

## 园艺作物花青素合成调控研究进展

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**摘要:**花青素是一类保护植物免受生物和非生物胁迫的重要次生代谢产物,因其赋予植物丰富的色彩和对人体的保健功能而受到广泛关注。花青素合成调控机理的相关研究是目前园艺作物分子生物学研究的前沿课题,对于园艺作物花青素含量的提高、种质品质的提升等具有重要的意义。结合国内外园艺作物中花青素生物合成调控方面的最新研究进展,介绍了环境因素、酶与激素、DNA甲基化与泛素化和调控基因等对花青素生物合成的作用,以及花青素抵御外界胁迫的功能机制,综述了近年来园艺作物中花青素生物合成调控的研究成果,以期利用基因工程为提升园艺作物的色彩丰富度提供理论参考。

**关键词:**园艺作物;花青素;转录因子;合成调控

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## Research Progress on the Regulation of Anthocyanin Synthesis in Horticultural Crops

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**Abstract:** Anthocyanin is an important secondary metabolite that protects plants from biotic and abiotic stress. It has received widespread attention because of its rich colors to plants and its benefit to human health. The related research on the regulation mechanism of anthocyanin synthesis is the current frontier subject of molecular biology of horticultural crops, which has important significance for the improvement of anthocyanin content and germplasm quality of horticultural crops. This article combined the latest research progress in the regulation of anthocyanin biosynthesis in horticultural crops at home and abroad, and introduced the effects of environmental factors, enzymes and hormones, DNA methylation and ubiquitination, and regulatory genes on anthocyanin biosynthesis, and the functional mechanism of anthocyanins against external stresses. The research results of anthocyanin biosynthesis regulation in horticultural crops in recent years were reviewed, in order to using genetic engineering to provide a theoretical reference for enhancing the color richness of horticultural crops.

**Key words:** horticultural crops; anthocyanin; transcription factor; biosynthesis and regulation

花青素是植物酚类色素中一个重要的大类,是某些植物的叶、花、果实、块茎呈现红色、紫色或蓝色的原因。花青素功能多样,在自然界发挥着吸引传粉者和种子传播者的生态生理作用;在抵御紫外线辐射、低温/高温、干旱和病原体侵袭等方面发挥着重要作用。作为自然界中含量最多最

重要的一类水溶性色素,花青素还具有广泛的抗氧化<sup>[1]</sup>、抗糖尿病、抗高脂血症、抗炎、抗癌和预防心血管疾病等功能,其含量对蔬果的品质具有重要影响。已有大量相关研究表明,植物中存在的花青素主要有飞燕草色素、矢车菊色素、矮牵牛色素、天竺葵色素、芍药色素和锦葵色素等6种。胡

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莉等<sup>[2]</sup>对黑米、黑豆、茄子(带皮)、甘蓝、紫甘薯、草莓、蓝莓、桑葚、葡萄等9种园艺作物的花青素成分研究发现,除茄子外,所有样品中均含有矢车菊素。在粮食中,黑米中的矢车菊素、芍药素含量最高;水果中以蓝莓中的花青素种类和含量最高。在环境修复方面,由于花青素中的黄酮类阳离子 $O^+$ 能通过静电力吸引 $I^-$ ,并通过离子交换控制吸附,因此,从农业废弃物中提取的花青素基材料能够可持续地用于从核电设施、水处理厂中去除放射性 $I^-$ <sup>[3]</sup>。花青素也是促进人体健康的重要抗氧化剂,因此,在分子水平上探索花青素对植物色彩和生理代谢等的影响具有重要的意义。

## 1 花青素抵御外界胁迫的功能

花青素在抵御胁迫、防御食草动物和病原体侵袭方面扮演着“多面手”的角色。植物可以通过花青素色素沉着抵抗非生物胁迫,从而对与全球变化相关的干旱和极端温度做出适应性或可塑性的应答。随着时间的推移,经历较大程度温度升高的物种色素沉着减少,而经历干旱增加的物种色素沉着增加<sup>[4]</sup>。花青素能中和由非生物胁迫产生的活性氧,减少由活性氧积累对植物生长发育产生的抑制。ROS相关基因*ZmSRO1e*在玉米和拟南芥中,通过与*ZmR1*(MBW转录激活复合物的核心基本螺旋-环-螺旋亚基)竞争,从而与*Zm-PL1*(复合物的核心MYB亚基)结合,导致复合物的形成受到抑制。该表达增加了植物对非生物胁迫的敏感性,抑制了花青素的生物合成和活性氧清除活性<sup>[5]</sup>。花青素的生物合成有助于降低过量糖分的积累,保护光系统II(photosystem II, PS II)免受多余光子到达叶绿体,这种糖缓冲作用能够积极影响光合作用的反馈调节<sup>[6]</sup>。碳饥饿会影响果实发育以及花青素和碳水化合物代谢产物浓度,花青素和碳水化合物生物合成途径的基因编码酶均下调,海藻糖6-磷酸盐和活性抑制因子MYB27参与感知碳饥饿状态,标志着植物为了节约资源会减少果实中花青素的含量<sup>[7]</sup>。拟南芥中Pi反应的保守调控因子SPX4与MYB转录因子PAP1依靠肌醇多磷酸盐相互作用,进而阻止PAP1与其靶基因启动子的结合。磷饥饿时,在无肌醇多磷酸的情况下,SPX释放出PAP1来激活花青素的生物合成<sup>[8]</sup>。在磷缺乏的苹果叶片中,

miR399d和高亲和性Pi转运蛋白McPHT1;4正向调控花青素合成;甲基转移酶基因*McMET1*和组蛋白乙酰化酶基因*McHDA6*可能对McMYB10启动子进行甲基化和乙酰化调节,通过表观遗传修饰调控花青素的合成<sup>[9]</sup>。这种miR399d和表观遗传修饰共调节模型解释了缺磷条件下苹果叶片变红的现象。以上结果揭示了碳饥饿和磷饥饿与类黄酮代谢之间的直接联系。

砷(As)是一种对动植物均有毒性的非金属。过量的As可导致茶叶中光合系统II的最大光化学效率显著降低,活性氧积累和脂质过氧化反应增加,从而引起严重的氧化应激。而外源性褪黑素可以通过选择性上调花青素生物合成基因的表达,减缓植物As中毒,并使花青素含量增加,且褪黑素对As胁迫的耐量增强很大程度上依赖于茶树中花青素的基础水平<sup>[10]</sup>。

在干旱胁迫下,MdERF38与花青素生物合成的正向调节因子MdMYB1相互作用,促进MdMYB1与其靶基因的结合,从而促进花青素的生物合成。此外,MdBT2是花青素合成的负调控因子,其通过加速MdERF38蛋白的降解来减弱MdERF38促进的花青素合成作用<sup>[11]</sup>。

在许多植物中,花青素的生物合成是由低温诱导的。在桃果(中华寿桃)中,花青素的积累发生在16℃的贮藏条件下,该温度条件下编码花青素生物合成酶、运输蛋白谷胱甘肽S-转移酶和关键转录因子的基因转录水平升高。在≤12℃贮藏时,花青素没有积累<sup>[12]</sup>。R2R3-MYB TF基因*BrMYB2*和*bHLH*调控基因*BrTT8*在紫头白菜中低温诱导后表达量显著升高,而2个负调控基因*BrMYBL2.1*和*BrLBD38.2*在白头白菜中表达量显著升高。低温诱导紫头白菜后,*BrMYB2*和*BrTT8*可能在共激活花青素结构基因中发挥重要作用,而*BrMYB2*的下调和一些负调控因子的上调可能是白头白菜表型形成的主要原因<sup>[13]</sup>。

## 2 花青素合成调控的影响因素

### 2.1 外界环境对花青素生物合成的影响

花青素的生物合成易受外界环境因子的影响。已有研究显示,适宜的温度和光照条件可以通过激活正调控因子PsMYB10.1的表达,进而诱导花青素生物合成和转运相关基因的表达,从而

诱导 Akihime——李子果皮中花青素的积累<sup>[14]</sup>。强光可以促进花青素生物合成途径结构基因和调节基因的表达,光质也会对花色苷生物合成产生影响,尤其是光照中紫外线和蓝光的强度。光环境的调控是改良园艺作物花青素的重要手段,LED补光技术已成为调控园艺作物色泽的关键技术<sup>[15]</sup>。在桃中,PpHY5的表达被UV-A和UV-B上调,PpHY5通过与自身启动子中的E-box相互作用正向调控下游花青苷生物合成基因*PpCHS1*、*PpCHS2*、*PpDFR1*和*PpMYB10.1*以及自身转录<sup>[16]</sup>。UV-A、UV-B和UV-AB处理过的“紫燕”茶叶片中,总花青素以及3种主要花青素——飞燕草素、矢车菊素和天竺葵素的分子含量均显著高于单独白光处理下的茶叶片。UV-A处理下,花青素合成途径的结构基因黄酮3-羟化酶(F3H)、F3'5'H、DFR、ANS和调控基因TT8上调;在UV-AB处理下,F3'5'H、DFR、ANS和UFGT以及调控基因EGL1和TT2均上调;但与对照组相比,UV-B处理下,苯丙素和黄酮途径的大部分结构基因表达下调。表明UV处理抑制了花青素还原酶LAR和ANR的表达,导致ANR活性降低,代谢通量向花青素生物合成的方向转移<sup>[17]</sup>。

作为世界上最受欢迎的蔬菜之一,番茄果实中最丰富的抗氧化剂是亲脂的类胡萝卜素——番茄红素,尽管也含有水溶性类黄酮(包括花青素),但水平并不理想。番茄基因组包含4个高度同源的与花青素相关的R2R3-MYB转录因子:SLANT2、SIANT1、SIANT1-like和SLANT2-like/Aft。大多数番茄品种中不产生花青素,而紫番茄品种“靛蓝玫瑰”(indigo rose)在果皮中表现出依赖光的花青素积累,该品种具有Aft显性基因位点和atv隐性基因位点。Sun等<sup>[18]</sup>报道了Aft编码一种名为SIANT2-like的花青素转录因子,而atv编码转录抑制因子SIMYBatv。受光照条件影响的SIANT2-like既能激活花青素生物合成基因的表达,又能激活花青素生物合成的调控基因,SIANT2-like直接与SIMYBatv启动子结合来激活其转录<sup>[19]</sup>。对SIANT2进行靶向诱变的靛蓝玫瑰番茄突变体,其组织中花青素的含量和几个花青素相关基因的表达量均显著低于对照组,此外,番茄下胚轴和子叶的花青素合成受到不同调控因子的控制<sup>[20]</sup>。

光照诱导MdMYB1在苹果皮上表达,Md-

MYB1激活花青素合成途径中结构基因*MdCHS*、*MdF3H*、*MdDFR*和*MdUFGT*in的转录,促进花青素积累。An等<sup>[21]</sup>研究发现,在高强光条件下,苹果中MdTCP46与MdMYB1互作促进花青素的生物合成,并增强MdMYB1与其靶基因的结合。在弱光条件下,MdBT2泛素化并降解MdTCP46和MdMYB1蛋白,从而减弱MdTCP46对花青素积累的促进作用。随着光强的增加,MdBT2的表达被抑制,而MdTCP46的表达被激活,从而触发高光强诱导花青素的生物合成。由此推测,MdBT2可能作为光强的剂量响应器。MdMYB1是通过响应了花青素合成抑制剂硝酸盐的泛素化途径被降解<sup>[22]</sup>。MdCOP1蛋白在遮光条件下能通过泛素化降解MdMYB1,导致花青素含量降低,果皮颜色变浅<sup>[23]</sup>。苹果中MdWRKY72通过与MdHY5启动子中的W-box元件间接结合,与MdMYB1启动子中的W-box元件直接结合,促进了MdMYB1的表达,提高了UV-B辐射下转基因愈伤组织花青素合成<sup>[24]</sup>。B-box(BBX)蛋白MdBBX37是苹果光信号的负调控因子,在光信号转导中抑制花青素生物合成,并直接与光信号正调控子MdHY5的启动子结合,抑制其表达,从而缓解MdHY5介导的下胚轴抑制<sup>[25]</sup>。

## 2.2 酶与外源激素对花青素合成的影响

谷胱甘肽S-转移酶(PpGST1)基因的表达与桃果组织中花青素的积累密切相关<sup>[26]</sup>。病毒诱导的血肉桃*PpGST1*基因沉默不仅导致花青素积累减少,而且导致花青素生物合成和调控基因的表达下降;瞬时过表达PpGST1与PpMYB10.1在烟草和桃果中的花青素积累显著高于单独表达PpMYB10.1。Jiang等<sup>[27]</sup>报道了另一种被认为可以结合并稳定花青素的谷胱甘肽S-转移酶TRANSPARENT TESTA19(TT19),当TT19缺失时,RDR6、SGS3或DCL4的突变通过将碳元素推向类黄酮合成方向,从而抑制花青素的合成。还有研究发现黑色胡萝卜中GST1(LOC108205254)可能是一个重要的花青素转运体,其表达上调导致黑色胡萝卜样品中液泡花青素积累增加<sup>[28]</sup>。GST phi亚家族成员RsGSTF12-1和RsGSTF12-2的转录本可能编码胭脂红萝卜花青素转运蛋白<sup>[29]</sup>。

乙烯利是诱导花青素积累的有效刺激物,诱导后花青素积累可达82%;在乙烯利的作用下,毛状根中SOD和GST活性升高,这2种酶与花青素



在维持毛状根内部氧化还原稳态中具有相互作用<sup>[30]</sup>。但也有研究表明,乙烯利处理的草莓果实绿色发育期表现出抑制花青素合成和下调花青素合成必需基因的作用<sup>[31]</sup>。另有研究表明,茉莉酸在叶片着色过程中显著富集,与花青素含量变化一致<sup>[32]</sup>。在苹果中,ABA信号转导的重要调控因子MdABI5通过调节MdbHLH3-MdMYB1复合物正向调控ABA诱导的花青素合成<sup>[33]</sup>。E3泛素连接酶PacCOP1通过抑制PacMYBA转录水平,进而下调结构基因的表达丰度,最终导致花青素在果实中的积累减弱,从而在花青素生物合成中发挥负调控作用<sup>[34]</sup>。Maritim等<sup>[35]</sup>首次全面阐明了季节性诱导花青素降解、植物激素调节以及抑制因子TFs在茶叶花青素积累中的作用。

由于受分子特性固有因素,如食物加工和消化过程中的转化和花青素在食物中的含量等的影响,花青素的生物利用率极低<sup>[36]</sup>。PAL、ANS和UFGT在桃果实采后花青素的生物合成中起着重要作用,这3种酶均受到HA、UV-C、蔗糖、柠檬酸和苹果酸的刺激。研究表明,对采后的桃子采用热风(hot air)处理或UV-C处理,可以增强相关酶的活性和基因表达,促进花青素的积累<sup>[37]</sup>。在草莓采后贮藏过程中,用果胶寡糖(pectin oligosaccharides, POS)处理可以保持草莓的品质属性,减少腐烂,进一步提高花青素的含量和抗氧化能力,这可能与苯丙氨酸解氨酶(phenylalanine ammonia-lyase, PAL)活性的提高导致花青素的合成和积累有关<sup>[38]</sup>。用食品保鲜剂1-甲基环丙烯(1-methylcyclopropene, 1-MCP)处理桃、杏、李果实,能够在贮藏早期抑制合成相关结构基因和转录因子PsMYB10的表达,在贮藏后期增强其表达,从而延迟了贮藏过程中总花青素和主要个体花青素的增加,1-MCP处理有利于保持桃、杏、李的品质,特别是果实的化学性状,延长贮藏寿命,降低贮藏期间的经济损失<sup>[39]</sup>。玉米籽粒中存在乙酰化和琥珀化花青素,这些化合物是在提取过程中产生的人工色素,因此需要使用酸化溶液提取玉米花青素<sup>[40]</sup>。

### 2.3 甲基化与泛素化对花青素合成的影响

DNA甲基化可以引发由于染色质结构的变化而不是DNA序列变化引起的基因表达差异,即表观遗传现象。DNA甲基化或者蛋白质泛素化的研究对深入了解植物着色机理和发现MYB转

录因子的上游调控机制具有重要的意义。

苹果MdMYB308L转录因子通过与MdbHLH33互作,对苹果的耐寒性和花青素积累起到正向调节作用,但是MdMYB308L的1个互作蛋白E3泛素连接酶MdMIEL1会促进其泛素降解,从而对苹果耐寒性和花青素积累起到负调控作用<sup>[41]</sup>。在RNA介导的DNA甲基化途径中,苹果MdAGO4s与MdMYB1启动子结合,实现MdMYB1位点的甲基化修饰,调控花青素的生物合成<sup>[42]</sup>。萝卜白色肉质突变体是RsMYB1启动子DNA甲基化改变的结果,这种可遗传的表观遗传变化是由于高甲基化的CACTA转座子诱导DNA甲基化扩散到RsMYB1的启动子区域,RsMYB1在白肉突变体中的表达显著下调,抑制了花青素的生物合成<sup>[43]</sup>。DNA甲基化抑制剂5-氮杂胞苷的应用诱导了桃果肉中花青素的积累,进一步揭示了DNA去甲基化在调节桃果肉中花青素积累中的关键作用<sup>[42]</sup>。1项对土豆基因组甲基化分析的研究表明,在一些基因组位点上,生产花青素的细胞的甲基化程度高于无性系白细胞<sup>[44]</sup>。

### 2.4 调控基因对花青素生物合成积累的作用

GhPAP1D编码1个R2R3-MYB转录因子,促进花青素的合成和积累,与拟南芥花青素调节因子PAP1同源<sup>[45]</sup>。在棉花的GhPAP1A启动子中存在1个50 bp的串联重复序列,该重复序列驱动花瓣下游基因表达的活性较强,推测亚红色棉中花青素的适度积累是由启动子结构不同导致GhPAP1A转录增加造成的<sup>[46]</sup>。

研究发现,黄毛草莓花青素合成的核心转录激活因子FnMYB10的上游调控区存在序列变异,导致FnMYB10基因低表达,影响了花青素的合成,这可能与黄毛草莓的白果表型有关<sup>[47]</sup>。另有研究发现,草莓FaRAV1通过直接激活花青素途径基因启动子和上调FaMYB10来促进草莓花青素积累,而FaMYB10也正向调控这些基因的表达<sup>[48]</sup>。苹果中MdMYB114虽然不能形成MBW复合物,但可以通过直接与MdANS、MdUFGT、MdGST启动子结合促进其表达,从而增强花青素的生物合成和转运<sup>[49]</sup>。

R3 MYB取代MBW复合体中的R2R3 MYB家族TFs之一,可能使该复合体从花青素基因转录的激活因子转变为抑制因子。茄子中SmelMYB11属于R3 MYB,在MBW复合体中作为抑制剂,

通过与MYB活化剂(SmELANT1和SmELAN2)竞争结合SmELJAF13和SmELAN1,从而阻碍了新MBW复合物的形成<sup>[50]</sup>。Huang等<sup>[51]</sup>研究表明甜橙CsMYB3能抑制MBW复合体的活化能力,并能被CsRuby1激活。在紫薯中,抑制因子IbMYB44通过竞争性抑制IbMYB340-ibbHLH2-ibNAC56a或IbMYB340-ibbHLH2-ibNAC56b调控复合物的形成而影响花青素的合成<sup>[52]</sup>。杨梅中MrMYB6与MrbHLH1和MrWD40-1相互作用形成功能复合物,直接抑制原花青素特异基因*MrLAR*和*MrANR*以及花青素特异基因*MrANS*和*Mrrufgt*的启动子活性,从而对杨梅花青素和PA的积累具有负调控作用<sup>[53]</sup>。Xu等<sup>[54]</sup>研究表明,苹果中MdMYB6转录因子通过调节MdTMT1,降低UDP-葡萄糖和UDP-半乳糖的含量来抑制花青素的生物合成。Li等<sup>[55]</sup>鉴定猕猴桃的AaMYBC1为R2R3型转录因子,且miR858通过抑制红色猕猴桃的目的基因*AaMYBC1*来负调控花青素的生物合成。光敏茄子品种“Lanshan Hexian”的转录因子SmMYB86能直接与SmCHS、SmF3H和SmANS的启动子结合并抑制其活性,使花青素积累减少<sup>[56]</sup>。Xu等<sup>[57]</sup>研究发现胡萝卜中DcMYB113的根特异性表达是由启动子决定的,该转录因子可能调控花青素的转运。以上研究结果表明,MYB转录因子以不同的形式调控花青素合成的途径,有的作为转录激活子,起正向调控作用;有的作为抑制子,抑制目标基因的表达。

除了MYB、bHLH、WD40及三者组成的复合体等与花青素合成相关的主要转录因子,Zhang等<sup>[58]</sup>首次发现了与红肉苹果花青素积累相关的*MdNAC*基因,其在体内外均与MdMYB10存在明显的相互作用。Ning等<sup>[59]</sup>在紫肉甘薯花色苷的生物合成中发现了一个新的调控网络,IbERF71和IbMYB340-IbbHLH2形成了调控复合物IbERF71-IbMYB340-IbbHLH2,通过结合IbANS1启动子共调控花青素积累,为紫肉甘薯花色发育的研究提供了新的思路。

### 3 展望

目前,关于花青素的研究已有丰富的成果,科研工作者对花青素的生物合成途径已经解析得比

较清楚,但花青素的代谢调控网络仍需不断完善。从药食用、包装到环保领域,花青素的应用领域不断扩展,而花青素的合成调控一直以来都是园艺作物及观赏植物分子育种的关注点之一,未来在基因工程方面,系统阐明花青素的转录调控机制和利用代谢工程改良花青素的相关研究仍需继续探索。

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