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植物花青素生物合成途径相关基因研究进展及其基因工程修饰

赵德勇[1,2]

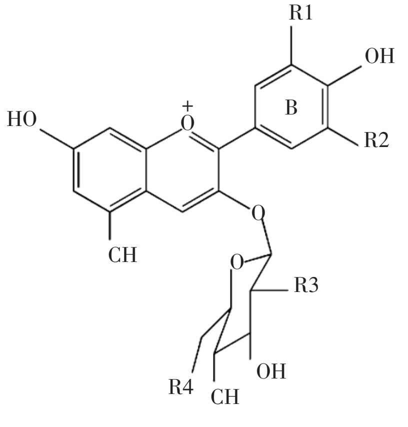
(1. 中国科学院 西北高原生物研究所,青海 西宁 810001; 2. 中国科学院 研究生院,北京 100049)

摘　要: 对植物花青素生物合成及调控基因的研究进展、基因工程在调控花青素合成途径中的应用进行了综述。植物花青素生物合成属次生代谢途径,对该途径关键酶基因的调控可降低或提高目标化合物的产量,可通过调控植物次生代谢的方式对植物进行遗传改良。对植物通过积累花青素来适应紫外线辐射、防卫害虫及真菌侵害的分子机制进行研究,有助于培育抗病、抗逆的植物新品种。

关键词: 花青素; 生物合成途径; 次生代谢; 基因工程

中图分类号: Q 786　　　**文献标志码:** A

花青素是植物类黄酮色素中最丰富的一类,分布于植物的茎、叶、花、果实、种子等组织中,使其呈现出黄、红、紫、蓝等颜色。在植物中,包括花青素在内的类黄酮化合物参与多种生物过程,例如使花器官具有特定颜色来吸引传粉媒介[1]、花粉管萌发[2]、适应紫外线辐射[3]、防卫害虫及真菌的侵害[4-6]。花青素主要有 6 种生色团,分别为花葵素、矢车菊素、甲基花青素、翠雀素、矮牵牛素、锦葵花素(见图 1),花葵素衍生物通常产生红色,矢车菊素衍生物产生紫色,翠雀素呈现紫或蓝色[7]。由于花青素具有清除自由基、防血小板凝结、预防心血管疾病、免疫调节活性、抗癌活性等营养和药理作用而备受关注[8-9]。对花青素生物合成及其调控基因的深入研究,有助于利用基因工程手段(如反义 RNA、干扰 RNA、基因敲除等技术)来调控植物花青素生物合成途径,从而获得具有某一特定性状(如花色)的植株。笔者参阅了国内外的大量资料,对花青素生物合成及调控基因的研究进展、基因工程在调控花青素合成途径中的应用进行了综述,旨在为花青素生物合成的进一步研究提供参考。



R1,R2=H, pelargonidin-3-O-glycoside 花葵素 -3-O- 糖苷
R1=OH,R2=H, cyanidin-3-O-glycoside 矢车菊素 -3-O- 糖苷
R1,R2=OH, delphinidin-3-O-glycoside 翠雀素 -3-O- 糖苷
R1=OCH3,R2=H, peonidin-3-O-glycoside 甲基花青素 -3-O- 糖苷
R1=OCH3,R2=OH,pelunidin-3-O-glycoside 矮牵牛素 -3-O- 糖苷
R1,R2=OCH3, malvidin-3-O-glycoside 锦葵花素 -3-O- 糖苷
R3=xylose, R4=OH, anthocyanidin-3-O-sambubioside
花青素 -3-O- 桑布双糖苷
R3=OH,R4=rhamnose, anthocyanidin-3-O-rutioside
花青素 -3-O- 芸香苷
R3=glucose,R4=OH, anthocyanidin-3-O-sophoroside
花青素 -3-O- 槐糖苷

图 1　花青素的化学结构

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作者简介: 赵德勇(1984 -),男,山东乐陵人,中国科学院研究生院 2011 级植物育种学专业博士研究生.

1　花青素生物合成基因

花青素生物合成途径如图 2 所示。

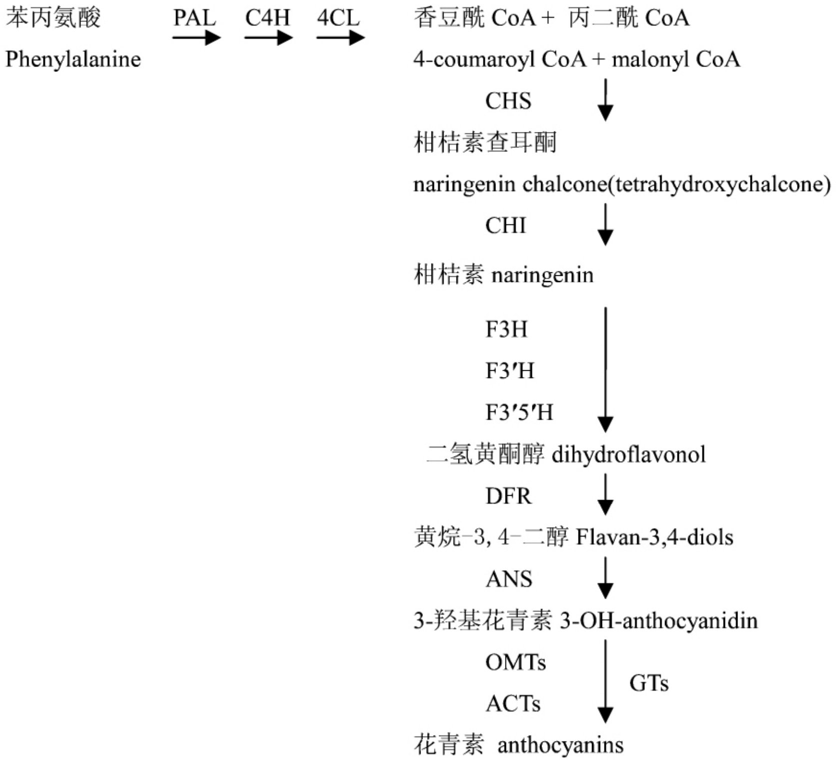

图 2　花青素生物合成途径

ACTs(acetyl transferases) 乙酰基转移酶; ANS(anthocyanidin synthase) 花色素苷合成酶; C4H(cinnamate-4-hydroxylase) 肉桂酸 - 4 - 羟化酶; CHI(chalcone isomerase) 查尔酮异构酶; CHR(chalcone reductase) 查耳酮还原酶; CHS(chalcone synthase) 查耳酮合酮; 4CL(4-coumaroyl: CoA-ligase) 香豆酰辅酶 A 连接酶; DFR(dihydroflavonol 4-reductase) 二氢黄酮醇 4 - 还原酶; F3H(flavanone 3-hydroxylase) 黄碱酮 3 - 羟化酶; F3′H(flavonoid 3′ -hydroxylase) 类黄酮 3′羟化酶; F3′5′H(flavonoid 3′5′ -hydroxylase) 类黄酮 3′5′羟化酶; OMTs (O-methyltransferase) 氧 - 甲基转移酶; PAL(phenylalanine ammonia-lyase) 苯丙氨酸氨裂合酶; GTs(glucosyl transferases) 葡萄糖基转移酶。

查耳酮合酶(CHS，chalcone synthase) 是花青素合成途径中的关键酶[10]，其编码基因具有很高的保守性，因此也被用于进化研究[11-12]。*CHS* 基因在不同科植物中的拷贝数差异较大，例如欧芹、拟南芥、金鱼草中只存在 1 个拷贝[13-15]，而其他物种中均有多个拷贝。*CHS* 基因编码区被不同长度的内含子分隔成外显子 1 和外显子 2，其中外显子 1 较短，只编码 60 个氨基酸，长度变异较大; 外显子 2 编码 340 个氨基酸，*CHS* 一般仅有 1 个内含子[16]。*CHS* 基因表达可被真菌或机械损伤[17]、紫外光[18]诱导。自从 *CHS* 基因被分离后，后人一直致力于分离克隆其他控制花青素途径的结构基因[19-20]。

查尔酮异构酶(CHI，chalcone isomerase) 催化柚配基查尔酮异构化形成二羟基黄烷酮，其基因最早是利用抗体技术从法国菜豆中分离[21]，NORIMOTO 等[22]将植物 *CHI* 蛋白基因家族分为两大类，一类 *CHI* 只能将查尔酮异构化为(2S) - 黄烷酮，另一类 *CHI* 除能将查尔酮异构化为(2S) - 5 - 脱氧黄烷酮之外，还能将 6′ - 脱氧查尔酮异构化为(2S) - 5 - 脱氧黄烷酮。矮牵牛基因组中存在 *CHI* A 和 *CHI* B 2 个 *CHI* 基因，*CHI* A 在花冠和成熟的雄蕊中表达，*CHI* B 在未成熟的花药中表达[23]。

黄烷酮 3 - 羟化酶(F3H，flavanone 3-hydroxylase) 催化黄烷酮生成黄酮醇，是花青素代谢途径的关键酶。*F3H* 基因最早从金鱼草(*Antirrhinum majus*) 中克隆出来[24]，经 NCBI 检索程序(http: //www. ncbi.

nlm. nih. gov/gene/? term = *CHS*)和查阅文献[25]可知，目前研究人员已从拟南芥、大豆、玉米、葡萄、矮牵牛、茄子、苜蓿、苹果、柑橘、康乃馨、翠菊等植物中分离出 *F3H* 基因。*F3H* 在大多数物种中以单拷贝形式存在[26]。

黄烷酮3′-羟化酶(F3′H，flavonoid 3′-hydroxylase,)和黄烷酮3′5′-羟化酶(F3′5′H，flavonoid 3′,5′-hydroxylase,)控制花青素B环的羟化，是控制矢车菊素和翠雀素生物合成的重要决定因子。

二氢黄酮醇4-还原酶(DFR，dihydroflavonol 4-reductase)催化二氢黄酮醇类生成无色原花色素，它在花青素生物合成中的关键作用最初是在紫罗兰突变体中发现的。*DFR* 基因一般以单拷贝形式存在于植物基因组中[27]，但有些植物中存在多个拷贝并呈现组织特异性表达，例如百脉根 *DFR*1 在结节、根、茎、叶、花和豆荚中表达，*DFR*2 在叶以外的其他组织中表达，*DFR*3 只在茎和叶中表达，*DFR*4 和 *DFR*5 不在结节中表达，但在其他组织中都能表达[28]。

花色素苷合成酶(ANS，anthocyanidin synthase)，亦称无色花色素双加氧酶(LDOX，leucoanthocyanidin dioxygenase)，催化无色的原花色素氧化产生有色的花色素。*ANS* 最初是在玉米的A2突变体中克隆到的[29]，大多数 *ANS* 基因由1个内含子和2个外显子组成，且剪接位点一致。*ANS* 基因的表达具有组织特异性，例如其只在金钟连翘的萼片中表达，而不在花药花瓣中表达[30]。

氧-甲基转移酶(OMTs，O-methyltransferase)、乙酰基转移酶(ACTs，acetyl transferases)、葡萄糖基转移酶(GTs，glucosyl transferases)分别催化花青素的甲基化、乙酰化和糖基化从而导致多种花青素的产生[31]。例如在牵牛花和金鱼草的花中发现了花青素-3-O-芸香糖苷，在番薯属的花中及有色素沉淀的拟南芥叶子中检测到花青素-3-O-槐糖苷和桑布双糖苷衍生物的存在[32-36]。花青素-3-O-芸香糖苷和花青素-3-O-槐糖苷的产生分别受到UDP-鼠李糖: 花青素3-O-葡糖苷-6″-O-鼠李糖转移酶和UDP-葡萄糖: 花青素3-O-葡糖苷-2″-O-葡萄糖基转移酶的调控，这2种酶分别催化鼠李糖和葡萄糖与花青素3-O-葡糖苷的结合反应[33-34,37]。

2 花青素生物合成途径的调控基因

在双子叶植物中花青素生物合成基因可分为早基因和晚基因2类，而在单子叶植物玉米中花青素合成基因呈协调作用[38-41]。这种区别常被认为源于单子叶植物与双子叶植物的差异[38-39]，而有研究表明在双子叶的番薯属中花青素合成基因也呈协调作用[37,42-45]。

花青素的合成需要转录因子的协同作用，因此，编码转录因子的调控基因突变常会影响多个生物合成酶基因的表达。参与花青素合成的转录调控因子包括 *R2R3-MYB*，*bHLH*(basic-helix-loop-helix)和 *WD*40 蛋白家族，这些转录因子之间的结合及相互作用决定着一系列基因的表达[39,46-48]。在玉米中花青素的积聚受到成对重复转录因子的调控，比如属于 *bHLH* 蛋白的 *R*1 和 *B*1[49-50]及属于 *MYB* DNA 结合蛋白的 *C*1 和 *PL*1[51]。在种子糊粉粒中花青素积累受到 *R*1 和 *C*1 控制，而在植物体部分的花青素积累受到 *B*1 和 *PL*1 的控制[52]。CAREY 等发现 *pac*1 基因编码 *WD*40 重复蛋白与下游转录因子 *R*1 和 *C*1 共同作用诱导花青素的产生[53]。

R2R3-MYB 基因是一种特殊亚型，包括玉米 *C*1 基因[54]、牵牛花 *AN*2 基因[55]、拟南芥 *PAP*1/*PAP*2 基因[56]，对花青素生物合成基因的调控方式较特殊，与3-脱氧类黄酮生物合成调控因子 *P*1 相比，*R2R3-MYB* 转录因子只在具有螺旋-转角-螺旋结构的辅激活蛋白R/B家族存在时才发挥作用。

3 基因工程在调控植物花青素合成的应用

3.1 调控植物的花色 MEYER 等将玉米 *DFR* 基因导入牵牛花而使其产生新花色[57]，VANDERKROL A R 等将反义 *CHS* 基因转入矮牵牛，抑制了相应基因的表达，从而使矮牵牛花色由紫色变成白色[58]，邵莉等[59]从矮牵牛中克隆到 *CHS-A* 基因，并将正向 *CHS-A* 基因转入矮牵牛中，成功地改变了花的颜色。BOREVITZ 等的研究表明，过量表达编码 *MYB* 转录因子的 *PAP*1 基因可使多种营养器官紫色加深[56]。ROSA-

TI 等将紫罗兰的 *ANS* 基因在金钟连翘中过表达，使花色由黄变为棕色[60]。FUKUSAKI 等利用 RNAi 技术调控 *CHS* 的表达来改变蓝猪耳月季(*Torenia hybrida*)的花色[61]。TANAKA 等[62]的研究表明，转入 *F3'5'H* 基因的康乃馨能呈现蓝色或紫色，而相应的转基因玫瑰只呈现蓝色。

3.2　调控植物次生代谢物合成　WISEMAN 等阻断拟南芥 *F3H* 基因的表达而导致黄酮和花色素水平的下降[63]。YU 等[64]将玉米中的 *P* 和 *C* 转录因子构建为嵌合基因转入大豆，激活了整个花色素苷代谢途径，同时利用基因敲除使 *F3H* 基因沉默，将已经增加的代谢流量转到异黄酮合成途径中，从而提高了大豆种皮中异黄酮含量。AMBAVARARM 等[65]将 *ANS* 基因在水稻 NP(Nootripathu)突变体中过表达，使花青素和黄酮含量升高，原花青素减少，在转化植物的稻壳、节间、叶鞘中有不同程度的花色素苷积累。

4　展　望

通过生物技术手段调控植物花青素生物合成及调控基因的表达可人为地降低或提高目标化合物的产量。由于植物的次生代谢途径是一个错综复杂的网络结构，某一代谢途径中的某一基因的沉默或过表达有可能对其他代谢途径产生影响，从而使植物具有特定的性状(如形态、生理、品质上的改变)，因此，可通过基因工程对植物次生代谢途径进行调控的方式对植物进行遗传改良。

有些植物通过在体内积累花青素的方式来适应紫外线辐射、害虫及真菌的侵害，表明花青素在植物的抗病、抗逆过程发挥着重要作用。随着生物技术手段的革新、化学物质检测及结构鉴定技术的改进，人们可以深入地研究植物积累花青素来适应逆境的分子机理，这将有助于今后抗病、抗逆植物新品种的培育。

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Advances in research of genes involved in anthocyanin biological synthesis in plant and the genetic modification of the pathway

ZHAO De-yong[1,2]

(1. Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China;
2. Graduate University of Chinese Academy of Sciences, Beijing 100049, China)

Abstract: This paper reviews the advances in research of synthetic genes and regulator genes involved in the anthocyanin biological synthesis process as well as in genetic engineering in regulating the anthocyanin biological synthesis. Anthocyanin biological synthesis process of plants belongs to the secondary metabolic pathway, regulates the expression of key enzymes involved in the pathway, and could hence lead to a reduced or increased yield of target compound. Genetic improvement of plants may be realized through modifying the secondary metabolic process. Anthocyanin accumulation helps the plants to act against the UV radiation, insects and fungi. Further study on the defense molecular mechanism of the anthocyanin facilitates breeding of new plant cultivars with resistance to diseases and adversities.

Key words: anthocyanin; biological synthesis pathway; secondary metabolism; genetic engineering