

脱落酸(ABA)促进果实着色研究进展

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摘要: 着色状况是衡量果实成熟程度和质量优劣的重要评价指标。影响果实着色的因素诸多,其中生长调节物质是影响果实着色的因素之一,笔者对生长调节物质脱落酸(abscisic acid, ABA)影响果实着色的研究进行综述,主要包括ABA影响葡萄、草莓、苹果、桃等果实着色的作用时间、浓度及分子生物学机制,从生理和分子水平阐述ABA促进果实着色机制。详细综述了外源ABA对内源乙烯、ABA等激素的含量及其之间平衡的影响,以及对花色苷合成途径中关键基因和转录因子的影响。旨在通过归纳ABA促进果实着色的研究报道,为外源生长调节物质以及植物内源激素的研究提供参考,为果树高效生产奠定理论基础。

关键词: 果实; ABA; 调控; 着色; 花色苷

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Advances in ABA promoting fruit coloration

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Abstract: Fruit color is a basic evaluation index of maturity and quality. Chlorophyll, carotenoids and flavonoids are the three major coloring pigments. Most immature fruits contain large amounts of chlorophyll. For ripened fruits, the color is primarily composed of flavonoids and carotenoids. Fruits showing either red or purple color are primarily determined by the anthocyanins which are a group of important flavonoids and synthesized by a series of intermediate products. Anthocyanins occur abundantly as glycosides. Different anthocyanin glycoside types determine different fruit colors. With the fruit ripening, the chlorophyll content decreases and the anthocyanin content gradually increases. The fruit coloring process is not only controlled by genetic factors but also regulated by light, temperature, plant growth regulators and other external factors. Abrupt environmental condition changes can cause poor color, and reduce the value of the product. It is therefore necessary to take effective measures to promote the coloring for some fruits. Applying growth regulators is a convenient and quick method. Abscisic acid (ABA), as an important plant hormone, which plays an important regulatory role in the maturation of climacteric and non-climacteric fruits, and can effectively promote fruit coloring and improve fruit quality. Currently, ABA is widely used to improve grape fruit quality and nutrition in the United States and Japan. It is being used to improve the coloring of grapes, peaches, litchis, oranges, and strawberries in China. According to a research report, the concentration of endogenous ABA significantly increases after ripening. Spraying exogenous ABA during the color-change period increases the accumulation of the anthocyanins and antioxidant ability of the fruit. Exogenous application of ABA promotes fruit coloration and maturation by affecting the balance and endogenous levels of ethylene, ABA, IAA, GA and ZR. The biosynthesis of anthocyanins is regulated by a variety of enzymes. Exogenous ABA can promote the

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synthesis of anthocyanins by affecting activities of anthocyanin related enzymes. ABA treatment was found to enhance the activities of PAL and UFGT in pericarp which promoted the synthesis of anthocyanin and the accumulation of soluble solids in the fruit peel. During fruit coloration, related genes of the anthocyanin pathway were significantly increased in the transcriptional level that primarily related to the anthocyanin contents. The biosynthesis of anthocyanins is controlled by the expression of structural genes and transcription factors. The structural genes including *chalcone synthases (CHS)*, *chalcone isomerase (CHI)*, *flavonoid 3-hydroxylase (F3H)*, *flavonoid 3'-hydroxylase (F3'H)*, *flavonoid 3', 5'-hydroxylase (F3' 5' H)*, *dihydroflavonol 4-reductase (DFR)*, *leucoanthocyanidin dioxygenase (LDOX)* and *UDP glucose-flavonoid 3-O-glucosyl-transferase (UFGT)*. The anthocyanin biosynthesis pathway was regulated by the highly conserved MYB-bHLH-WD repeat (MBW) transcriptional complex model. In the dicot *Arabidopsis*, anthocyanin biosynthesis genes can be divided in two subgroups: early biosynthesis genes (EBGs) reactivated by co-activator independent R2R3-MYB transcription factors, whereas late biosynthesis genes (LBGs) require an MBW complex. It has a MBW complex and anthocyanin regulatory system in grapes that are similar to *Arabidopsis*. Many researches have broadened our understanding of the regulation of anthocyanin synthesis in fruits, indicating that a regulatory system based on the cooperation of MYB, bHLH and WD40 proteins that control fruit pigmentation is common to many species. MYB is a family of important regulator genes, which can regulate the expression of the UFGT gene. UFGT is a key enzyme in the anthocyanin biosynthesis pathway, and it is also one of the most affected enzymes by transcription factors in the biosynthesis pathway. The expression of structural genes determines the content and species of anthocyanin. The type and number of MYB genes plays an important role in anthocyanin synthesis. Exogenous ABA can promote fruit coloring by regulating the expression of structural and MYB regulatory genes in the pathway of anthocyanin biosynthesis. The fruit coloring problem has been the hotspot of agricultural research. Exogenous application of growth regulators is a simple, effective and inexpensive method. Many researches have confirmed that ABA can promote fruit color, and improve fruit quality. However, the required time and concentration of ABA in different fruit trees still needs further study. In order to provide a definite theoretical foundation for improving fruit color, many experiments have been performed using exogenous ABA to treat different fruit trees. The mechanism as to how exogenous ABA treatment improves fruit color is still debated. One approach is that ABA treatment can increase the level of endogenous ABA, so as to promote fruit ripening and coloring. The other is that ABA can change the dynamic balance of the endogenous hormone in fruit to promote fruit coloration and maturity. It is not absolutely clear which process ABA affects. However, to date, the mechanism of how ABA is promoting fruit coloring is elusive, which needs further study in order to reach the best conclusion for efficient cultivation. In this review, we summarize recent research progress on the role of ABA in fruit coloring and transcriptional regulation, and also the functional verification of both ABA-responsive and coloring-related genes. In addition, we suggest possible commercial applications of genetic manipulation of ABA signaling to improve fruit quality and yields.

Key words: Fruit; ABA; Regulation; Coloring; Anthocyanin

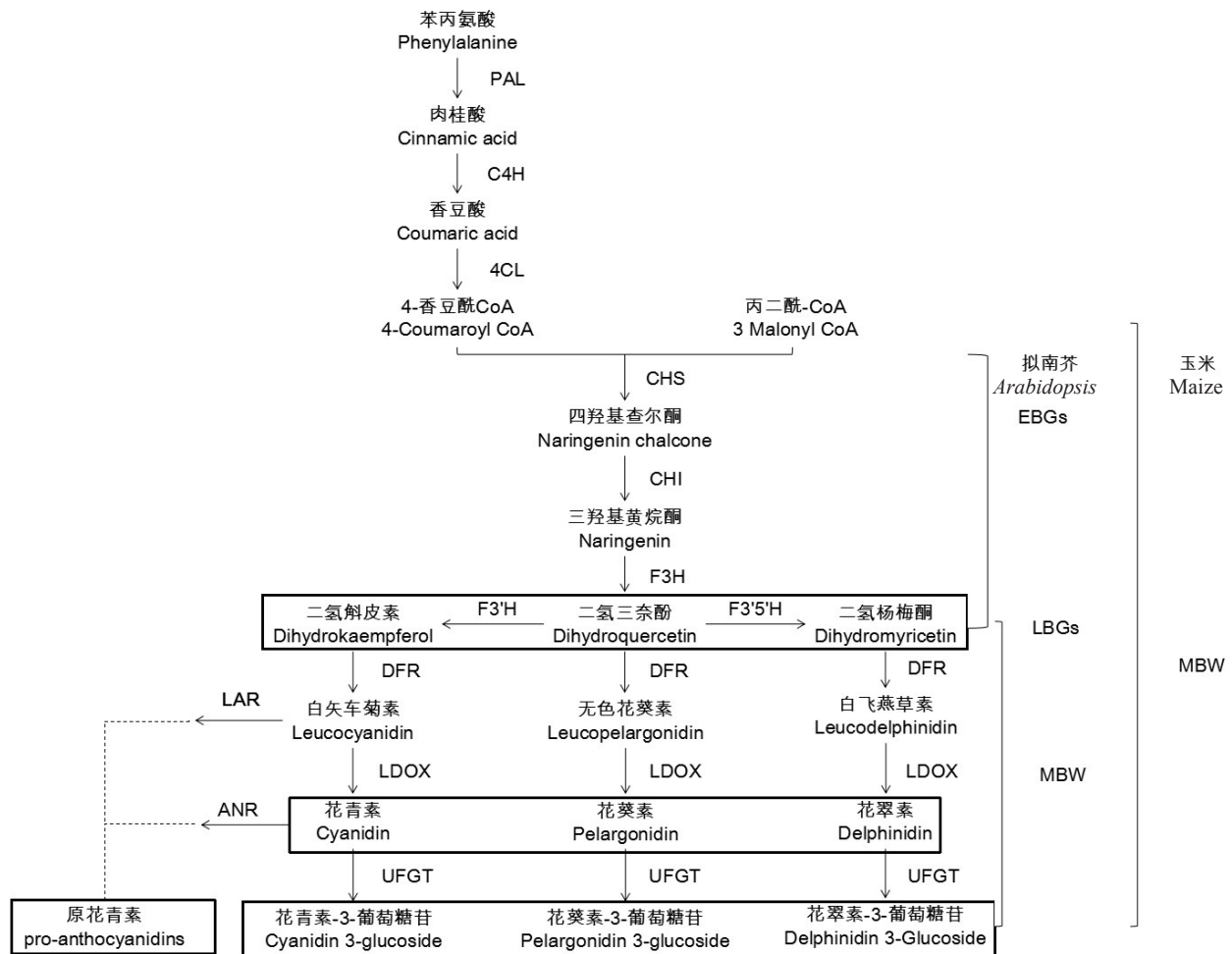
色泽是果实外观品质的重要指标,更是某些果实成熟程度的重要评价依据。花色苷、类胡萝卜素、甜菜素和叶绿素及其组合使植物呈现不同的颜色。花色苷是花青素的配糖体形式,在自然条件下,花青素多以花色苷形式存在。在大多数果树中,未成熟果实含有大量的叶绿素,成熟果实的颜色则主要由

花色苷和类胡萝卜素的含量和比例决定^[1],果实呈现红色或紫色,主要由花色苷决定^[2]。随着果实成熟,果皮中叶绿素含量逐渐降低,花色苷含量逐渐升高。果实充分成熟后,叶绿素的含量降到最低,此时花色苷的种类和含量决定果实的着色程度^[1]。

花色苷的生物合成分为两个阶段,首先由苯丙

氨酸转化为4-香豆酰 CoA,这一阶段称为苯丙烷类代谢途径,该步骤受苯丙氨酸解氨酶(phenylalanine ammonia lyase, PAL)控制;第2阶段为类黄酮途径,由4-香豆酰 CoA 转化为各种黄酮类化合物^[3],该途径受WBM蛋白复合体(WBM蛋白复合体由WD40蛋白、bHLH及R2R3-MYB转录因子形成的蛋白复合体)调控。在拟南芥花色苷合成途径中早期生物合成基因(EBGs)由MYB转录因子单独调控,晚期生物合成基因(LBGs)由WBM蛋白复合体调控,而玉米花色苷合成途径仅由WBM蛋白复合体调控^[4-5]

(图1)。花色苷生物合成途径涉及许多基因和转录因子,花色苷的含量与这些基因的转录水平密切相关。在花色苷合成途径中,直接参与合成的酶主要为查尔酮合酶(CHS)、查尔酮异构酶(CHI)、黄酮酮3-羟化酶(F3H)、类黄酮3'-羟化酶(F3'H)、类黄酮3',5'-羟化酶(F3'5'H)、黄酮酮醇4-还原酶(DFR)、无色花色素双加氧酶(LDOX)和UDP-类黄酮-3-O-葡萄糖基转移酶等^[6-7](图1)。花色苷的合成受WBM蛋白复合体调控,其中MYB^[8]基因对花色苷类型和含量的影响更大,主要通过调节UFGT基因的



MBW. MYB(M)、bHLH(B)和 WD 40(W)转录因子蛋白复合体;EBGs、LBGs. 花色苷合成途径早期合成基因和晚期合成基因;PAL. 苯丙氨酸解氨酶;C4H. 肉桂酸 4-羟化酶;4CL. 4 香豆素 A 连接酶;CHS. 查尔酮合酶;CHI. 查尔酮异构酶;F3H. 黄酮酮 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. 黄酮酮醇 4-还原酶;LDOX. 无色花色素双加氧酶;UFGT. 鸟苷二磷酸葡萄糖基转移酶;ANR. 花青素还原酶;LAR. 无色花色素还原酶。

MBW complexes consisting of MYB (M), bHLH (B) and WD40 (W) transcription factors; EBGs, LBGs. The early and late biosynthetic genes of the flavonoid pathway; PAL. Phenylalanine ammonia lyase; C4H. Cinnamic acid 4-hydroxylase; 4CL. 4 coumarate CoA ligase; CHS. Chalcone synthase; CHI. Chalcone isomerase; F3H. Flavanone 3-hydroxylase; F3'H. Flavanone 3'-hydroxylase; F3'5'H. Flavanone 3'5'-hydroxylase; DFR. Dihydroflavonol reductase; LDOX. Leucoanthocyanidin dioxygenase; UFGT. UDP-flavonoid glucosyl transferase; ANR. Anthocyanidin reductase; LAR. Leucoanthocyanin reductase.

图 1 花色苷生物合成途径
Fig. 1 Biosynthetic pathway of anthocyanins

表达从而调控花色苷的合成。

果实的着色过程不仅受遗传因素调控,也受光照、温度及植物生长调节物质等外部因素的影响^[9],环境因素不适会造成果实着色不良,从而影响果实品质、降低商品价值。对于这些种类果实来说,采取有效措施促进着色是必要的,其中采取生长调节物质调控果实着色是一种方便快捷的措施。ABA是促进非呼吸跃变型果实成熟和衰老的主要激素之一,在高等植物体内,C40类胡萝卜素在9-顺式环氧类胡萝卜素双加氧酶(NCED)的作用下氧化裂解形成ABA^[10],ABA在CYP707A酶的作用下进行分解代谢。ABA在植物信号传导中有着重要作用,其信号传导途径主要有3种^[11]:(1)ABA-PYR/PYL/Rcar-PP2C-SnRK2s;(2)ABAR/CHLH;(3)GPCR-型GTGS。研究发现,外源ABA处理可有效促进果实着色,提高果实品质^[12-13]。

1 ABA调控果实着色研究概述

1.1 ABA对果实花色苷含量的影响

果实果皮中花色苷的生物合成受植物内源激素ABA的调节^[14],研究发现,施加外源ABA可促进花色苷的生物合成^[15],调节果实成熟过程中的色素组成及含量^[16-18]。无论是跃变型果实还是非跃变型果实,ABA处理均可增加果实中花色苷的含量^[19-20],使不同种类花色苷含量均有不同程度的提高^[21-22]。对于葡萄,经ABA处理后,果皮中矮牵牛素糖苷和锦葵素糖苷2种花色苷增加最为显著^[23-24]。

外源ABA处理桃果实,果实内花色苷含量显著增加,果实糖酸比及糖含量明显提高,改善风味,提高品质^[25]。在苹果^[26]以及杨梅^[27]、荔枝^[19,28-29]等非呼吸跃变型果实上也有相似研究报道。目前,ABA在美国、日本广泛应用于改善葡萄果实着色和提高果实品质,在国内也被有些产区用于改善葡萄^[30-33]、桃^[25]、荔枝^[19,28-29]、脐橙^[34]、甜樱桃^[11]、草莓^[35]等果实的着色。

1.2 ABA对果实其他色素的影响

研究表明,大多数果实果皮表面的红色通常由花色苷^[5]决定,但柑橘类、番茄果皮和血橙果肉^[36]的红色主要由类胡萝卜素和番茄红素决定。柑橘果实的着色是果皮中叶绿素降解、类胡萝卜素合成作用的结果^[37-38],叶绿素、类胡萝卜素的含量直接关系到果品的色泽品质。红肉脐橙果肉中内源ABA含量

与番茄红素含量呈显著正相关^[39]。外源ABA处理加速了红肉脐橙、柑橘、番茄等果实果皮叶绿素的降解,促进花色苷、类胡萝卜素和番茄红素的合成^[34]。Li等^[40]通过转录组分析发现,ABA可以上调与叶绿素降解相关基因的表达,加速叶绿素的降解。ABA处理苹果^[41]、番茄^[37,42]加速了叶绿素的降解,同时增加了苹果花色苷与番茄类胡萝卜素含量。这些研究都表明外源ABA可以促进果实着色。

1.3 ABA促进果实着色的施用方法

不同果树不同品种,使用ABA促进着色的最适时间、浓度^[15,43]各有差异。以葡萄为例,硬核期至转色期是调控果实着色的关键时期,在硬核期^[44]、转色初期^[45]及转色后期^[46]施用ABA均可促进葡萄果实的着色。Davies等^[44]研究认为,对于不同品种葡萄,ABA促进着色的最适时间不同,转色期前7~14 d为最适时间区间。对于施用方式,研究表明,叶面喷施^[25]、果实喷施^[23,47]、果穗浸蘸^[48-49]3种方式均可促进果实的着色。果穗浸蘸方式最适质量浓度为100~250 mg·L⁻¹,喷施方式最适质量浓度为600~1 000 mg·L⁻¹。采用果穗浸蘸的方式,其最适浓度低于喷施最适浓度,节约药剂成本,但较喷施方式费时费工。外源ABA在桃^[25,50-51]、苹果^[41,52-53]、草莓^[40,54-55]、荔枝^[19,28-29]等果树上的施用方式与葡萄相似。ABA对于不同树种或品种的最适施用浓度存在一定差异,生产上应根据品种和施用方式进行确定。

2 ABA促进果实着色机制

2.1 ABA通过影响内源激素促进果实着色

外源ABA处理果实,对内源激素的影响主要有以下几点:(1)外源ABA促进了内源ABA的生物合成,增加果实内源ABA含量;(2)外源ABA促进果实内源乙烯的合成,增加果实成熟后乙烯释放量;(3)外源ABA改变ABA、乙烯、吲哚乙酸(indole-3-acetic acid, IAA)、赤霉素(gibberellic acid, GA)、玉米素核苷(trans-zeatin-riboside, ZR)等之间的动态平衡关系,促进果实花色苷的合成,进而促进果实着色。

ABA参与果实的生长发育,对离体培养的葡萄悬浮细胞施用外源ABA 6 h后,细胞内游离ABA含量大幅增加^[56]。ABA代谢途径中,NCED是促进ABA合成的关键酶,CYP707A是分解途径的关键酶^[12],ABA的含量由PacNCED1和PacCYP707A协

同调控^[57]。*VvNCED1* 基因表达水平与 ABA 的积累大致呈线性关系,施用外源 ABA 会影响果实中 *NCED* 基因的表达水平^[42,58]。*FaCHLH/ABAR* 和 *FaPYL1* 是 ABA 信号通路中的受体,Jia 等^[59]利用 RNAi 技术沉默 *FaCHLH/ABAR* 和 *FaPYL1* 基因,草莓内源 ABA 含量显著降低,果实不着色,外源 ABA 可以启动 *FaCHLH/ABAR* 和 *FaPYL1* 基因的表达。这些研究证明了在果实成熟过程中,果实内源 ABA 含量上升与成熟进程一致,外源 ABA 处理上调了 ABA 合成、受体相关基因的表达,提高了果实内源 ABA 含量,并促进了果实花色苷的合成和可溶性固形物的积累。

乙烯是公认的果实成熟衰老激素,同样是调控花色苷生物合成的关键激素,在果实成熟时,乙烯浓度与总花色苷含量呈显著正相关,其通过影响细胞膜透性、增加糖分流通和积累,从而提供反应底物或直接调节相关生理生化过程,进而促进花色苷合成^[60]。大量试验证明,外源 ABA 处理能够促进果实后熟衰老过程中乙烯合成、呼吸升高和果实完熟等生理进程^[61],并且在跃变型果实中 ABA 的积累出现在乙烯释放之前^[12,57]。在模式植物番茄果实上的相关研究表明,ABA 可能触发了乙烯的大量合成并启动果实的成熟,外源 ABA 处理番茄果实能促进内源 ABA 和乙烯的提前释放,而外源乙烯处理则只促使内源乙烯释放提前。用 ABA 合成抑制剂 Fluridone 处理,不仅抑制了 ABA 的合成,也降低了乙烯的产量^[12]。这些结果说明,ABA 诱导了乙烯的合成,而乙烯对 ABA 合成没有影响。在苹果^[52-53]、葡萄^[62]、甜樱桃^[17]、番木瓜^[18]、草莓^[55]上也有相关报道,适宜浓度 ABA 可以促进果实中乙烯的生成。另外,ABA 处理可促进果实中 *ACO* 和 *ACS* 基因的表达,导致 ACC 氧化酶以及与 ACC 合酶相关多肽的积累,从而加速果实中乙烯的合成,最终促进果实成熟与着色^[41]。但也有研究认为,果实成熟受 ABA 调控,与乙烯功能无关,在鳄梨后熟过程中,ABA 含量的升高是在乙烯增加之后,故 ABA 没有促进乙烯的合成^[63]。综上所述,大多数研究表明,ABA 处理可以促进乙烯的合成,增加乙烯的释放量;少数研究结果表明,ABA 没有促进乙烯的合成,对于这一争论需要进一步研究来解释。

植物的生长发育是一个受激素网络交叉作用的调控系统^[64],果实中存在着内源激素之间的动态平

衡^[52]。外源 ABA 是通过改变植物内源激素的动态平衡而促进果实着色和成熟的。ABA 处理使果实中内源 ABA 含量增多,抑制 GA 合成,也抑制前期 ZR 的合成,由于 GA 和 ZR 具有抑制叶绿素降解作用,二者含量的降低利于果皮叶绿素的降解,叶绿素降解产物与花色苷生成的活化作用有关,这样也为花色苷的生成创造有利条件^[41]。也有研究认为,外源 ABA 处理抑制了果实 IAA 的合成,提高了果实乙烯的释放速率,促进了果实花色苷的合成和可溶性固形物的积累^[52]。

2.2 ABA 通过影响花色苷合成相关基因促进果实着色

2.2.1 ABA 对结构基因的影响

果实发育进入着色期,花色苷合成过程中苯丙烷类代谢途径和类黄酮途径的主要相关基因表达水平都显著升高^[6],Li 等^[40]通过转录组分析发现,内源 ABA 调控花色苷合成途径相关基因的表达。外源 ABA 处理显著增加了果实内源 ABA 含量,并诱导花色苷苯丙烷类代谢途径和类黄酮途径中相关基因表达上调^[65]以及转录因子的合成^[56,66],使花色苷迅速积累,从而促进果皮着色^[55]。

花色苷合成第 1 阶段苯丙烷类代谢途径受苯丙氨酸解氨酶(PAL)控制,果实着色期, PAL 活性与花色苷含量呈显著正相关^[55,67],ABA 处理后,果皮中 PAL 的活性显著增加,苯丙氨酸解氨酶基因的表达上调^[49,53]。查尔酮合成酶(CHS)是花色苷合成第 2 阶段类黄酮途径的第 1 个关键酶,*CHS*、*CHI* 基因家族调控类黄酮物质合成,其表达水平与花色苷合成紧密相关。外源 ABA 处理后,*CHS*、*CHI* 家族中的 *CHS3*、*CHI2* 随花色苷合成而大量表达^[6],Jeong 等^[61]研究结果也证明这一点。黄烷酮醇 4-还原酶(DFR)是催化黄烷酮醇生成无色花色苷的关键酶,外源 ABA 可以促进 *DFR* 基因表达上调,进而促进花色苷的合成^[51,61]。UDP-类黄酮-3-O-葡萄糖基转移酶基因(UFGT)是参与花色苷合成过程的最后一个酶,在花色苷整个合成途径中有着至关重要的地位,其在细胞质和液泡协同作用下,将不稳定花色苷修饰形成稳定花色苷,对花色苷合成起着决定性作用^[68]。外源 ABA 处理果实,多种花色苷合成基因表达上调,其中 *UFGT* 基因上调效果最明显^[6,69],并促进了 *UFGT* 基因提前表达^[51],加速着色进程^[19]。外源 ABA 处理还可以降低无色花青苷还原酶(LAR)和

花青苷还原酶(ANR)活性并抑制其基因的表达,从而抑制无色花青素和花青素被催化为原花青素,促进反应朝着花色苷合成方向进行,从而促进果皮着色^[70]。

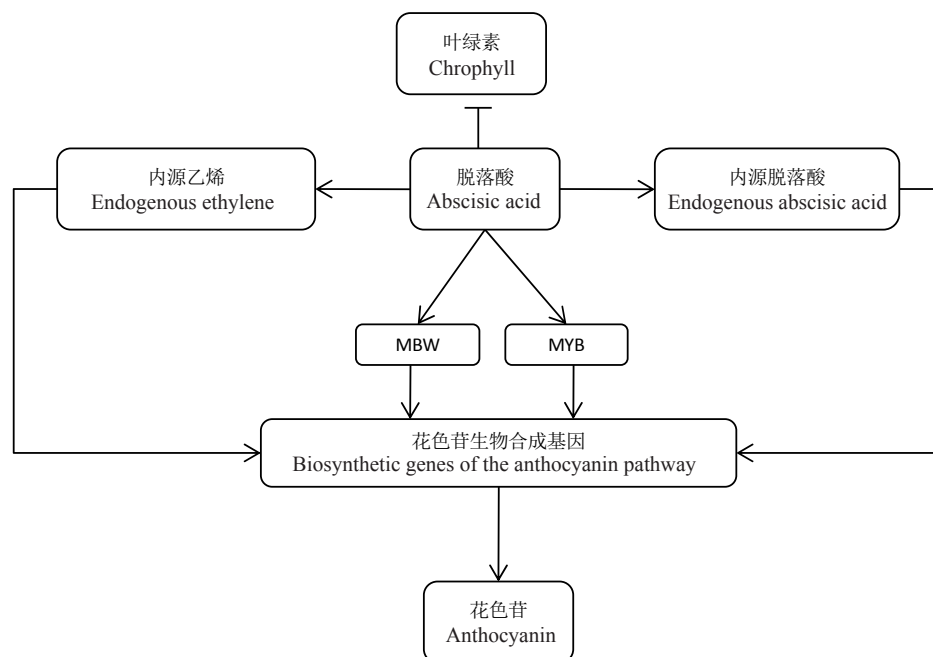
外源 ABA 处理可以增强花色苷合成途径中相关酶的活性,抑制原花青素的合成,促进花色苷的合成,增加花色苷含量,从而促进果实着色。

2.2.2 ABA 对转录因子的影响 大多数基因的表达由转录因子调控,花色苷基因受 W BM 蛋白复合体的直接调控,而无中间调控物^[71]。M BW 复合物是调控花色苷 LBG s 基因的关键。M YB、bHLH 和 W D 40 转录因子组合及其相互作用具有多样性, W BM 蛋白复合体的类型决定花色苷生物合成途径中相关基因的表达水平,进而决定花色苷的种类与含量^[72]。根据 M YB 结构域的个数, M YB 蛋白被分为 3 类:单一 M YB 结构域(R1)蛋白、2 个重复 M YB 结构域(R2R3)蛋白、3 个重复结构域(R1R2R3)蛋白。其中 R2R3-M YB 转录因子能够调控花色苷合成途径酶的合成,对花色苷类型和含量的影响起决定性作用,这已在多种植物中得到证明^[8]。

在葡萄中,2 个 MYB 基因 (*VvMYBA1* 和 *VvMYBA2*) 共同调节 *UFGT* 基因的表达,从而调控花色苷

代谢途径的最后合成步骤。UFGT 是合成途径中受转录因子影响程度最大的一种酶^[73-75]。*VvMYB5a/5b* 在烟草中过表达时,表现出更广泛的作用,控制着包括花色苷在内的苯丙烷类生物合成的所有途径^[76]。目前已经克隆了 2 个 WD40 蛋白基因 (*VvWDR 1* 和 *VvWDR 2*) 和 bHLH 蛋白基因 (*VvMYC 1* 和 *VvMYCA 1*)^[77-78],其表达模式与 *VvMYBA 1*、*UFGT* 和 *ANR* 的表达有关,共同促进了葡萄花色苷积累。*VvWDR1* 在拟南芥中过表达时,激活了花色苷合成途径^[77]。这些研究都表明,花色苷生物合成途径由 MYB、bHLH 和 WD 40 蛋白共同控制,间接证明了葡萄中存在与拟南芥相似的 MBW 复合体和花色苷调控系统。外源 ABA 处理可上调 MYB 调控基因的表达,促进花色苷的合成,进而促进果实着色(图 2)。ABA 处理葡萄果实,进入着色期后,*VvMYB A1*、*VvMYB A1-2* 和 *VvMYB5b* 随花色苷合成而大量表达,其表达水平与花色苷合成紧密相关^[24]。

在苹果中, *MdMYB1*、*MdMYBA* 和 *MdMYB10* 基因对红皮苹果品种的花色苷合成起着重要作用^[79-81]。*MdMYB10* 蛋白诱导花色苷合成,依赖 *MdbHLH3* 和 *MdbHLH33* 两种不同的 bHLH 蛋白的共同作用^[81],当 MYB 与 bHLH 两种不同蛋白共同表达时,花色苷



MBW 是 MYB(M)、bHLH(B)和 WD 40(W)转录因子蛋白复合体。

MBW complexes consisting of MYB (M), bHLH (B) and WD40 (W) transcription factors.

图 2 ABA 促进果实着色机制示意图

Fig. 2 Mechanism of ABA promoting fruit coloration

合成途径结构基因被激活。苹果中的 WD40 蛋白 MdTTG1 已被鉴定,但其与来自苹果的 MYB 和 BHLH 蛋白相互作用仍有待确定。

MYB10 转录因子已在梨、李、樱桃、桃、覆盆子和草莓等其他水果中被发现^[73,82-84]。在草莓中,ABA 可以激活 MYB10 基因,该基因调控草莓果实花色苷生物合成途径,促进了花色苷的积累^[85]。在甜樱桃中,ABA 直接在转录水平上调控 *PacMYBA* 的表达,促进花色苷合成与果皮着色^[86]。在柿果上同样有相关报道^[87],ABA 参与了 *DkMYB4* 调控花色苷的生物合成过程。

花色苷 R2R3-MYB 调控因子含有相当保守序列,如 C 末端结构域的 KPRPR[S/T]F 保守序列^[88]和 MYB 结构域 R3 重复中一个 ANDV 保守序列^[73]。在番茄等作物中,同一组合中 MYB 和 bHLHs 通常是可交换的^[88-91]。研究表明,调控花色苷的转录因子在功能域上有很大的保守性,并且在一个物种和近缘物种之间的功能多样化通常更多地存在于调控序列中,而不是在编码区域。这种高度的保守性更加支持了外源调节物质通过代谢工程调控花色苷的含量。目前研究已经证实,外源 ABA 处理是通过影响 MYB 调控因子,进而调控花色苷的合成,对于 ABA 是否影响 bHLH 和 WD40 调控因子,以及影响 MWD 蛋白复合体的组成仍有待研究。ABA 可以上调花色苷合成途径中相关基因的表达,但其是直接作用于相关基因还是作用于转录因子间接促进花色苷的合成目前还有待考证。

3 问题与展望

目前,国内外对于外源 ABA 调控果实着色的作用,在表观上进行了大量研究,对于调控花色苷代谢途径也有了初步探究。花色苷合成途径在模式植物上的研究也很深入,但在果树中,目前只有苹果、葡萄、草莓等少数种类发现了 MYB、bHLH、WD40,并对其编码基因进行了研究,这需要对其他果树进行转录组分析,借鉴拟南芥、玉米的相关研究,对果树中 MBW 蛋白复合体如何调控着色等代谢途径进行深入探究。而外源 ABA 对 MYB、bHLH、WD40 的影响等相关研究更少,该过程是直接还是间接调控反应尚未确定,今后需在 MBW 复合蛋白体的研究基础上,在转录组、蛋白组、代谢组水平进一步研究。外源 ABA 对内源激素的合成存在影响已得到

证实,但对于作用后各内源激素之间以及果实着色过程的信号通路的转导还不清晰,需对信号分子的传递、代谢途径的调控和关键基因的表达进行深入研究。

果实着色问题一直备受国内外学者关注,利用外源生长调节物质处理,方法简便、经济有效,并且调控花色苷的转录因子高度的保守性更加支持了可利用外源调节物质,通过合成代谢调控花色苷的含量,这一方法无疑将会受到广大果农的喜爱。虽然 ABA 能够促进果实着色,提高果实品质,但对于不同树种和品种的作用浓度、作用时间仍需进行系统的试验,针对不同品种特性确定出不同方案,以期在生产提供明确的技术指导。

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