生物技术通报
· 综述与专论 · BIOTECHNOLOGY BULLETIN 2026, 42(10):13-26

类胡萝卜素调控植物花色和果色机制研究进展

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摘 要： 类胡萝卜素是形成园艺植物花器官和果实色泽的重要色素，直接影响产品的观赏和经济价值。与叶片等光合器官不同，植物花、果发育着色过程中，类胡萝卜素的积累常伴随叶绿素降解及类黄酮等次生代谢物的显著变化，该过程受多层级调控网络协同调控。近年来，类胡萝卜素介导园艺植物花果着色的分子调控机制的研究发展迅速。本文全面总结该领域研究进展，明确*PSY*等类胡萝卜素合成关键酶基因和有色体分化与色素储存在代谢通路多样性中的核心作用。该代谢过程受到转录、转录后及表观遗传层面协同调控。在转录调控水平，MYB、bHLH、NAC、WRKY、AP2/ERF等转录因子构成复杂调控网络，通过靶向*PSY*、*LCYB*、*CCD4*等关键基因精准维持类胡萝卜素合成与降解的动态平衡。转录后调控层面，ORANGE蛋白对PSY的稳定作用、泛素化介导的蛋白降解、PPR蛋白调控以及miRNA介导的转录后沉默等多种机制，协同实现代谢通量的精细微调。表观遗传方面，DNA甲基化与组蛋白修饰动态调控关键基因染色质状态，影响色素积累的时空模式。同时，光照、温度等环境因子与乙烯、脱落酸等植物激素信号可整合至上述调控网络，共同决定花果颜色。本文全面梳理该多层面协同互作调控体系，深入揭示类胡萝卜素在花果着色中的合成与降解平衡机制，并基于此分析园艺产品色泽改良与分子育种实践中的关键问题及发展路径，为园艺产品色泽性状的精准调控与品质提升提供理论支撑和技术指导。

关键词： 类胡萝卜素；花色；果色；转录调控；表观遗传调控；转录后调控；代谢途径
DOI: 10.13560/j.cnki.biotech.bull.1985.2025-1235

Research Progress in the Mechanism of Carotenoids Regulating Plant Flower Color and Fruit Color

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Abstract: Carotenoids are important pigments that determine the color of floral organs and fruits in horticultural plants, directly influencing their ornamental and economic value. Unlike that in photosynthetic organs such as leaves, the accumulation of carotenoids during the development and coloration of plant flowers and fruits is often accompanied by significant changes in chlorophyll degradation and levels of secondary metabolites such as flavonoids, a process that is coordinately regulated by a multi-level regulatory network. In recent years, research on the molecular regulatory mechanisms of carotenoid-mediated flower and fruit coloration in horticultural plants has developed rapidly. This paper comprehensively summarizes research progress in this field, clarifying the core roles of key enzymes encoded by carotenoid biosynthetic genes such as *PSY* and the processes of chromoplast differentiation and pigment storage in the diversity of metabolic pathways. This metabolic process is coordinately regulated at the transcriptional, post-transcriptional, and epigenetic levels. At the transcriptional level, transcription factors such as MYB, bHLH, NAC, WRKY, and AP2/ERF form complex regulatory networks, precisely maintaining the dynamic balance between carotenoid biosynthesis and degradation by targeting key genes including *PSY*, *LCYB*, and *CCD4*. At the post-transcriptional level, multiple mechanisms, including the stabilization of PSY by ORANGE proteins, ubiquitination-mediated protein degradation, PPR protein regulation, and miRNA-mediated post-transcriptional silencing, coordinately achieve fine-tuning of metabolic flux. Epigenetically, DNA methylation and histone modifications dynamically regulate the chromatin state of key genes, thereby affecting the spatiotemporal patterns of

收稿日期：2025-11-15
基金项目：国家自然科学基金项目（32371957），辽宁省种质创新藏粮于技专项计划项目（2023JH1/10200010）
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pigment accumulation. Meanwhile, environmental factors such as light and temperature, as well as phytohormone signals like ethylene and abscisic acid, can be integrated into the above regulatory network to jointly determine flower and fruit color. This paper comprehensively reviews this multi-level coordinated and interactive regulatory system, deeply reveals the balance mechanism of carotenoid biosynthesis and degradation in flower and fruit coloration, and based on this, analyzes key issues and development pathways for color improvement and molecular breeding of horticultural products, providing theoretical support and technical guidance for the precise regulation of color traits and quality improvement of horticultural products.

Keywords: carotenoids; flower color; fruit color; transcriptional regulation; epigenetic regulation; post-transcriptional regulation; metabolic pathways

园艺作物的花色与果实颜色是评价其经济价值的重要指标。植物色素包括花青素类、类胡萝卜素以及甜菜素3大类。其中，类胡萝卜素不仅赋予花朵和果实鲜艳的色泽，也作为维生素A前体和强效抗氧化剂，在人体视觉健康、免疫调节及慢性病预防中发挥重要作用[1]。类胡萝卜素的种类、积累水平以及代谢转变，直接影响花朵和果实的色泽和品质。与叶片等光合器官不同，花朵和果实的着色伴随着叶绿素降解、质体分化以及色素代谢流的复杂生物学过程，并受到发育信号、环境因子及多层级基因网络的精密协同调控。

近年来，随着分子生物学和遗传工程技术的进步，类胡萝卜素着色机制成为植物次生代谢研究热点。研究重点由类胡萝卜素生物合成与降解途径转向转录调控机制，逐步揭示了多个转录因子家族通过复杂互作网络，精准调控关键酶基因的时空表达。近期研究进一步延伸至蛋白稳定性调控、miRNA介导的基因沉默及表观遗传修饰，初步揭示代谢通量在转录后与染色质水平的精细调控[2]。全面阐明类胡萝卜素参与花、果等有色器官着色的调控网络，不仅有助于深化对植物色素代谢途径的认识，也为通过代谢工程与分子设计育种精准改良园艺作物色泽与营养品质提供了关键靶标与策略。本文旨在系统总结近年来在园艺植物花果着色过程中，类胡萝卜素合成与降解代谢途径中受到的多层级调控网络，以及光照、温度等环境因子与乙烯、脱落酸等植物激素信号的整合作用机制，并探讨其在花果色泽定向改良及高品质分子育种中的应用。

1 类胡萝卜素与植物花色和果色的关系

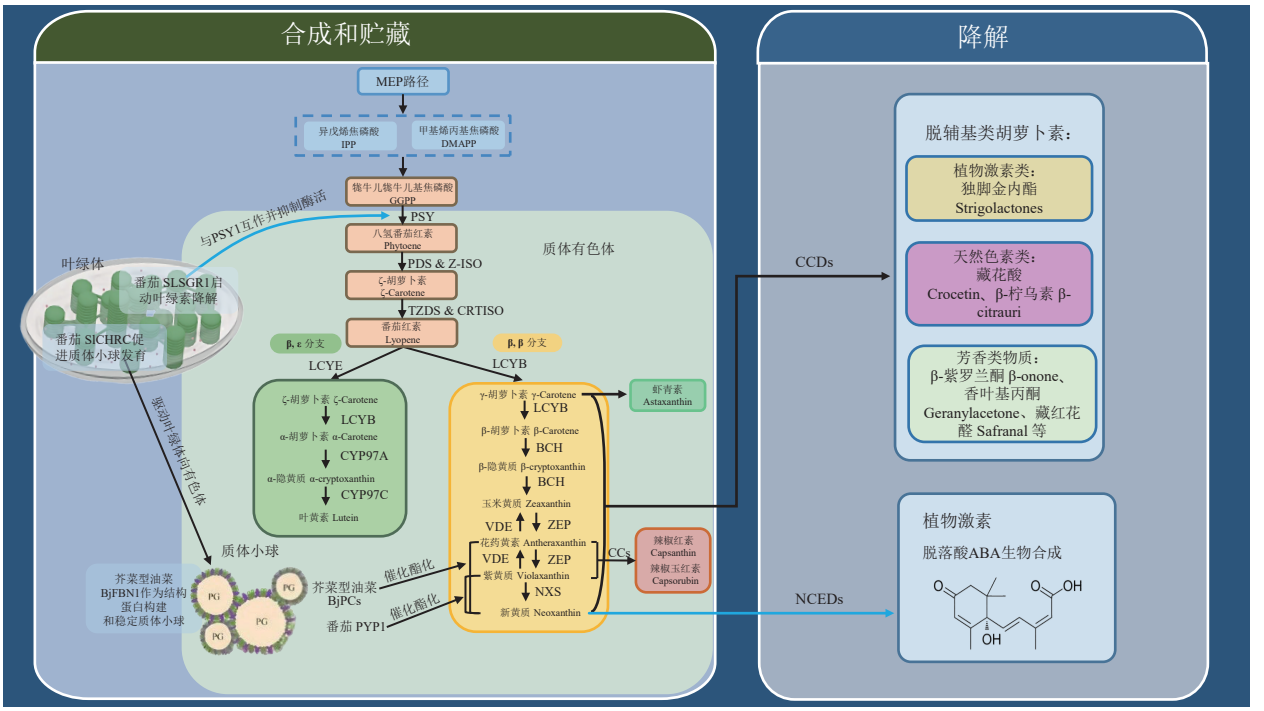
类胡萝卜素的基本结构单元包含C40共轭多烯链及末端碳环结构，根据是否存在氧原子，分为胡萝卜素与叶黄素两类。在光合组织中，叶黄素主要以游离形式存在[3]，而在多数非光合组织中，叶黄素常以酯化形式在有色体中积累，但番茄成熟果实是特例[4]。各种类胡萝卜素在花与果实中吸收特定波长的光线，使其呈现红、橙、黄等色泽。红色的花朵和果实通常源于番茄红素、辣椒红素等吸收蓝绿光的类胡萝卜素。例如番茄（*Solanum lycopersicum*）的红色果实主要源于番茄红素的积累[5]，而辣椒的红色果实则主要由辣椒红素决定[6]。虾青素在大多数高等植物中无法合成，天然分布极为有限[7]。浅黄色至深黄色的花和果实中，往往积累大量吸收蓝光的叶黄素酯。例如，白菜（*Brassica rapa*）的黄色花由叶黄素、紫黄质和新黄质3种类胡萝卜素决定[8]。橙黄色花朵中积累的类胡萝卜素成分比较复杂。β-胡萝卜素主要吸收蓝紫光，呈现橙黄色。然而，橙色的花和果实，往往源于多种类胡萝卜素的共同积累。例如，百合属（*Lilium* spp.）植物橙色花是红色辣椒红素和多种叶黄素共同积累的结果[9]。胡柚（*Citrus changshanensis*）中，红褐色的β-柠乌素（β-citraurin）是橙红色果皮着色的关键[10]。此外，在植物花和果实发育中，类胡萝卜素水平受其合成和代谢平衡的直接影响。例如，布朗百合（*Lilium brownii*）花朵开放初期呈黄色，后因降解过程被激活而褪白，最终呈白色[11]。总体上，类胡萝卜素的种类、积累水平及酯化程度共同决定花和果实的色泽。

2 植物类胡萝卜素生物合成和降解的途径

类胡萝卜素的代谢涉及合成、储存、转运和降解过程。合成途径以质体MEP途径提供的碳源为起点，经GGPPS催化生成前体GGPP，不同GGPPS亚型具有明显的组织表达特异性，分别调控叶片与花

果的代谢流向[12]。PSY催化GGPP缩合为八氢番茄红素是首个限速步骤，其功能缺失或定位异常（如番茄黄色突变体）是合成受阻的主因[13-14]。PDS、ZDS与CRTISO功能异常干扰下游色素合成，CRTISO活性差异可阻碍顺式异构体向反式构型转化，进而引发花色改变[15-16]。番茄红素处于代谢分支点，LCYE与LCYB竞争性地将其分配至β,ε-与β,β-分支，分支代谢流比例对色泽多样性具有重要作用。德国鸢尾（*Iris germanica*）*IgLCYB2*的表达水平调控代谢物流向β,β-分支的强度，使花色在粉、橙、黄间转变[17]。在合成通路下游，油菜BnaZEP家族成员影响花瓣叶黄质与紫黄质的比例，调控花色由黄转橙[18-19]。可见，类胡萝卜素合成途径的限速酶、分支点及下游关键酶共同决定色素积累水平与组成比例（图1），并与降解动态平衡。

在类胡萝卜素储存过程中，有色体作为储存色



类胡萝卜素在质体中合成，经GGPPS催化生成前体GGPP，再经PSY缩合及多步脱氢异构反应生成番茄红素，随后分为β,β和β,ε两个分支。β,β分支中，LCYB催化生成β-胡萝卜素，进一步衍生出玉米黄质、紫黄质、新黄质及脱落酸等；β,ε分支中，LCYE与LCYB协同催化生成α-胡萝卜素并最终形成叶黄素。箭头代表酶促代谢反应方向，黑色箭头代表直接调控，蓝色箭头代表间接调控。PSY：八氢番茄红素合酶；PDS：八氢番茄红素脱氢酶；Z-ISO：ζ-胡萝卜素异构酶；ZDS：ζ-胡萝卜素脱氢酶；CRTISO：类胡萝卜素异构酶；LCYE：番茄红素ε-环化酶；LCYB：番茄红素β-环化酶；CYP97A/C：细胞色素P450羟化酶；BCH：β-胡萝卜素羟化酶；CCS：辣椒红素/辣椒玉红素合酶；VDE：紫黄质脱环氧化酶；ZEP：玉米黄质环氧化酶；NXS：新黄质合酶；CCD：类胡萝卜素裂解双加氧酶；NCED：9-顺式环氧类胡萝卜素双加氧酶。蓝色为前体MEP途径，橘红色为上游主干路径，绿色为β,ε-支路，黄色为β,β-支路，右侧为β,β-分支衍生物合成通路

Carotenoids are synthesized in plastids, where GGPPS catalyzes the formation of the precursor GGPP, which is subsequently converted to lycopene via PSY-mediated condensation and multi-step desaturation and isomerization reactions. The pathway then diverges into two branches: in the β,β-branch, LCYB catalyzes the cyclization of lycopene to β-carotene, which is further hydroxylated and epoxidized to yield zeaxanthin, violaxanthin, neoxanthin, and abscisic acid; in the β,ε-branch, LCYE and LCYB act cooperatively to produce α-carotene, which is ultimately converted to lutein. Arrows indicate the direction of enzymatic metabolic reactions; black arrows represent direct regulation, and blue arrows represent indirect regulation. PSY: phytoene synthase; PDS: phytoene desaturase; Z-ISO: ζ-carotene isomerase; ZDS: ζ-carotene desaturase; CRTISO: carotenoid isomerase; LCYE: lycopene ε-cyclase; LCYB: lycopene β-cyclase; CYP97A/C: cytochrome P450 hydroxylase; BCH: β-carotene hydroxylase; CCS: capsanthin/capsorubin synthase; VDE: violaxanthin de-epoxidase; ZEP: zeaxanthin epoxidase; NXS: neoxanthin synthase; CCD: carotenoid cleavage dioxygenase; NCED: 9-*cis*-epoxycarotenoid dioxygenase. Blue represents the MEP pathway for carotenoid precursor synthesis; orange indicates the upstream core backbone pathway; green indicates the β,ε-branch; yellow indicates the β,β-branch; the right side shows derivative synthesis from the β,β-branch

图1　类胡萝卜素生物合成途径

Fig. 1　Carotenoid biosynthesis pathways

素的特化质体，其分化过程和结构类型直接决定色素的积累模式与稳定性。有色体的发育受质体转换、微观结构变化和酯化作用的协同调控。一方面，*SGR*基因通过促进叶绿素降解，参与叶绿体向有色体的转变，并协同调控类胡萝卜素的合成与积累[20]。另一方面，不同类型有色体通过其独特的超微结构，影响类胡萝卜素的积累效率与代谢稳定性[21-23]。通常，晶体型有色体通过高浓度堆积产生强烈色泽[23]，膜片型有色体通过膜系统重组提供丰富的颜色层次[24]，而小球型有色体则依靠酯化类胡萝卜素与脂质基质结合形成稳定的复合体[25-26]。此外，纤维蛋白对质体小球发育的促进作用、类胡萝卜素酯化基因对结构完整性的维持[26]，甚至淀粉降解的延迟均可通过影响色素稳定储存调控花朵颜色[27]。可见，质体转换、酯化沉积与有色体发育相互关联、层层递进，与生物合成途径共同决定了植物花果的颜色表型。

在类胡萝卜素降解阶段，CCDs可识别并裂解多种有色类胡萝卜素，从而产生脱辅基类胡萝卜素[28-29]。CCDs与菊花（*Chrysanthemum* × *morifolium*）、矮牵牛（*Petunia* × *hybrida*）、百合、番红花（*Crocus sativus*）等多种植物白色花的形成密切相关[30]。在日本牵牛花（*Ipomoea nil* (L.) Roth）中，CRISPR/Cas9敲除*InCCD4*可使花瓣由白色转为淡黄色[31]。*CCDs*对果色的调控则更为复杂。红皮柑橘中，*CsCCD4b1*虽参与β-柠乌素合成，但其表达水平与果皮颜色或β-柠乌素积累并不呈简单正相关。β-柠乌素含量可能受转录后调控、底物供应及质体发育等多因素共同影响[32]。总体而言，CCDs对花色的影响较为直接，果色的形成则有赖于合成、储存与降解过程的协同调控。

综上，植物类胡萝卜素代谢的动态平衡由合成、储存与降解三大过程共同维持。合成通路的关键酶基因的差异性表达，直接决定色素组分与含量；有色体作为储存载体，为色素稳定积累提供物质支撑；CCD家族介导的降解过程，通过反向调控进一步完善代谢网络。三者共同构成园艺植物花果颜色形成的代谢基础。

3 影响植物花和果实中类胡萝卜素积累的因素

植物类胡萝卜素的代谢受到外界环境信号与内源激素水平的协同调控。光照、温度及各类植物激素作为关键调节因子，通过不同的途径调控代谢相关基因表达，从而影响花与果实的着色。

3.1 光照

光照是调控植物次生代谢的核心环境因子，其强度、光质及周期共同调控类胡萝卜素积累。不同遮光条件下，类胡萝卜素生物合成基因表现出差异积累模式。黑暗处理后，百日菊（*Zinnia elegans*）花瓣中光响应转录因子*ZeMYB32*表达量显著增加，结合并抑制*ZeCCD4-2*的转录、减少类胡萝卜素降解，使花瓣亮度、黄度和颜色饱和度显著增强[33]。光强对柑橘果皮类胡萝卜素合成的调控存在发育阶段特异性。在克里曼丁橘（*Citrus clementina*）和甜橙（*Citrus sinensis*）中，遮光可下调*PSY*、*PDS*、*ZDS1*、*LCY2a*、*LCY2b*、*CHX*的表达，进而抑制果皮中类胡萝卜素积累，而强光可增强果皮着色。成熟后期，遮光持续抑制但未完全阻断这些基因的表达[34]。除光强外，光质也是影响色素合成的重要因素。在甜橙、番茄、苹果（*Malus domestica*）、草莓（*Fragaria* × *ananassa*）、葡萄（*Vitis vinifera*）等多种植物果皮着色中，红光促进类胡萝卜素积累，导致果实呈橙色/黄色；蓝光促进花青素积累，导致果实呈红/紫色[35]。不同光质对类胡萝卜素合成的影响存在差异。辣椒果实发育中，红光特异性上调类胡萝卜素合成的中下游基因*LCYb*、*CrtZ*、*CCS*，促进辣椒红素积累和果实着色，而蓝光虽能在早期强烈诱导*PSY*表达，但对果实着色的促进弱于红光[36]。进入成熟期后，采收前的红光处理可加速辣椒果实由绿转红[37]。此外，光周期也在一定程度上影响类胡萝卜素合成[38]。总体而言，光照强度和光质对类胡萝卜素合成的调控具有物种与发育阶段特异性，且红光与蓝光的作用机制存在明显差异。

3.2 温度

温度是影响植物发育的重要环境因子。对于番茄果实，20-25 ℃是番茄红素合成的适宜温度，30 ℃以上的高温抑制番茄红素积累，并促进β-胡萝卜素合成，使果色变浅[39]。类似地，对于克莱门丁柑橘（*Citrus clementina* Hort. ex Tan.），土壤温度20-23 ℃有利于果皮类胡萝卜素积累和色泽发育；

当土温高于23 ℃，则延迟果皮颜色转变[40]。此外，在桂花（*Osmanthus fragrans*）中，高温抑制*OfLCYB1*并激活*OfCCD4-1*，减少类胡萝卜素积累，花色由黄转为黄白色；低温则促进类胡萝卜素积累，使花色由黄转为淡橙色[41]。温度对花朵和果实中类胡萝卜素积累的调控复杂且具有物种特异性，这一过程中温度信号的感知与转录整合机制仍不明确，有待深入研究。

3.3　植物激素

乙烯和脱落酸是调控器官成熟的重要激素，参与调控花和果实成熟过程中的类胡萝卜素积累。在番茄果实成熟过程中乙烯和光信号传导途径相互影响，协同调节类胡萝卜素合成。番茄*hp2*突变体对光信号超敏感，其果实成熟阶段过量富集类胡萝卜素，可能与乙烯代谢紊乱和信号传导输出增强相关。外源乙烯处理能够更强烈地促进*hp2*突变体果实中类胡萝卜素合成基因的表达[5]。ABA可激活桂花花瓣多个类胡萝卜素合成基因，导致花色加深[42]。总体而言，乙烯与脱落酸虽作用方式与调控节点各异，但均可正向促进类胡萝卜素积累。激素信号与光信号通路间的交叉互作，进一步揭示了类胡萝卜素代谢调控网络的复杂性与整合性。

4　花色果色形成中类胡萝卜素合成的转录调控

大量研究表明多种转录因子家族通过激活或抑制类胡萝卜素生物合成与降解途径中关键酶基因的表达，调控植物花、果等器官的色泽形成。

4.1　影响类胡萝卜素代谢的关键转录因子

4.1.1　MYB转录因子　MYB是植物基因组中最大的转录因子家族之一，常通过激活类胡萝卜素合成基因，促进其在花和果实中的大量积累。在桂花中，*MYB43*能够被CPTA诱导上调，进而促进*PDS*、*ZISO*、*ε-LCY*和*CCD4*的表达，增加花瓣类胡萝卜素含量，使花色转红[43]。在辣椒中，R-R型MYB转录因子DIVARICATA1直接结合*PSY*、*β-CH1*、*CCS*的启动子，促进辣椒红素积累、加速果实转色[6]。此外，CaMYB306也正向调控辣椒果实着色，沉默该基因可显著降低*CaPSY*、*CaBCH*、*CaZEP*表达与类胡萝卜素积累，使红果转为黄色[44]。鹅掌楸属植物*L. tulipifera*的R2R3-MYB转录因子RCP激活*LCYE*基因，促进类胡萝卜素合成进而形成花瓣橙色条纹；而中国鹅掌楸（*L. chinense*）*RCP*基因两个Indel变异后，无法激活*LCYE*，导致花瓣呈黄绿色[45]。此外，少量MYB家族成员可负向调控类胡萝卜素代谢基因的表达。瓯柑（*Citrus reticulata* cv Suavissima）的CrMYB68直接抑制*BCH2*和*NCED5*的表达，阻碍α-和β-胡萝卜素向叶黄素与ABA转化，造成果皮胡萝卜素过度积累、叶黄素缺乏，进而呈现留绿的着色异常表型[46]。综上，MYB转录因子家族通过多种方式调控植物类胡萝卜素代谢，多数成员正向激活合成基因以促进色素积累，少数起抑制作用，其调控模式具有明显的物种特异性与功能多样性。

4.1.2　NAC转录因子　NAC转录因子是植物特有的转录因子家族，多个成员通过调控类胡萝卜素合成影响果实着色。在番茄中，SlNAC4与SNAC9是类胡萝卜素积累的正向调控因子。沉默*SlNAC4*导致*SlPSY1*表达显著下降，总类胡萝卜素含量降低约30%，果实呈橙色而非正常红色[47]。SNAC9直接激活*PSY1*、*DXS2*、*SGR1*、*CrtR-b2*转录，敲除后总类胡萝卜素与番茄红素显著降低，叶绿素降解延缓，果实黄化且成熟延迟[48]。SlNAC1发挥负向调控作用，直接结合*SlPSY1*启动子并抑制其表达，同时上调*SlLCYb*、*SlLCYe*、*SlCYCB*以重定向类胡萝卜素代谢流，过表达该基因使成熟果实由红色变为黄色或橙色[49-50]。木瓜（*Carica papaya*）中，CpNAC1和CpNAC2直接结合并激活*CpPDS2/4*等基因的启动子，促进类胡萝卜素积累，调控果实转向黄色或红色[51-52]。金柑（*Fortunella crassifolia*）*FcrNAC22*受红光诱导表达，激活*FcrLCYB1*、*FcrBCH2*和*FcrNCED5*的启动子，促进类胡萝卜素积累和果实褪绿转色[53]。辣椒中，CaNAC2直接激活*CaCCS*促进辣椒红素和辣椒玉红素积累，并抑制ABA降解基因*CaCYP707A2*以提高ABA水平，后者经CaABF3形成正反馈回路进一步激活*CaNAC2*表达。*CaNAC2*沉默后，红色素积累减少而叶黄素含量相对增多，导致果实颜色由红转橙黄[54]。除影响类胡萝卜素合成外，CaNOR可通过激活*CaSGR*促进叶绿素分解，为类胡萝卜素合成创造条件，驱动辣椒果实由绿转红[55]。综上，NAC转录因子通过调控色素合成基因、介导激素信号反馈、促进叶绿素降解等多种方式，调控植物类

胡萝卜素代谢和果实色泽。

4.1.3 bHLH转录因子 bHLH是植物中仅次于MYB的第二大转录因子家族。番茄中，SlBZR1和SlPRE2分别是果实色素积累的正向和负调节因子。SlPRE2通过下调*SlPSY1*、*SlPDS*、*SlZDS*降低果皮叶绿素和类胡萝卜素含量，产生淡绿色的未成熟果实和黄化的成熟果实，而SlBZR1通过激活*SlPSY1*促进类胡萝卜素积累和果实着色[56-57]。木瓜中，CpbHLH1/2直接结合*CpCYC-B*和*CpLCY-B*启动子，分别抑制或促进其转录，调控番茄红素向β-胡萝卜素转化，从而影响果肉红/黄色转变[58]。在辣椒果实中，*bHLH032*、*bHLH048*、*bHLH095*和*bHLH100*等多个基因表达与叶黄素、玉米黄质和辣椒红素合成谱相似[59-60]。瓦伦西亚橙（*Citrus natsudai*）中，CsTT8可上调*CsDXR*、*CsHDS*、*CsHDR*、*CsPDS*、*CsLCYE*、*CsZEP*和*CsNCED2*的表达，增加果实类胡萝卜素含量，促进果皮转橙[61]。此外，甜橙（*Citrus sinensis* cv. Newhall）CsMYC2是茉莉酸信号通路中正向调控果皮类胡萝卜素积累的关键转录因子，可直接激活*CsCCD4b*、*CsLCYb*、*CsBCH*，协同促进β-柠乌素积累。同时，CsMYC2可转录激活*CsMPK6*，后者通过磷酸化降解CsMYC2并抑制其DNA结合活性，形成负反馈回路，精确调控着色强度以防止过度反应[62]。芒果（*Mangifera indica*）中，MiMYC2上调*MiSGR*、*MiRCCR*、*MiPSY*和*MiBCH*的表达，协同调控叶绿素降解与类胡萝卜素合成，促进果皮变黄[63]。可见，bHLH转录因子不仅在转录水平调控类胡萝卜素合成，部分成员还能通过负反馈回路在转录后水平精确控制着色强度。

4.1.4 AP2/ERF转录因子 AP2/ERF与多种植物的花和果实中类胡萝卜素代谢密切相关。番茄SlAP2a和SlERF6是乙烯合成的负调控因子，能够整合乙烯和类胡萝卜素合成通路。其中，SlAP2a抑制乙烯合成基因*ACS2*和*ACS4*的表达，同时促进*PSY1*表达、抑制*CYC-B*表达，影响果实中番茄红素与β-胡萝卜素的比例[64]，而SlERF6抑制乙烯合成的*ACS2*和*ACO1/3*基因，同时抑制类胡萝卜素途径的*DXS*和*HSP21*，阻碍果色转红[65]。晚熟甜橙（*Citrus sinensis* L. Osbeck）果实发育中，CsERF061受乙烯诱导后，直接转录激活*CsLCYb2*，促进果实着色。此外，CsERF061具有多靶向调控功能，可激活多个关键类胡萝卜素途径的基因，包括*PSY1*、*PDS*、*CRTISO*、*LCYb1*、*BCH*、*ZEP*、*NCED3*、*CCD1*和*CCD4*[66]。津巴多橘（*Citrus reticulata Blanco* '*Shiranui*'）CitERF5通过直接激活*CitBCH1*，促进β-隐黄质等的积累，增强果皮的橙红色泽[67]。AP2/ERF转录因子家族以多样化的方式调控果实类胡萝卜素代谢，其调控作用常与乙烯信号通路密切相关。

4.1.5 WRKY转录因子 WRKY转录因子也参与类胡萝卜素生物合成的调控。在番茄果实中，SlWRKY35可直接激活MEP途径关键基因*DXS1*，促进代谢流向类胡萝卜素合成和果实着色，而*SlWRKY16/17/53/54*的沉默会显著抑制番茄果实正常转红[68-69]。柑橘［(*C. unshiu* × *C. sinensis*) × *C. reticulata*］中，CrWRKY42是叶绿素降解和类胡萝卜素合成的双重正调节因子，可直接激活*CrBCH1*表达，过表达*CrWRKY42*可以促进果实由绿转黄[70]。可见，WRKY转录因子不仅直接调控类胡萝卜素合成基因，还可能调控MEP途径为色素合成提供前体。

4.1.6 PRR转录因子 PRR通过调控光周期感知和生物钟，间接影响植物花与果实的色素合成。PRR2亚家族基因*APRR2*及其同源基因可影响番茄、辣椒、西葫芦（*Cucurbita pepo*）等多种植物的果实颜色[71]。辣椒'Micropep Yellow'中，沉默*PRR2*显著降低类胡萝卜素水平[72]。而Lee等[73]进一步证实，c1位点的*CcPRR2*影响成熟果实中类胡萝卜素含量，而不是类型。目前，PRR转录因子调控类胡萝卜素代谢的功能已被多项研究证实，但其具体分子机制仍有待深入研究。

4.1.7 BBX转录因子 BBX是一类具有1个或2个B-box结构域的锌指转录因子，参与调控光形态建成。辣椒中，沉默*CaBBX20*会导致*CCS*表达下降、辣椒红素积累减少，果实颜色由红转橙[74]。番茄SlBBX20是光信号通路的重要正调控因子，直接激活*PSY1*并促进番茄果实着色[75]。某些BBX转录因子能协同调控多条色素代谢通路。芒果中，两种蓝光诱导的锌指蛋白转录因子MiBBX24和MiBBX27，激活花青素合成的正调节因子*MiMYB1*的同时启动*MiPSY*的表达[76]，协同调控花青素和类胡萝卜素合成，促进果实色素积累。综上，BBX转录因子调控

类胡萝卜素代谢的作用常与光信号通路密切相关。

4.1.8　MADS转录因子　MADS-box转录因子主要影响果实成熟和转色。辣椒（*Capsicum annuum*）中，MADS-RIN可直接转录激活*PSY1*和*CCS*以及*DIVARICATA1*，直接或间接调控类胡萝卜素合成，促进果实转红[77]。榴莲（*Durio zibethinus*）果实中，DzAGL6-1激活了*DzPSY*的启动子，瞬时表达可上调*PSY*转录水平和β-胡萝卜素含量[78]。在甜橙果实中，CsMADS5与CsMADS3促进类胡萝卜素的积累和果实着色。CsMADS5直接结合并激活*PSY*、*PDS*和*LCYb1*的启动子，而CsMADS3能直接激活*CsPSY1*、*CsLCYb2*和叶绿素降解基因*CsSGR*启动子，协同调控色素代谢平衡[79-80]。可见，MADS-box转录因子在果实类胡萝卜素积累过程中主要发挥正向调控作用。

4.1.9　其他转录因子　除了上述关键转录因子外，其他类型转录因子也可参与类胡萝卜素代谢调节。温州蜜柑（*Citrus unshiu* Marc.）果实着色中，CitZAT4直接激活*CitPSY*启动子，促进类胡萝卜素合成[81]。甜橙（*C. sinensis* L. Osbeck）果皮中，三螺旋转录因子（TTF家族）CsRP1直接激活*CsCCD4b*，催化β-柠乌素合成，调控果皮红化[82]。番茄CAMTA/SR转录因子SlSR3直接结合*PSY2*和*ZDS*的启动子并抑制其转录，使番茄红素合成受限，延缓果实着色[83]。

4.2　色素代谢通路协同调控机制

类胡萝卜素与类黄酮两大类色素的合成，常在转录水平上受到协同调控。如，猴面花（*Mimulus lewisii*）的黄色蜜导区，R2R3-MYB转录因子RCP1正向调控*PSY1*、*ZDS1*及*BCH1*等多个结构基因，促进类胡萝卜素在该区域积累。当*RCP1*以中等水平过表达时，在增强类胡萝卜素合成的同时，下调花青素合成途径的关键激活因子*PELAN*的表达，抑制*DFR*和*ANS*等花青素合成基因的转录。可见，RCP1在两条色素合成通路间建立起一种表达剂量依赖的拮抗调控关系[84]。除了拮抗调控外，某些MYB转录因子也可协同促进类胡萝卜素与花青素合成。在蒺藜苜蓿中，R2R3-MYB转录因子WP1不仅直接激活类胡萝卜素合成基因*MtLYCe*和*MtLYCb*，还与bHLH蛋白MtTT8及WD40蛋白MtWD40-1形成MBW复合体，进一步增强WP1对类胡萝卜素及花青素合成基因的转录激活能力，最终共同决定其黄底红脉的花色[85]。除MYB外，其他转录因子也可能具备整合两个通路的作用[76, 86]。番茄果实中，两个bHLH转录因子*SlBES1*与*SlBZR1*被油菜素内酯信号同时激活，SlBZR1直接激活*SlPSY1*，而SlBES1直接抑制类黄酮合成关键基因*SlMYB12*、*SlCHS1/2*和*SlF3′H*。二者协同作用，共同调控果实色泽与代谢分配[57, 87]。目前类胡萝卜素与类黄酮色素途径间的拮抗与协同调控机制备受关注，但其精细调控的系统性研究仍较有限，是未来花色形成与代谢调控研究的重要方向。

综上，尽管已鉴定出多个参与类胡萝卜素代谢的转录因子（表1），但对其转录调控网络的理解仍零散且不完整。多数研究缺乏内源功能验证、跨物种比较及多因子协同作用的探讨，完整的有色器官转录调控网络仍有待深入解析。

5　类胡萝卜素合成的转录后调控机制

除转录调控外，转录后调控在植物类胡萝卜素合成的精细调控中发挥重要作用。在蛋白水平上，类胡萝卜素合成关键酶PSY的丰度受到翻译后水平的严格调控。植物橙基因ORANGE（OR）家族蛋白是调控质体分化和类胡萝卜素生物合成的关键因子，它通过在蛋白质水平上与PSY直接互作，稳定PSY蛋白并防止其降解，提高花和果实类胡萝卜素含量[88-89]。番茄E3泛素连接酶PPSR1识别并泛素化修饰靶向PSY前体蛋白，使其经26S蛋白酶体降解，从而负向调控PSY的稳态水平。当PPSR1功能丧失时，PSY前体降解受阻，导致成熟PSY蛋白积累和类胡萝卜素含量提升[90]。ORANGE蛋白的稳定作用与PPSR1的降解作用相辅相成，共同在蛋白质水平上构成一个精细的双向调控网络，以精确控制类胡萝卜素的合成通量[89-91]。在辣椒（*Capsicum chinense*）中，PPR（pentatricopeptide repeat）蛋白被鉴定为类胡萝卜素代谢的关键转录后调控因子，通过CRISPR/Cas9敲除*PPR*后，导致叶黄素酯和玉米黄质酯等酯化色素水平下降，同时促进β-柠乌素等脱辅基类胡萝卜素的积累，从而改变类胡萝卜素的酯化谱与色素稳定性，最终影响果实颜色[92]。

在RNA水平上，非编码RNA，特别是miRNA，在植物基因表达调控中发挥重要作用。miRNA通过

表1 影响类胡萝卜素生物合成的关键转录因子

Table 1 Key transcription factors affecting carotenoid biosynthesis

转录因子 Transcription factors	物种 Species	作用机制 Regulatory mechanism	对色泽的作用 Impact on color		参考文献 Reference
			正向 Positive	负向 Negative	
MYB	桂花、辣椒、猴面花、鹅掌楸、柑橘、蒺藜苜蓿	直接结合启动子激活结构基因;少数成员抑制结构基因或招募抑制复合物	促进黄、橙、红色素积累	改变色素组成,导致留绿或褪色	[43-46, 84-85]
NAC	番茄、木瓜、柑橘、辣椒	部分成员直接激活合成基因,部分成员抑制限速步骤,部分成员调控叶绿素降解间接促进着色	促进果实转红或黄色积累	抑制番茄红素合成,导致黄/橙色果	[47-55]
bHLH	番茄、木瓜、柑橘、芒果	响应光照调控代谢流分支,部分成员直接激活/抑制结构基因,部分成员通过负反馈精确控制着色	促进类胡萝卜素合成与着色	淡绿色未成熟果实和黄化成熟果实	[56-58, 61-63, 87]
AP2/ERF	番茄、柑橘、津巴多橘	受乙烯诱导,广泛激活类胡萝卜素合成途径上游前体到下游修饰环节多个关键基因	上调柑橘类胡萝卜素,增强果皮橙红色泽与着色	下调番茄总类胡萝卜素和番茄红素含量,果色偏橙	[64-67]
WRKY	番茄、柑橘	激活MEP途径;激活合成基因;协同调控叶绿素降解	上调类胡萝卜素积累,驱动果实由绿色转为黄色或红色	—	[68-70]
BBX	辣椒、番茄、芒果	光形态建成调控因子,直接激活合成基因;部分成员协同调控花青素与类胡萝卜素通路	上调类胡萝卜素/花青素,促进辣椒、番茄、芒果着色	—	[74-76]
MADS	辣椒、柑橘、榴莲	直接激活合成结构基因启动子;部分成员同时激活叶绿素降解基因,协同调控色素代谢	促进类胡萝卜素积累,调控辣椒、柑橘、榴莲果实着色	—	[77-80]

与靶mRNA结合，使其降解或翻译抑制，从而负向调控基因表达。柑橘（*Citrus clementina*）中，多个miRNA靶向类胡萝卜素的代谢基因，可能调控柑橘果实着色[93]。在番茄中，7个miRNA靶向类胡萝卜素合成相关基因。miR169i-5p和miR1027a靶向*PSY*，miR482靶向*ZDS*，miR172靶向*CRTISO*，miR396靶向*LCYB*，而miR395则靶向*ZEP*[94]。这些不同类型的miRNAs通过靶向类胡萝卜素合成通路中的多个关键基因，构成一个转录后调控网络，从而实现对代谢流及终产物积累的精细控制。综上，转录后水平通过调控酶稳定性、质体发育、色素修饰和转录后沉默组成的多层次机制，协同调控类胡萝卜素积累和最终呈色。

6 类胡萝卜素生物合成的表观遗传修饰

表观遗传修饰通过改变染色质结构调控基因转录活性，是一类重要的基因表达调控方式。最近的研究表明，表观遗传修饰通过DNA甲基化与组蛋白翻译后修饰，实现对类胡萝卜素代谢相关基因表达的精细调控。

6.1 DNA甲基化

DNA甲基化是通过在特定碱基上添加甲基基团来调控基因表达的一种基因调控模式。在园艺植物中，DNA甲基化可抑制基因转录，进而调控花朵和果实中类胡萝卜素的积累。番茄果实的类胡萝卜素积累与DNA甲基化状态密切相关[95]。在番茄果实发育中，关键基因*PSY1*的启动子区域的DNA甲基化水平呈动态变化。在未成熟的绿色果实中，*PSY1*启动子呈高甲基化状态，基因沉默；进入成熟期后，其启动子发生主动去甲基化后被转录因子激活，从而驱动番茄红素的大量合成。这一过程是番茄果实由绿转红、类胡萝卜素爆发性积累的表观遗传开关[96]。花瓣中类胡萝卜素积累同样受到CCD等色素代谢关键基因启动子区域甲基化的影响。文心兰（*Oncidium*）中，*OgCCD1*是催化类胡萝卜素降解的关键基因。与黄色花‘Gower Ramsey’相比，白色花品种‘White Jade’的*OgCCD1*启动子呈现低甲基化状态，从而激活了该基因的转录，导致类胡萝卜素被大量降解，花瓣呈现白色[97]。在桂花中，

DNA甲基化抑制剂Aza处理后，诱导全基因组DNA低甲基化，激活*OfERFs*的表达，从而促进内源乙烯的合成与信号传递，协同增强类胡萝卜素积累，花色由黄转橙[98]。可见，类胡萝卜素代谢结构基因启动子区域的甲基化水平的动态变化，是调节花朵和果实色泽的重要方式。

6.2　组蛋白修饰

组蛋白修饰通过改变染色质结构，影响基因的转录活性。其中，组蛋白乙酰转移酶（HATs）与去乙酰化酶（HDACs）的动态平衡起着关键调控作用。HATs负责添加乙酰基，使染色质结构松弛，促进转录，而HDACs则移除乙酰基，使染色质结构紧缩，抑制转录。在番茄果实成熟过程中，这一平衡机制调控类胡萝卜素合成。沉默*HDAC*基因*SlHDT3*会导致*PSY1*表达下调，延缓果实成熟并抑制类胡萝卜素积累[99]。而转录因子SlAP2c通过其C端的EAR基序招募共抑制因子TPL2/4，进而与组蛋白去乙酰化酶HDA1/3形成复合体，直接抑制*SlPSY1*、*SlZISO*和*SlCRTISO*的表达[100]。在苹果（*Malus domestica* Borkh.）中，MdMYB44通过其EAR基序招募共抑制因子MdTPR1，进而与HDACs形成复合体，降低靶基因*MdCCD4*和*MdCYP97A3*启动区的组蛋白乙酰化水平来抑制其表达，从而调控类胡萝卜素组成和果实颜色[101]。由此可见，HATs与HDACs共同介导的组蛋白乙酰化动态平衡，在果实类胡萝卜素合成与积累过程中发挥调控作用。

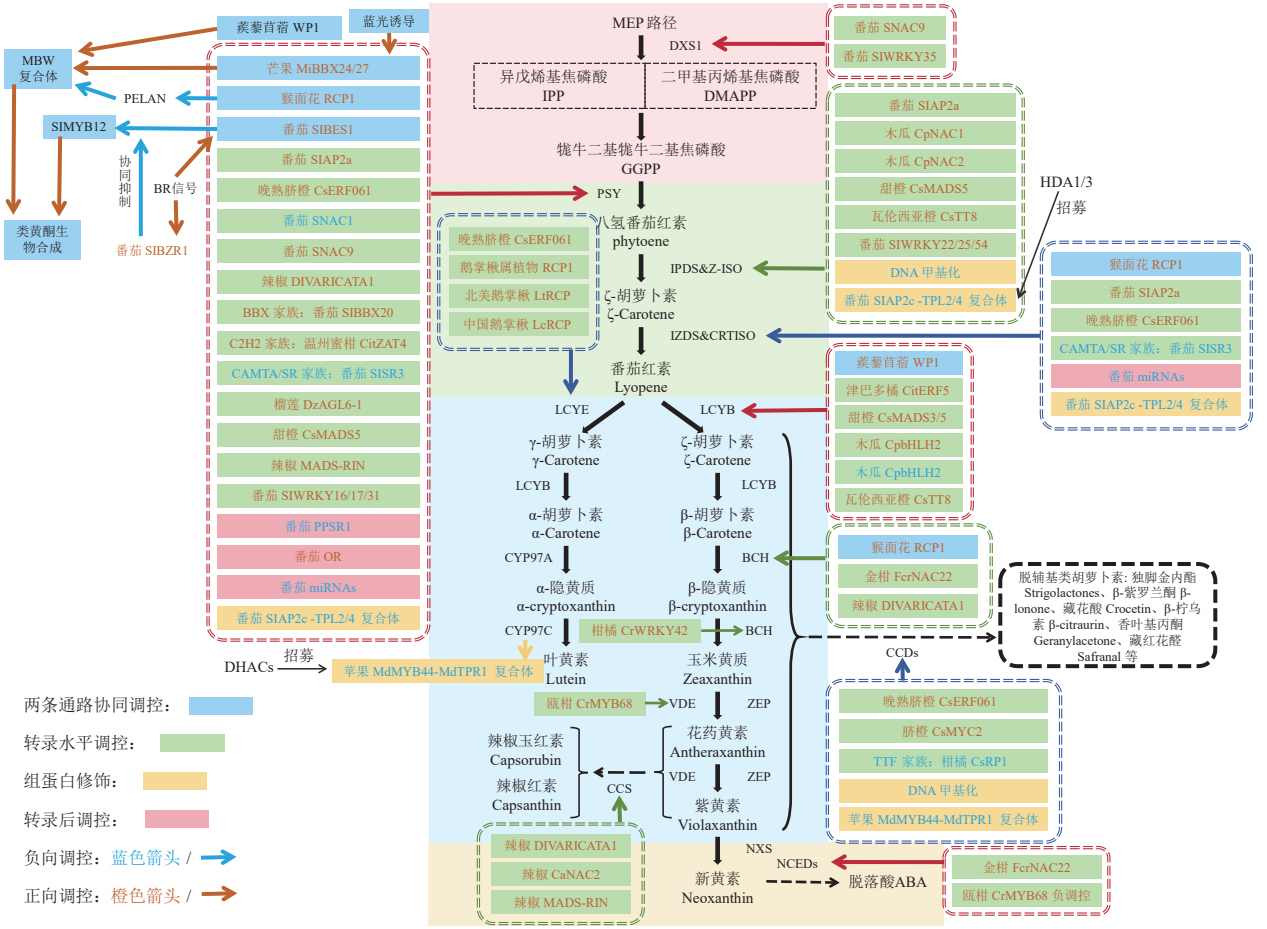
在植物花果着色过程中，类胡萝卜素代谢受多层次协同调控。在转录水平依赖多种转录因子家族激活或抑制合成基因，转录后水平通过蛋白稳定控制和miRNA精细调节代谢通量，表观遗传则通过DNA甲基化和组蛋白修饰动态重塑基因活性（图2）。

7　总结与展望

近年来，植物花与果实色泽形成的分子机制逐步被阐明。类胡萝卜素作为关键着色色素，其积累受内外多重因素调控。其中，类胡萝卜素生物合成途径是代谢基础，转录因子协调叶绿素降解、有色体形成及色素合成，并与转录后、表观遗传调控共同构成调控网络。同时，环境因素与植物激素通过复杂的信号传导途径，调控类胡萝卜素合成结构基因的表达及相关酶活性，最终影响植物花与果实的色泽。当前对类胡萝卜素调控植物色泽的研究虽已取得重要进展，但在揭示深层机制方面，仍面临以下关键挑战：（1）现有研究多聚焦于单个或少数基因的功能解析，缺乏对转录因子复合物形成、上下游级联关系、代谢反馈回路，以及色素代谢动态调控网的深入探讨，对转录调控网络的了解仍不完善；（2）多组学数据的整合应用仍显不足，难以系统解析类胡萝卜素合成相关转录调控网络的整体架构，不同转录因子间的互作关系尚未明确，转录因子与环境因子、内源激素间的协同调控机制也缺乏深入探究；（3）在色泽性状改良方面，虽然番茄、辣椒等重要作物取得了长足进展，然而对于多年生、无性繁殖的园艺植物，基因工程改良效率受限。传统转基因技术中外源基因表达易受植物内源调控系统干扰，导致类胡萝卜素积累效率不佳，且单一基因过表达难以突破代谢网络的整体限制，无法有效提升类胡萝卜素的合成通量。

针对上述挑战，基因编辑技术通过精准修饰植物内源基因，在规避外源DNA引入的同时实现代谢途径的精确调控，为突破育种瓶颈提供了新路径。目前，该技术虽已通过定向改造*PSY*、*LCY*等关键酶基因或敲除负调控因子提升了类胡萝卜素水平，但仍多局限于单一修饰，忽略了对色素稳定性及环境响应因子的协同改良，导致品种常面临稳定性差、适应性窄等局限。基于此，人们提出了多基因联合敲除等技术，并成功实现了番茄等少数植物果实色泽的有效改良[102]。未来的研究可重点发展“多基因联合编辑”引导代谢通路系统优化的新一代育种策略，具体包括：（1）整合基因组、转录组、代谢组及空间转录组数据，深度解析类胡萝卜素合成、修饰、转运及降解的代谢网络全景，精准锁定调控节点；（2）针对特定物种设计多基因协同编辑方案，通过“强化合成、削弱竞争”实现代谢流的定向汇聚与高效分配；（3）定向改良色素稳定性相关修饰酶及环境响应调控因子，系统性培育出色素含量高、化学稳定性强、环境适应性广的新品种。

综上，植物花与果实中类胡萝卜素代谢的调控网络呈现高度复杂性与精密性。随着多组学、基因编辑及分子互作等技术的快速发展，类胡萝卜素合成、降解、转运及储存的多层次调控机制研究将更



类胡萝卜素代谢受转录、转录后、翻译后及表观遗传水平的协同调控。在转录水平，MYB、NAC、bHLH、WRKY、AP2/ERF、MADS等转录因子发挥关键作用；其中，MYB、BBX和bHLH可协同调控类胡萝卜素与类黄酮代谢。PSY作为关键限速酶，LCYE/LCYB作为代谢分支点，均受到多层次调控。在转录后水平，ORANGE蛋白对PSY的稳定作用与PPSR1介导的降解作用形成互补的双向调控网络。在表观遗传层面，类胡萝卜素代谢受DNA甲基化与组蛋白乙酰化的动态变化的共同调控。橙色箭头和字体表示正向调控/促进作用；蓝色箭头和字体表示负向调控/抑制作用。浅绿色模块为转录因子家族；深粉色模块为转录后/翻译后调控；黄色模块为表观遗传修饰；蓝色模块为类黄酮与类胡萝卜素合成协同调控

Carotenoid metabolism is coordinately regulated at the transcriptional, post-transcriptional, post-translational, and epigenetic levels. At the transcriptional level, transcription factors such as MYB, NAC, bHLH, WRKY, AP2/ERF, and MADS play key roles; among them, MYB, BBX, and bHLH cooperatively regulate the biosynthesis of both carotenoids and flavonoids. PSY, as the key rate-limiting enzyme, and LCYE/LCYB, as metabolic branch points, are subject to multi-level regulation. At the post-transcriptional level, the stabilizing effect of ORANGE protein on PSY and the degradation mediated by PPSR1 form a complementary bidirectional regulatory network. At the epigenetic level, dynamic changes in DNA methylation and histone acetylation co-regulate the expression of key genes involved in carotenoid metabolism. Orange arrows and fonts indicate positive regulation/promotion; blue arrows and fonts indicate negative regulation/inhibition. Light green module is the transcription factor family; the dark pink module is post-transcriptional/post-translational regulation; the yellow module is epigenetic modification; the blue module is the synergistic regulation of flavonoid and carotenoid synthesis

图2 植物花果色泽形成中的类胡萝卜素代谢多层次调控机制

Fig. 2 Multi-level regulatory mechanism of carotenoid metabolism on color formation in plant flowers and fruits

加深入。揭示色素代谢的分子调控网络，能够完善植物次生代谢调控理论体系，为园艺作物色泽品质改良提供新思路与可行技术方案，最终推动优质、高价值园艺品种的培育与园艺产业高质量发展。

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