作为一种环境因子,其调控花色素苷合成主要通过对相关酶基因的直接或间接调控来完成(Jaakola 2013)。通常,转录因子决定了结构基因是否表达及表达强弱,而结构基因则决定了花色素苷生物合成的种类(谢兴斌2011)。通过对花色素苷生物合成结构基因的启动子序列分析发现,*CHS*等结构基因的启动子序列中均含有多个响应光信号的顺式作用元件,光受体在感知光信号后,通过光信号转导途径将其传递至转录因子;然后转录因子通过与这些顺式作用元件结合,调控结构基因的表达,合成花色素苷(Jaakola 2013; Zoratti等2014)。

3.1 光受体与植物花色素苷合成

高等植物至少有5类光受体参与植物对光信号的感知:吸收红光和FR的光敏色素受体(phytochrome, PHY)、吸收蓝光和UV-A的隐花色素受体(cryptochrome, CRY)、吸收蓝光的向光素受体(phototropin, PHOT)、吸收蓝光的ZTL家族(Zeitlupe family)蛋白和吸收UV-B的UV-B受体(UV Resistance Locus 8, UVR8) (程海燕和李德红2010; Somers等2000; Li等2012)。在这5类光受体中,PHYs (陈静等2004; Shin等2007)、CRYs (程海燕和李德红

2010; Hardtke和Deng 2000; Chatterjee等2006)、UVR8s (Brown等2009; Wu等2016)与植物花色素苷的合成有关。

PHYs是吸收红光的受体,广泛分布在膜系统、细胞溶胶和细胞核中(董愚德2004)。PHY感知光信号后,自身会发生磷酸化,同时还可引起其他相关蛋白发生磷酸化(如蓝光受体),并将信号传递给下游信号转导元件,最终诱导相关基因表达(Quail等1995)。经红光处理后,金鱼草(*Antirrhinum majus*)花瓣和番茄幼苗光敏色素感受光信号,通过一系列信号传递激活调节蛋白,最终诱导花色素苷合成结构基因的表达(如*CHS*) (陈静等2004; Weisshaar等1991)。与PHY蛋白相互作用的上游信号因子(如PIF3等)通过与*CCA1* (*CIRCADIAN CLOCK ASSOCIATED 1*)和*LHY* (*LATE ELONGATED HYPOCOTYL*)等光调控基因启动子区保守的G-box元件相互作用,从而实现光敏色素调控的基因表达(Martinez-Garcia等2000; Kim等2003)。

CRYs是吸收蓝光和UV-A的受体,参与多个植物生长发育和生物节律的信号传递(程海燕和李德红2010)。在拟南芥中,CRY1是蓝光诱导花色素苷积累的主要光受体,介导蓝光诱导的*CHS*基因表达(王曼和王小菁2004)。CRY吸收光信号后,引发其与其他蛋白质的相互作用,使光信号蛋白结构和分布发生变化,从而引起相关基因的表达(程海燕和李德红2010; Hardtke和Deng 2000)。大白菜(*Brassica rapa* subsp. *pekinensis*) *cry1*突变体的幼苗在光照下花色素合成含量显著降低,也证明了CRY参与植物花色素苷合成的调控(Chatterjee等2006)。

在光信号转导途径中,光形态建成的核心基因组成性光形态建成E3泛素连接酶(constitutively photomorphogenic, COP)在UV-B信号转导和可见光信号转导中功能截然相反(Lau和Deng 2012),而UVR8与COP1的互作决定了UVR8介导的UV-B信号感知以及光形态建成(Huang等2014)。2002年, Kliebenstein等发现拟南芥中存在一种新的UV-B敏感突变体(*uvr8-1*),该突变体由于改变了UV-B的信号转导而导致UV诱导的黄酮类化合物及*CHS*的mRNA和蛋白的缺失。*uvr8-1*在第5号染色体的末端出现单基因隐性突变,通过对该区域进行测序,发现其与野生型的序列相比,*uvr8-1*突变体的序列

在一个与人类鸟嘌呤核苷酸交换因子RCC1 (regulator of chromatin condensation 1)相似的基因内部有15 bp的碱基缺失,于是将该基因命名为UVR8 (Kliebenstein等2002)。无UV-B照射时,UVR8以二聚体的形式存在于细胞质和细胞核中;接收到UV-B光信号后,细胞质中的UVR8转移到细胞核中,蛋白构象发生变化从二聚体形式变为单体形式,并与COP1发生相互作用,从而开启UV-B信号通路,引起转录调节和下游应答(Favory等2009; Rizzini等2011)。UVR8通过与组蛋白的相互作用参与正向调节UV-B诱导类黄酮类化合物的合成(Brown等2009; Cloix等2012); UV-B照射可以显著增加萝卜苗花色素苷的含量和UVR8的表达, H_2O_2 和NO可能参与其发生过程(Wu等2016)。

3.2 光信号转导元件与植物花色素苷合成

一般认为,COP是植物光形态建成的负调控因子,COP1是一个E3泛素连接酶。黑暗条件下,COP1定位在细胞核内,可以泛素化核内外一些参与光形态建成的蛋白,可见光照射会促进COP1向核外运输解除其间接作用(Lau和Deng 2012; Lu等2016)。在UV-B信号转导途径中,HY5 (ELONGATED HYPOCOTYL 5)转录因子可以直接与花色素苷合成酶结构基因和转录因子启动子的顺式作用元件结合,调节花色素苷的合成(Shin等2013); UV-B可抑制核内COP1对HY5的降解,COP1可与UVR8直接正调控UV-B信号的光形态建成(Favory等2009)。最新研究表明FHY3 (FAR-RED ELONGATED HYPOCOTYL 3)和HY5通过与COP1启动子区域的FBS和ACE元件结合激活其转录,协同正向调控COP1介导的UV-B信号的光形态建成(Huang等2012)。

在苹果中,MdCOP1可以通过降解MdMYB1蛋白在转录后水平负调控花色素苷的合成(Li等2012);另一项研究中则指出,MdCOP1和MdHY5受UV-B诱导,且MdHY5可与*MdMYBA10*基因启动子结合调控其表达(Peng等2013)。两者结论不一致可能是由于两者使用的光源不同造成的,在可见光条件下,MdCOP1负调控花色素苷合成,而UV-B照射条件下MdCOP1表达受到诱导,这与拟南芥中的研究结果是一致的(Lau和Deng 2012)。在作用机制方面,COP1参与花色素苷合成的调控并非仅发生在转录后水平。在拟南芥中的研究表明,

COP1/SPA复合体能在转录水平和转录后水平,通过调节PAP1和PAP2的转录水平和蛋白稳定性,参与花色素苷的合成(Maier等2013)。HY5可以通过与MYBL2启动子的直接结合引起特定的组蛋白变性,抑制其表达;miR858a抑制了MYBL2的表达,是花色素苷生物合成的负调节子;HY5-MIR858a-MYBL2复合体通过转录和转录后调控响应光及其他环境因子,从而调节花色素苷合成(Wang等2016)。在茄子(*Solanum melongena*)上,光通过CRY1/CRY2-COP1与SmHY5和SmMYB1相互作用来调控花色素苷的积累(Jiang等2016)。对中国砂梨转录组学和共表达分析结果表明, HY5、CRY-DASH和COL (CONSTANS like)等转录因子可能在早期光信号响应促进花色素苷合成过程中扮演重要的角色(Bai等2017)。

PIF3和HY5直接与同一个花色素苷合成基因启动子的不同区域结合使其激活,正调节花色素苷的生物合成,但并不直接与光敏色素介导的信号相联系(Shin等2007)。在FR条件下,PIA2 (PHYTOCHROME-INTERACTING ANKYRIN REPEAT PROTEIN 2)和PIF3 (PHYTOCHROME INTERACTING FACTOR 3)是拟南芥种子中花色素苷积累的正调控子,PIA2通过抑制的phyA介导的PIF3磷酸化调控花色素苷的合成(Yoo等2016)。

花色素苷合成途径相关酶的结构基因几乎都受光调控,在强光下表达量上调,在弱光或黑暗条件下表达量下降或不表达(胡可等2010)。在拟南芥中,CHS、F3H、FLS、DFR、UFGT等光调节酶基因的启动子序列中含有ACE、MRE、I-box、Box II、G-box、ATCT-motif和GATA-motif等光响应元件,同时还含有多个MBS等MYB结合元件和E-box等MYC识别元件(Hartmann等2005)。这些结构基因的启动子中均含有MRE和ACE这两个顺式作用元件,在光诱导下,MRE和ACE通过与反式作用因子相互作用,激活相关基因的表达从而合成花色素苷(Hartmann等2005)。在苹果中,DFR和ANS等结构基因的启动子也存在ACE等光响应元件(Ban等2007)。

光信号通过影响转录因子与启动子的结合程度,调节结构基因的表达。在拟南芥中,强光可以诱导叶片积累花色素苷,除WD40 (TTG1)外,MYB

(PAP1)、bHLH (TT8、EGL8和GL3)都表现出较强光诱导特性(Cominelli等2008; Rowan等2009)。在白光诱导条件下,拟南芥幼苗中PAP1和TT8等转录因子的表达水平随着光照时间持续而逐渐增强,而CHS、F3H和DFR等花色素苷合成关键基因表达水平也相应增强(Cominelli等2008)。在玉米中,光照通过调节转录因子MYB和bHLH表达,从而调控结构基因的表达引起花色素苷的合成(Irani和Grotewold 2005)。遮光处理条件下,菊花(*Chrysanthemum* sp.)中MYB、WD40和MYB5-1等转录因子及CHS、F3H、DFR和ANS等结构基因的表达都受到明显的抑制(胡可等2010; Hong等2016)。黑暗条件下,亚洲百合(*Lilium* sect. *Sinomartagon*)中LhbHLH2和LhDFR等基因的表达量及花色素苷含量明显下降,光照2 d时LhbHLH1的表达量达到高峰(Nakatsuka等2009)。光照条件下,MPK4 (MAP KINASE 4)通过磷酸化MYB75来增强其稳定性,从而促进拟南芥花色素苷的积累(Li等2016)。可见,光信号通过调控MYB等转录因子的表达及其与结构基因启动子的结合而影响花色素苷的合成。

4 结语与展望

近年来,随着基因组学和蛋白组学的飞速发展及分子生物学实验手段的日新月异,植物花色素苷的合成和调控机制已逐步阐明,在拟南芥等模式作物和矮牵牛、苹果等多种园艺作物中都分离得到了花色素苷合成的关键结构基因和调控基因,并构建了花色素苷合成和调控的分子网络,同时利用基因工程技术实现了许多观赏植物的花色、叶色改良(唐杏姣和戴思兰2011)。光作为影响植物生长发育最重要的环境因子,也是影响植物花色素苷合成和积累的关键因素,通过调节大量的转录因子组成的复杂调控网络调控花色素苷的合成(Wang等2016),其调控网络尚未完全解析。且光照对花色素苷合成调控主要集中在拟南芥和矮牵牛模式植物中,对园艺作物尤其是果实颜色方面的研究尚不够系统。

根据当前的研究进展,笔者认为可以从以下两个方向继续深入开展光信号调控植物花色素苷合成机制的研究:(1)不同光质和光照强度下,哪一种或几种光受体参与了该途径光信号的感知,光信号如何通过信号转导传递并调控转录因子和结

构基因的表达, 以及整个过程中参与花色素苷合成的转录因子之间如何相互作用和协同调控等系列问题都亟待解决; (2)在光调控花色素苷合成的过程中, 还涉及到ABA等内源激素的合成、糖分积累及叶绿素降解等代谢过程(Lai等2014; Rodyoung等2016; Guan等2016), 这些生理过程之间存在哪些联系, 以及光和ABA等内源激素如何协同调控花色素苷的合成与积累过程? 这些问题的解决都将有助于花色素苷合成与积累调控网络的阐明, 也将对园艺植物新品种的选育、改良及栽培设施的改进起到巨大的推动作用。

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Regulation and mechanism of light on anthocyanin biosynthesis in plants

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Abstract: Anthocyanins are the main pigments in flowers, fruits, leaves and seed capsules of higher plants. Biosynthesis and accumulation of anthocyanins were co-regulated by their genetic background and environmental factors. Light is one of the major environmental factors limiting anthocyanin biosynthesis in plant. Different light qualities and light intensities have different effects on anthocyanin accumulation, but light quality play an even more critical role. In order to provide references for breeding of new horticultural varieties and improving cultivation facilities, this review summarizes research progresses of photoreceptors, light signal transduction and interacting with transcription factors and structural genes in the entirely process of light-regulating anthocyanin biosynthesis, and proposes future research interests.

Key words: light; anthocyanin; photoreceptor; transcription factor

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