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## 类胡萝卜素代谢途径基因变异导致园艺植物 色泽差异的研究进展

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**摘要** 类胡萝卜素是园艺植物中广泛存在的次生代谢物和色素物质,在植物生长发育和观赏价值中发挥重要作用。同时它也是高价值的天然活性物质,对人体健康有益。因此,类胡萝卜素的代谢调控一直是园艺植物的研究热点。类胡萝卜素组分和含量的差异是造成园艺植物色泽和营养成分多样性的重要原因之一,解析优质性状形成的分子机制是进行定向改良的前提和基础。目前,植物类胡萝卜素代谢途径已明确,大量研究表明代谢通路上基因的启动子和编码区变异是造成类胡萝卜素代谢多样性的关键因素之一。本文对园艺植物类胡萝卜素变异遗传机制的研究策略、启动子和编码区的变异类型及变异对类胡萝卜素代谢的影响进行综述,为园艺植物类胡萝卜素的定向改良提供理论依据。

**关键词** 类胡萝卜素;植物色泽;遗传变异;转录调控;分子标记辅助育种

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类胡萝卜素是自然界中广泛分布的一类次生代谢物,在植物的生长发育中发挥着重要的作用<sup>[1]</sup>。同时,在植物花瓣、果实和叶片等器官中由于类胡萝卜素种类及含量的差异,导致色泽的多样性<sup>[2-5]</sup>,形成五彩缤纷的世界(图1)。此外,类胡萝卜素可裂解产生紫罗酮等重要香气物质<sup>[6]</sup>。对植物而言,鲜艳的颜色

和芬芳的气味可有效吸引昆虫或其他动物为其传粉,提高生殖成功率<sup>[7]</sup>。在植物光合机构中,类胡萝卜素能辅助捕获光能并传递给叶绿素进行光合作用;也能有效清除自由基,避免光氧化对植物造成的损伤<sup>[8]</sup>。另外,类胡萝卜素的下游产物脱落酸(abscisic acid, ABA)和独角金内酯(strigolactone)是植

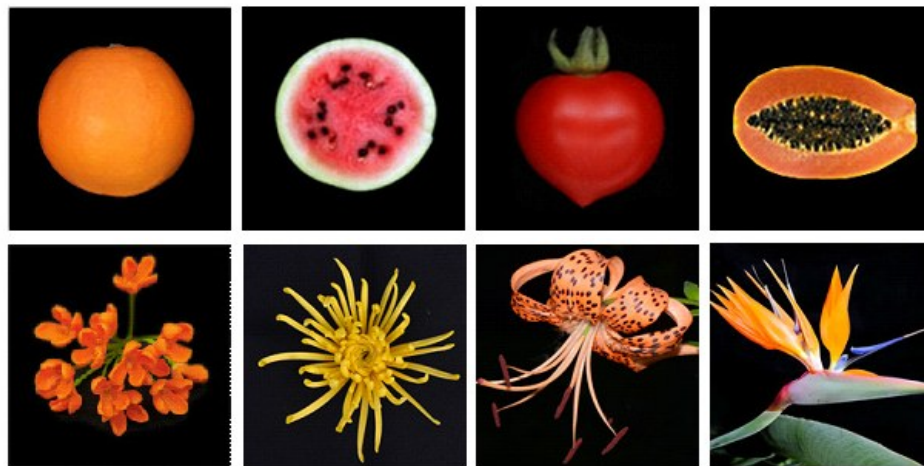


图1 含类胡萝卜素的常见园艺植物<sup>[2-5]</sup>

Fig. 1 Common horticultural plants containing carotenoids

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物抵御逆境、调控生长发育等重要的内源信号物质<sup>[9]</sup>。类胡萝卜素也是一类具有抗氧化能力的高价值天然活性物质,是人体膳食营养的重要组成部分<sup>[10]</sup>。因此,类胡萝卜素代谢途径的分子机制一直是园艺植物研究的热点。

在园艺植物中,类胡萝卜素的代谢通路已基本明晰。近年来,随着组学技术的不断发展以及与遗传学的深度融合,越来越多类胡萝卜素代谢途径的关键基因及其重要变异被挖掘并加以验证。这些研究表明,代谢途径中结构基因编码区和启动子的变异会导致基因功能及转录水平的显著变化,从而改变类胡萝卜素的种类和含量。分子标记辅助育种是未来种业的发展方向,解析优良性状形成的分子机制是开展定向改良的核心科学问题,开发可用于早期选择的分子标记是实现高效育种的关键技术手段。因此,本文总结了植物类胡萝卜素代谢通路、基因变异研究策略、基因变异对类胡萝卜素代谢的影响及转录调控的研究,以期加深对园艺植物类胡萝卜素多样性的生物学认识,同时为开发分子标记、提升育种效率提供理论依据。

## 1 园艺植物类胡萝卜素的多样性

类胡萝卜素的种类异常丰富,迄今为止已在植物、动物和微生物中发现800余种。它是一类含有40个碳的类异戊烯聚合物,由8个异戊二烯单位首尾相连形成。类胡萝卜素类物质主要分为两大类,一是只含碳氢元素的胡萝卜素类,包括番茄红素、八氢番茄红素、 $\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素等物质;二是胡萝卜素类的含氧衍生物(即叶黄素类),包括叶黄素、虾青素、玉米黄质等<sup>[11]</sup>。类胡萝卜素也因其分子结构中存在的共轭双键而呈现不同的颜色<sup>[12]</sup>。园艺植物中常见的类胡萝卜素有红色的辣椒红素、橙红色的 $\beta$ -胡萝卜素、粉色的番茄红素、橙黄色的紫黄质、黄色的黄体素和玉米黄质等<sup>[2,13-15]</sup>。不同种类和含量的类胡萝卜素积累可形成园艺植物中美丽多彩的色泽<sup>[3,16]</sup>。同时,在柑橘、辣椒、西瓜、番茄等同种植物的不同品种间也可因类胡萝卜素种类的不同而呈现色泽的差异(表1)。如柑橘中的‘温州蜜柑’果实积累 $\beta$ -隐黄质而呈橙红色,‘红夏橙’果实积累紫黄质而呈黄色<sup>[35]</sup>;辣椒中红色果实主要积累辣椒红素,橙色果实主要积累辣椒红素、玉米黄质,黄色果实主要积累叶黄素和 $\beta$ -胡萝卜素<sup>[20-21]</sup>。此外,同一种植物

也可积累不同含量的类胡萝卜素而显示色泽多样性。如桂花中 $\alpha$ -胡萝卜素和 $\beta$ -胡萝卜素含量的高低是区分丹桂(橙红色)、金桂(橙黄色)、银桂(黄白色)的关键因素<sup>[26,36]</sup>。因此,类胡萝卜素的种类和含量是决定园艺植物色泽多样性的重要原因。

## 2 植物类胡萝卜素的主要代谢通路

植物类胡萝卜素的代谢途径已被阐述清楚,主要包括合成及降解两个部分<sup>[37]</sup>。类胡萝卜素合成始于异戊二烯焦磷酸(IPP)与二甲基丙烯焦磷酸(DMAPP)的缩合,在牻牛儿苗基焦磷酸合酶(GGPPS)的作用下生成的前体物质——牻牛儿苗基焦磷酸(geranylgeranyl pyrophosphate, GGPP)。两分子的GGPP通过八氢番茄红素合成酶(phytoene synthase, PSY)的作用产生无色的八氢番茄红素(phytoene),然后,在八氢番茄红素脱氢酶(phytoene desaturase, PDS)、 $\delta$ -胡萝卜素异构酶(zeta-carotene isomerase, ZISO)、 $\zeta$ -胡萝卜素脱氢酶(zeta-carotenodesaturase, ZDS)和胡萝卜素异构酶(carotenoid isomerase, CRTISO)等一系列酶的作用下生成番茄红素(lycopene)。随后,类胡萝卜素代谢途径被分为2个分支点,由番茄红素 $\epsilon$ -环化酶(lycopene epsilon cyclase, LCYe)和番茄红素 $\beta$ -环化酶(lycopene beta cyclase, LCYb)的环化分别产生 $\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素两个重要产物<sup>[38]</sup>。 $\alpha$ -胡萝卜素在 $\beta$ -胡萝卜素羟化酶( $\beta$ -carotene hydroxylase, BCH)和 $\epsilon$ -胡萝卜素羟化酶(ECH)作用下生成叶黄素;而 $\beta$ -胡萝卜素在 $\beta$ -胡萝卜素羟化酶(BCH)、玉米黄质环氧化酶(zeaxanthin epoxidase, ZEP)、紫黄质脱环氧化酶(violaxanthin deepoxidase, VDE)、新黄质合成酶(neoxanthin synthase, NXS)等作用下,生成 $\beta$ -隐黄质、玉米黄质、新黄质等,其中新黄质是脱落酸(abscisic acid, ABA)的合成前体物质,也是 $\beta$ 分支的最后一个产物。

植物类胡萝卜素的降解由酶促反应和非酶促反应完成,可生成多种脱辅基类胡萝卜素,如香气物质、激素、色素及信号分子等<sup>[9,39]</sup>。其中,酶促降解过程在植物中主要由类胡萝卜素裂解氧化酶(carotenoid cleavage oxygenases, CCOs)催化完成;非酶促降解过程通常与逆境胁迫应答相关。CCOs可以特异性剪切 $C_{40}$ 类胡萝卜素多烯链的共轭双键,形成多种脱辅基类胡萝卜素,部分产物还可进一步裂解<sup>[12]</sup>。CCOs家族具有双加氧酶特性,根据酶所裂解的底物

表1 园艺植物中的主要类胡萝卜素组分

Table 1 Important carotenoids in different horticultural plants

物种名 Name	拉丁学名 Latin name	表型 Color	主要类胡萝卜素 Major carotenoids	参考文献 Reference
番木瓜 Papaya	<i>Carica papaya</i> L.	黄/红色果肉 Yellow/red pulp	$\beta$ -隐黄质、 $\beta$ -胡萝卜素、番茄红素等 $\beta$ -Cryptoxanthin, $\beta$ -carotene, lycopene, etc.	[2]
桃 Peach	<i>Prunus persica</i> L. Batsch.	黄色果肉 Yellow pulp	花药黄质、黄体呋喃素 Antheraxanthin, luteoxanthin	[17]
芒果 Mango	<i>Mangifera indica</i> L.	黄色果肉/果皮 Yellow pulp/peel	紫黄质、 $\beta$ -胡萝卜素、 $\alpha$ -胡萝卜素、黄体素等 Violaxanthin, $\beta$ -carotene, $\alpha$ -carotene, lutein, etc.	[18-19]
柑橘 Citrus	<i>Citrus</i> L.	红/黄色果肉/果皮 Red/yellow pulp/peel	$\beta$ -隐黄质、紫黄质、花药黄质、柠乌素、八氢番茄红素 $\beta$ -Cryptoxanthin, violaxanthin, antheraxanthin, citraurin, phytoene	[3,13]
西瓜 Watermelon	<i>Citrullus lanatus</i>	红/橙/黄色果肉 Red/orange/yellow pulp	番茄红素、 $\beta$ -胡萝卜素、八氢番茄红素、紫黄质、黄体素、玉米黄质 Lycopene, $\beta$ -carotene, phytoene, violaxanthin, lutein, zeaxanthin	[1,4]
辣椒 Pepper	<i>Capsicum annuum</i>	红/橙/黄色果肉 Red/orange/yellow pulp	辣椒红素、玉米黄质、黄体素、 $\beta$ -胡萝卜素、 $\alpha$ -胡萝卜素、隐黄质 Capsanthin, zeaxanthin, lutein, $\beta$ -carotene, $\alpha$ -carotene, cryptoxanthin	[20-21]
胡萝卜 Carrot	<i>Daucus carota</i> L.	红/橙/黄色块根 Red/orange/yellow root tubers	番茄红素、 $\beta$ -胡萝卜素、 $\alpha$ -胡萝卜素、黄体素 Lycopene, $\beta$ -carotene, $\alpha$ -carotene, lutein	[22]
番茄 Tomato	<i>Lycopersicon esculentum</i>	红/黄色果肉 Red/yellow pulp	番茄红素、 $\beta$ -胡萝卜素、八氢番茄红素、六氢番茄红素 Lycopene, $\beta$ -carotene, phytoene, phytofluene	[5]
白菜 Chinese cabbage	<i>Brassica rapa</i> L. spp. <i>pekinensis</i>	橙色叶片 Orange leaf	$\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素、番茄红素 $\alpha$ -Carotene, $\beta$ -carotene, lycopene	[23]
万寿菊 Marigold	<i>Tagetes erecta</i> L.	黄/橙色花瓣 Yellow/orange petals	黄体素、玉米黄质、紫黄质、 $\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素、番茄红素、辣椒红素等 Lutein, zeaxanthin, violaxanthin, $\alpha$ -carotene, $\beta$ -carotene, lycopene, capsanthin, etc.	[24-25]
桂花 Sweet osmanthus	<i>Osmanthus fragrans</i>	橙/黄色花瓣 Orange/yellow petals	$\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素 $\alpha$ -Carotene, $\beta$ -carotene	[26]
菊花 Chrysanthemum	<i>Chrysanthemum morifolium</i>	黄色花瓣 Yellow petals	黄体素、 $\beta$ -胡萝卜素 Lutein, $\beta$ -carotene	[27]
石斛兰 Dendrobium	<i>Dendrobium nobile</i> Lindl.	黄色花瓣 Yellow petals	黄体素、 $\alpha$ -隐黄质、玉米黄质、花药黄质 Lutein, $\alpha$ -cryptoxanthin, zeaxanthin, antheraxanthin	[28]
文心兰 Oncidium	<i>Oncidium</i> Gower Ramsey	黄色花瓣 Yellow petals	紫黄质 Violaxanthin	[29]
大花蕙兰 Cymbidium	<i>Cymbidium hybrida</i>	黄色花瓣 Yellow petals	$\beta$ -胡萝卜素 $\beta$ -Carotene	[30]
百合 Lily	<i>Lilium lancifolium</i> Thunb.	橙/黄色花瓣 Orange/yellow petals	花药黄质、紫黄质、辣椒红素、辣椒玉红素等 Antheraxanthin, violaxanthin, capsanthin, capsorubin, etc.	[31-33]
忍冬 Honeysuckle	<i>Lonicera japonica</i> Thunb.	黄色花瓣 Yellow petals	紫黄质、玉米黄质、 $\alpha$ -胡萝卜素、 $\gamma$ -胡萝卜素等 Violaxanthin, zeaxanthin, $\alpha$ -carotene, $\gamma$ -carotene, etc.	[34]

是否发生环氧化,可将其分为类胡萝卜素裂解双加氧酶(carotenoid cleavage dioxygenases, CCDs)和9-顺式-环氧类胡萝卜素双加氧酶(9-cis-epoxycarotenoid dioxygenases, NCEDs)<sup>[40]</sup>。在类胡萝卜素降解过程中,CCD1和CCD4在植物的色泽和香气物质代谢中发挥重要作用<sup>[6]</sup>。桂花、拟南芥、月季、矮牵牛等

植物中,CCD1和CCD4以C<sub>40</sub>类胡萝卜素和C<sub>27</sub>脱辅基类胡萝卜素为底物分解产生香叶基丙酮、 $\beta$ -紫罗兰酮、假紫罗酮、 $\alpha$ -紫罗酮等C<sub>13</sub>或C<sub>14</sub>香气物质<sup>[41-46]</sup>。同时,类胡萝卜素被CCD4所裂解产生胭脂素、 $\beta$ -柠乌素及 $\beta$ -citraurinene等天然色素物质,使红木、柑橘等植物的种子或果实呈现诱人的红色<sup>[15,47-50]</sup>。此

外,植物激素 ABA 和独角金内酯也是类胡萝卜素裂解的重要产物<sup>[9]</sup>。番茄、水稻、鳄梨、葡萄及草莓等植物中 *NCED* 基因参与到 ABA 生物合成过程,导致果实内源 ABA 含量变化,果实表皮呈现不同色泽<sup>[51-56]</sup>。

### 3 植物类胡萝卜素遗传变异的常用研究方法

为了揭示色泽的遗传变异规律,利用正向遗传学方法进行研究,一般采取以下3种手段:其一是挖掘突变体材料,如在番茄<sup>[57-58]</sup>、桃<sup>[59]</sup>、白菜<sup>[60]</sup>等研究中通过比较野生型和突变型的差异锁定了关键变异基因。其二是用2种不同表型的植株进行杂交产生性状分离,再结合组学等技术明确差异区域,筛选并验证关键基因<sup>[15,61-62]</sup>。如在柑橘的研究中,利用红橘(红果皮)和枳(黄果皮)F<sub>1</sub>代杂交子代混池 RNA-seq 测序产生的 SNP 进行混合样本分组分析(BSA, bulked segregant analysis),再结合分子标记进行精细定位,揭示出 *CCD4b* 对色泽变异起到关键作用<sup>[15]</sup>。在花椰菜的花色研究中,对白花和黄花杂交的 F<sub>2</sub> 分离群体进行了 BSA 分析结合全基因组重测序,筛选到了关键变异基因 *CCD4*<sup>[63]</sup>。其三是利用丰富的自然品种寻找普遍规律。如在菊花研究中发现 *CmCCD4a* 在黄色品种中无法表达,而在白色品种中大量表达,进一步通过 RNAi 验证了 *CmCCD4a* 对类胡萝卜素降解起重要作用,是黄色和白色花瓣差异的关键<sup>[16]</sup>。在桃中也利用不同基因型种质资源筛选得到果肉色泽差异基因<sup>[59]</sup>。

### 4 类胡萝卜素代谢途径关键基因变异研究与应用

关键代谢通路基因的编码区及启动子变异是造成植物类胡萝卜素种类和含量差异的重要原因(表2)。在花椰菜<sup>[63]</sup>、胡萝卜<sup>[72]</sup>及菊花<sup>[77]</sup>等植物中证实,重要基因编码区的变异可使基因功能和基因表达量发生变化,从而导致表型差异。PSY 是类胡萝卜素生物合成途径的限速酶,研究显示在木薯和辣椒中,*PSY* 编码区多个 SNPs 和 InDels 的变异,可影响类胡萝卜素的合成,使其呈现丰富的色泽<sup>[71,73]</sup>。番木瓜中的红色果肉是由番茄红素环化酶基因 *LCYb2* 的编码区突变引起番茄红素大量积累而产生<sup>[68]</sup>。再如,桃子黄色与白色果实相比,*CCD4* 编码

区发生了多处 SNPs、转座子及逆转座子插入、氨基酸替代等变化,从而导致酶活性丧失,类胡萝卜素积累<sup>[59,64-67]</sup>。油菜的黄色花瓣中,由于 *CCD4* 基因编码区插入了一个 CACTA 类型转座子导致降解功能丧失,下游的紫黄质大量积累;而未发生转座子插入的白色花瓣中类胡萝卜素裂解产生大量香气物质紫罗酮<sup>[60]</sup>。拟南芥种子、甘蓝花瓣中 *CCD4* 编码区的 SNPs 变异导致其裂解功能下降,类胡萝卜素含量升高<sup>[62,78]</sup>。

除了编码区之外,启动子的变异则可直接影响基因的转录水平,从而改变类胡萝卜素代谢。如柑橘中的 *CCD4b* 基因启动子中增加了 Harbinger 类型 MITE 转座子。经烟草双荧光素酶和 GUS 酶活性检测表明,MITE 转座子上的 SNP2<sup>G</sup>(CAACTG)可增强启动子活性,促进 *CCD4b* 大量表达形成红皮柑橘中特有的红色  $\beta$ -柠乌素<sup>[15]</sup>。除此之外,还有部分植物类胡萝卜素代谢途径关键基因的编码区和启动子同时发生了变异,如白菜的类胡萝卜素异构酶基因 *CRTISO* 的编码区突变导致功能丧失,同时启动子的 88 bp 缺失导致调控它的转录因子及代谢通路其他基因表达均受影响,最终前番茄红素(prolycopene)在突变体中大量积累<sup>[60]</sup>。拟南芥种子中的 *CCD4*<sup>[78]</sup>、*ZEP*<sup>[79]</sup> 的启动子和编码区变异影响了种子类胡萝卜素的积累。玉米 *LCYe*<sup>[75]</sup> 的改变则直接影响了  $\alpha$ -和  $\beta$ -分支的流向。大量研究表明,植物类胡萝卜素的种类及含量与相关基因表达量密切相关<sup>[1,9,12]</sup>,而启动子活性直接调控基因表达,因此启动子变异是造成色泽差异的另一主因。

在深入解析类胡萝卜素变异的分子机制基础上,利用差异片段开发可用于早期选择的分子标记能有效提升育种效率。如在白菜的研究中发现, *CRTISO* 启动子 88 bp 缺失可导致白色叶片突变为黄色叶片,由此开发了 InDel 共显性分子标记 Br-Pro-Indel,可有效鉴别叶色,缩短育种周期<sup>[60]</sup>。玉米中的类胡萝卜素含量与 *LCYe* 紧密相关,它的编码区变异可引起  $\alpha$ -胡萝卜素、 $\beta$ -胡萝卜素、 $\beta$ -隐黄质等重要类胡萝卜素代谢变化。根据编码区变异片段设计特异引物,对后代进行 PCR 扩增可快速鉴定变异并推断表型<sup>[75]</sup>。因此,对类胡萝卜素代谢通路基因变异的解析不仅可以丰富色泽多样性的生物学理论,还可有效设计用于定向改良的分子标记。

表2 植物类胡萝卜素代谢关键基因启动子和/或编码区变异的遗传学机制  
**Table 2 Genetic mechanism of variation of promoter and/or coding regions of key genes of carotenoids metabolism in plants**

物种名 Name	拉丁学名 Latin name	表型 Color	基因 Gene	变异 Variation	文献 Reference
桃 Peach	<i>Prunus persica</i> L. Batsch.	黄/白果肉 Yellow/white pulp	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区STR变异、转座子插入、逆转录转座子插入、序列插入、SNPs变异、移码突变等 STR variation in coding region, transposon insertion, retrotransposon insertion, sequence insertion, SNPs mutation and frameshift mutation etc.	[59, 64-67]
番木瓜 Papaya	<i>Carica papaya</i> L.	红/黄果肉 Red/yellow fruit meat	番茄红素β-环化酶基因 <i>LCYB</i>	编码区2个SNPs变异 Variation of two SNPs in coding region	[68]
柑橘 Citrus	<i>Citrus</i> L.	黄/红果皮 Yellow/red peel	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	启动子MITE转座子插入 MITE transposon insertion in promoter region	[15]
油菜 Rape	<i>Brassica napus</i> L.	黄/白花瓣 Yellow/white petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区CACTA-like转座子插入 CACTA-like transposon insertion in coding region	[61]
甘蓝 Cabbage	<i>Brassica oleracea</i> L. var. <i>alboglabra</i> Bailey	黄/白花瓣 Yellow/white petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区多个SNPs变异 Variation of multiple SNPs in coding region 编码区CACTA-like转座子插入 CACTA-like transposon insertion in coding region	[62] [69] [70]
辣椒 Pepper	<i>Capsicum annuum</i> L.	橙/黄果实 Orange/yellow fruit	八氢番茄红素合成酶基因 <i>PSY</i>	编码区多个SNPs变异 Variation of multiple SNPs in coding region	[71]
胡萝卜 Carrot	<i>Daucus carota</i>	橙/黄/白块根 Orange/yellow/white root	β-胡萝卜素羟化酶 <i>BCH</i>	编码区多个SNPs变异 Variation of multiple SNPs in coding region	[72]
木薯 Cassava	<i>Manihot esculenta</i>	黄/白块根 Yellow/white root	八氢番茄红素合成酶基因 <i>PSY</i>	编码区多个InDels变异 Variation of multiple InDels in coding region	[73]
花椰菜 Broccoli	<i>Brassica oleracea</i> var. <i>botrytis</i>	黄/白花瓣 Yellow/white petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区CACTA-like转座子插入 CACTA-like transposon insertion in coding region	[63]
番茄 Tomato	<i>Solanum lycopersicum</i> L.	红/白花瓣 Red/white petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区多个InDels变异 Variation of multiple InDels in coding region	[74]
番茄 Tomato	<i>Solanum lycopersicum</i> L.	黄/红果实 Yellow/red fruit	番茄红素β-环化酶基因 <i>LCYB</i>	启动子多个SNPs变异 Multiple SNPs variation in promoter region	[57]
白菜 Chinese cabbage	<i>Brassica rapa</i> L. ssp. <i>pekinensis</i>	橙/白叶片 Orange/white leaves	类胡萝卜素异构酶基因 <i>CRISO</i>	启动子88 bp插入、编码区氨基酸变异和序列插入 Insertion of 88 bp sequence in promoter region, amino acid variation and sequence insertion in coding region	[60]
玉米 Maize	<i>Zea mays</i> L.	黄/白籽粒 Yellow/white grain	番茄红素ε-环化酶 <i>LCYE</i>	启动子InDels和编码区氨基酸变异 The variation of InDels in promoter region and variation of amino acid in coding region	[75]
矮牵牛 Petunia hybrida	<i>Petunia</i> × <i>hybrida</i>	黄/白花瓣 Yellow/white petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区MITE重复插入 MITE repeat insert in coding region	[76]
菊花 Chrysanthemum	<i>Chrysanthemum morifolium</i>	黄/粉花瓣 Yellow/pink petals	类胡萝卜素裂解双加氧酶基因4 <i>CCD4</i>	编码区大片段缺失 Large fragment deletion in coding region	[77]

## 5 植物类胡萝卜素代谢途径中关键基因的转录调控

类胡萝卜素代谢调控一直是园艺植物研究的热点,而转录因子通过直接或间接调控植物类胡萝卜素代谢途径关键基因的表达量,影响类胡萝卜素的含量。在柑橘中,CsMADS5既可直接结合 *PSY*、*PDS*、*LCYB1* 的启动子,从而激活其转录,也可与 CsMADS6 形成增强子复合物,协同促进类胡萝卜素的积累,调控果实着色<sup>[80]</sup>;CsERF061 激活 *PSY1*、*PDS*、*CRTISO*、*LCYb1*、*BCH*、*ZEP*、*NCED3*、*CCD1* 和 *CCD4* 等9个关键类胡萝卜素途径基因的启动子,参与类胡萝卜素代谢的多靶点调节<sup>[81]</sup>。在番茄果实中证实,SIBBX20 可通过直接结合 *PSY1* 启动子中 G-box 基序激活类胡萝卜素生物合成关键酶基因的表达,从而导致类胡萝卜素水平升高<sup>[82]</sup>;再如 SIMYB72 与八氢番茄红素合成酶、胡萝卜素异构酶和番茄红素  $\beta$  环化酶基因结合,调控类胡萝卜素含量,使番茄果实呈现不均匀着色<sup>[83]</sup>。同时,在猕猴桃<sup>[84]</sup>、番木瓜<sup>[85]</sup> 等果实中,AdMYB7、CpMYB1/2 分别调控类胡萝卜素的合成,影响果实的风味与色泽。转录因子也调节类胡萝卜素裂解酶基因,导致园艺植物色泽和香气物质不同。桂花 ERF61<sup>[86]</sup> 和 WRKY3<sup>[87]</sup> 与 *OjCCD4* 启动子上的作用元件结合促进类胡萝卜素裂解双加氧酶基因的表达,调节花瓣中挥发性香气物质(如  $\beta$ -紫罗兰酮)的合成,从而导致品种间色泽和香气的差异。葡萄 MADS4 转录因子负调控 *VvCCD4b* 的表达,影响其主要香气成分(如  $\beta$ -大马士酮、 $\beta$ -紫罗兰酮及  $\alpha$ -紫罗兰酮等)<sup>[88]</sup>。此外,番茄果实成熟过程中,研究显示 RIN 也可激活与成熟相关的基因,间接促进类胡萝卜素的积累<sup>[89]</sup>。因此,转录因子调控类胡萝卜代谢通路的关键基因,对园艺植物色泽差异也具有重要作用。

## 6 展望

园艺植物与人们生活密切相关,色泽改良一直是园艺植物的重要育种目标之一。在柑橘、桃、葡萄、番茄、油菜等园艺植物及作物中,学者们已经逐渐探明类胡萝卜素代谢途径关键基因变异的分子机制,并在此基础上开发了一系列辅助育种分子标记。分子标记辅助育种可直接针对特定农艺性状对大量

杂交后代开展快速且精确的检测,大幅提高育种效率,具有重要的产业价值。

## 参考文献 References

- [1] HARRIS J R. Carotenoids in nature: biosynthesis, regulation and function[M]. Germany: Springer, 2016: 111-133.
- [2] SCHWEIGGERT R M, STEINGASS C B, HELLER A, et al. Characterization of chromoplasts and carotenoids of red and yellow-fleshed papaya (*Carica papaya* L.) [J/OL]. *Planta*, 2011, 234: 1031 [2022-03-15]. <https://doi.org/10.1007/s00425-011-1457-1>.
- [3] LU S W, ZHANG Y, ZHU K J, et al. The citrus transcription factor *CsMADS6* modulates carotenoid metabolism by directly regulating carotenogenic genes[J]. *Plant physiology*, 2018, 176: 2657-2676.
- [4] FANG X F, LIU S, GAO P, et al. Expression of *CIPAP* and *CIPSY1* in watermelon correlates with chromoplast differentiation, carotenoid accumulation, and flesh color formation[J/OL]. *Scientia horticulturae*, 2020, 270: 109437 [2022-03-15]. <https://doi.org/10.1016/j.scienta.2020.109437>.
- [5] FRASER P D, ENFISSI E M, GOODFELLOW M, et al. Metabolite profiling of plant carotenoids using the matrix-assisted laser desorption ionization time of flight mass spectrometry [J]. *Plant journal*, 2007, 49: 552-564.
- [6] WALTER M H, STRACK D. Carotenoids and their cleavage products: biosynthesis and functions[J]. *Natural product reports*, 2011, 28(4): 663-692.
- [7] KANTSA A, RAGUSO R A, DYER A G, et al. Community-wide integration of floral colour and scent in a Mediterranean scrubland[J]. *Nature ecology & evolution*, 2017, 1(10): 1502-1510.
- [8] DALL'OSTO L, CAZZANIGA S, BRESSAN M, et al. Two mechanisms for dissipation of excess light in monomeric and trimeric light-harvesting complexes[J/OL]. *Nature plants*, 2017, 3: 17033 [2022-03-15]. <https://doi.org/10.1038/nplants.2017.33>.
- [9] YUAN H, ZHANG J, NAGESWARAN D, et al. Carotenoid metabolism and regulation in horticultural crops[J/OL]. *Horticulture research*, 2015, 2: 15036 [2022-03-15]. <https://doi.org/10.1038/hortres.2015.36>.
- [10] MILANI A, BASIRNEJAD M, SHAHBAZI S, et al. Carotenoids: biochemistry, pharmacology and treatment [J]. *British journal of pharmacology*, 2017, 174(11): 1290-1324.
- [11] VARGAS-SINISTERRA A F, RAMÍREZ-CASTRILLÓN M. Yeast carotenoids: production and activity as antimicrobial biomolecule [J]. *Archives of microbiology*, 2021, 203(3): 873-888.
- [12] NISAR N, LI L, LU S, et al. Carotenoid metabolism in plants[J]. *Molecular plant*, 2015, 8: 68-82.
- [13] KATO M, IKOMA Y, MATSUMOTO H, et al. Accumulation of carotenoids and expression of carotenoid biosynthetic genes during maturation in citrus fruit[J]. *Plant physiology*, 2004, 134: 824-837.

- [14] LÜ P, LI N, LIU H, et al. Changes in crotenoid profiles and in the expression pattern of the genes in carotenoid metabolisms during fruit development and ripening in four watermelon cultivars [J]. Food chemistry, 2015, 74: 52-59.
- [15] ZHENG X J, ZHU K J, SUN Q, et al. Natural variation in *CCD4* promoter underpins species-specific evolution of red coloration in citrus peel [J]. Molecular plant, 2019, 12 (9): 1294-1307.
- [16] OHMIYA A. Qualitative and quantitative control of carotenoid accumulation in flower petals [J]. Scientia horticulturae, 2013, 204: 10-19.
- [17] BRANDI F, BAR E, MOURGUES F, et al. Study of 'Redhaven' peach and its white-fleshed mutant suggests a key role of *CCD4* carotenoid dioxygenase in carotenoid and norisoprenoid volatile metabolism [J/OL]. BMC plant biology, 2011, 11: 24 [2022-03-15]. <https://doi.org/10.1186/1471-2229-11-24>.
- [18] MERCADANTE A Z, RODRIGUEZ-AMAYA D B, BRITTON G. HPLC and mass spectrometric analysis of carotenoids from mango [J]. Journal of agricultural and food chemistry, 1997, 45: 120-123.
- [19] LIANG M H, SU X G, YANG Z F, et al. Carotenoid composition and expression of carotenogenic genes in the peel and pulp of commercial mango fruit cultivars [J/OL]. Scientia horticulturae, 2020, 263, 109072 [2022-03-15]. <https://doi.org/10.1016/j.scienta.2019.109072>.
- [20] RODRIGUEZ-URIBE L, GUZMAN I, RAJAPAKSE W, et al. Carotenoid accumulation in orange-pigmented *Capsicum annuum* fruit, regulated at multiple levels [J]. Journal of experimental botany, 2011, 63: 517-526.
- [21] 李全辉, 邵登魁, 李江, 等. 辣椒果实类胡萝卜素生物合成研究进展 [J]. 植物遗传资源学报, 2019, 20 (2): 239-248. LI Q H, SHAO D K, LI J, et al. Research progress of carotenoid biosynthesis in pepper fruit [J]. Journal of plant genetic resources, 2019, 20 (2): 239-248 (in Chinese with English abstract).
- [22] RODRIGUEZ-CONCEPCION M, STANGE C. Biosynthesis of carotenoids in carrot: an underground story comes to light [J]. Archives of biochemistry and biophysics, 2013, 539: 110-116.
- [23] 马帅, 王若凡, 陈霖, 等. 不同产地的两种橙色大白菜类胡萝卜素积累差异分析 [J]. 西北农业学报, 2021, 30 (3): 395-405. MA S, WANG R F, CHEN L, et al. Analysis of carotenoid accumulation differences between two kinds of chinese cabbage with orange head in different production areas [J]. Acta agriculturae boreali-occidentalis sinica, 2021, 30 (3): 395-405 (in Chinese with English abstract).
- [24] 刘晓丛. 不同花色万寿菊色素含量及类胡萝卜素代谢途径关键酶基因表达分析 [D]. 上海: 上海交通大学, 2017. LIU X C. Expression analysis of different pigment content and key enzymes of carotenoid metabolism gene of marigold [D]. Shanghai: Shanghai Jiaotong University, 2017 (in Chinese with English abstract).
- [25] ZHANG H, ZHANG S, ZHANG H, et al. Carotenoid metabolite and transcriptome dynamics underlying flower color in marigold (*Tagetes erecta* L.) [J/OL]. Scientific reports, 2020, 10 (1): 16835 [2022-03-15]. <https://doi.org/10.1038/s41598-020-73859-7>.
- [26] WANG Y G, ZHANG C, DONG B, et al. Carotenoid accumulation and its contribution to flower coloration of *Osmanthus fragrans* [J/OL]. Frontiers in plant science, 2018, 9: 1499 [2022-03-15]. <https://doi.org/10.3389/fpls.2018.01499>.
- [27] KISHIMOTO S A, OHMIYA A. Regulation of carotenoid biosynthesis in petals and leaves of chrysanthemum (*Chrysanthemum morifolium*) [J]. Physiologia plantarum, 2006, 128 (3): 436-447.
- [28] 黄昕蕾, 王雁, 张辉. 3种石斛属植物类胡萝卜素成分及代谢途径分析 [J]. 林业科学研究, 2019, 32 (5): 107-113. HUANG X L, WANG Y, ZHANG H. Analysis of carotenoids compounds and their biosynthesis pathways in flowers of three *Dendrobium* species [J]. Forest research, 2019, 32 (5): 107-113 (in Chinese with English abstract).
- [29] HIEBER A D, MUDALIGE-JAYAWICKRAMA R G, KUEHNLE A R. Color genes in the orchid oncidium gower ramsey: identification, expression, and potential genetic instability in an interspecific cross [J]. Planta, 2006, 223 (3): 521-531.
- [30] WANG L, ALBERT N W, ZHANG H, et al. Temporal and spatial regulation of anthocyanin biosynthesis provide diverse flower colour intensities and patterning in *Cymbidium* orchid [J]. Planta, 2014, 240 (5): 983-1002.
- [31] OHMIYA A. Diversity of carotenoid composition in flower petals [J]. Japan agricultural research quarterly, 2011, 45 (2): 163-171.
- [32] JEKNIĆ Z, MORRÉ J T, JEKNIĆ S, et al. Cloning and functional characterization of a gene for capsanthin-capsorubin synthase from tiger lily (*Lilium lancifolium* Thunb. 'Splendens') [J]. Plant and cell physiology, 2012, 53 (11): 1899-1912.
- [33] YAMAGISHI M, KISHIMOTO S, NAKAYAMA M. Carotenoid composition and changes in expression of carotenoid biosynthetic genes in tepals of Asiatic hybrid lily [J]. Plant breeding, 2010, 129 (1): 100-107.
- [34] XIA Y, CHEN W, XIANG W, et al. Integrated metabolic profiling and transcriptome analysis of pigment accumulation in *Lonicera japonica* flower petals during colour-transition [J/OL]. BMC plant biology, 2021, 21 (1): 98 [2022-03-15]. <https://doi.org/10.1186/s12870-021-02877-y>.
- [35] 郑雄杰. 柑橘果皮红色性状形成的生化基础及遗传机制 [D]. 武汉: 华中农业大学, 2018. ZHENG X J. The biochemical and genetic mechanism underlying red color trait of citrus peel [D]. Wuhan: Huazhong Agricultural University, 2018 (in Chinese with English abstract).
- [36] 曾祥玲. 桂花 *TPS* 和 *CCD* 功能分析及其对花瓣色香形成的影响研究 [D]. 武汉: 华中农业大学, 2015. ZENG X L. Research of *TPS* and *CCD* function analysis and their influence on petal color and scent in *Osmanthus Fragrans* Lour [D]. Wuhan: Huazhong Agricultural University, 2015 (in Chinese with English abstract).
- [37] MOISE A R, AL-BABILI S, WURTZEL E T. Mechanistic aspects of carotenoid biosynthesis [J]. Chemical reviews, 2014, 114: 164-193.
- [38] SATHASIVAM R, KI J S. A Review of the biological activities of microalgal carotenoids and their potential use in healthcare and cosmetic industries [J]. Marine drugs, 2018, 16 (1): 1856-1865.
- [39] ZHENG X, YANG Y, AL-BABILI S. Exploring the diversity and regulation of apocarotenoid metabolic pathways in plants [J/

- OL]. *Frontiers in plant science*, 2021, 12: 787049 [2022-03-15]. <https://doi.org/10.3389/fpls.2021.787049>.
- [40] LIANG M H, ZHU J H, JIANG J G. Carotenoids biosynthesis and cleavage related genes from bacteria to plants[J]. *Critical reviews in food science and nutrition*, 2018, 58 (14): 2314-2333.
- [41] SCHWARTZ S H, QIN X, ZEEVAART J A. Characterization of a novel carotenoid cleavage dioxygenase from plants[J]. *Journal of biological chemistry*, 2001, 276 (27): 25208-25211.
- [42] SIMKIN A J, SCHWARTZ S H, AULDRIDGE M, et al. The tomato carotenoid cleavage dioxygenase 1 genes contribute to the formation of the flavor volatiles  $\beta$ -ionone, pseudoionone, and geranylacetone[J]. *Plant journal*, 2004, 40: 882-892.
- [43] BALDERMANN S, KATO M, KUROSAWA M, et al. Functional characterization of a carotenoid cleavage dioxygenase 1 and its relation to the carotenoid accumulation and volatile emission during the floral development of *Osmanthus fragrans* Lour[J]. *Journal of experimental botany*, 2010, 61(11): 2967-2977.
- [44] ZHANG X S, PEI J J, ZHAO L G, et al. Overexpression and characterization of *CCD4* from *Osmanthus fragrans* and  $\beta$ -ionone biosynthesis from  $\beta$ -carotene *in vitro*[J]. *Journal of molecular catalysis A: chemical*, 2016, 134: 105-114.
- [45] HAN Y J, WANG H Y, WANG X D, et al. Mechanism of floral scent production in *Osmanthus fragrans* and the production and regulation of its key floral constituents,  $\beta$ -ionone and linalool[J/OL]. *Horticulture research*, 2019, 6: 106 [2022-03-15]. <https://doi.org/10.1038/s41438-019-0189-4>.
- [46] WANG J M, ZHANG N, ZHAO M Y. Carotenoid cleavage dioxygenase 4 catalyzes the formation of carotenoid-derived volatile beta-ionone during tea (*Camellia sinensis*) withering[J]. *Journal of agricultural and food chemistry*, 2020, 68(6): 1684-1690.
- [47] GIULIANO G, ROSATI C, BRAMLEY P M. To dye or not to dye: biochemistry of annatto unveiled[J]. *Trends biotechnol*, 2003, 21: 513-516.
- [48] PACHECO S D G, GASPARIN A T, JESUS C H A, et al. Antinociceptive and anti-inflammatory effects of bixin, a carotenoid extracted from the seeds of *Bixa orellana* [J]. *Planta medica*, 2019, 85(16): 1216-1224.
- [49] MA G, ZHANG L, MATSUTA A, et al. Enzymatic formation of  $\beta$ -citraurin from  $\beta$ -cryptoxanthin and zeaxanthin by carotenoid cleavage dioxygenase4 in the flavedo of citrus fruit[J]. *Plant physiology*, 2013, 163(2): 682-695.
- [50] RODRIGO M J, ALQUEZAR B, ALÓS E, et al. A novel carotenoid cleavage activity involved in the biosynthesis of citrus fruit-specific apocarotenoid pigments[J]. *Journal of experimental botany*, 2013, 64(14): 4461-4478.
- [51] BURBIDGE A, GRIEVE T M, JACKSON A, et al. Characterization of the ABA-deficient tomato mutant notabilis and its relationship with maize Vp14 [J]. *Plant journal*, 1999, 17 (4) : 427-431.
- [52] VALLABHANENI R, BRADBURY L, WURTZEL E T. The carotenoid dioxygenase gene family in maize, sorghum, and rice [J]. *Archives of biochemistry & biophysics*, 2010, 504 (1) : 104-111.
- [53] CHERNYS J T. Characterization of the 9-*cis*-epoxycarotenoid dioxygenase gene family and the regulation of abscisic acid biosynthesis in avocado[J]. *Plant physiology*, 2000, 124(1) : 343-353.
- [54] RODRIGO M J, ALQUEZAR B, ZACARÍAS L. Cloning and characterization of two 9-*cis*-epoxycarotenoid dioxygenase genes, differentially regulated during fruit maturation and under stress conditions, from orange (*Citrus sinensis* L. Osbeck) [J]. *Journal of experimental botany*, 2006, 57(3) : 633-643.
- [55] 朱海生, 李永平, 花秀凤, 等. 草莓9-顺式-环氧类胡萝卜素双加氧酶基因 *FaNCED* 的克隆及表达分析[J]. *园艺学报*, 2012, 39(1): 40-48. ZHU H S, LI Y P, HUA X F, et al. Cloning and expression analysis of 9-*cis*-epoxycarotenoid dioxygenase gene *FaNCED* in strawberry [J]. *Acta horticulturae sinica*, 2012, 39 (1): 40-48 (in Chinese with English abstract).
- [56] JIA H F, CHAI Y M, LI C L, et al. Abscisic acid plays an important role in the regulation of strawberry fruit ripening [J]. *Plant physiology*, 2011, 157(1): 188-199.
- [57] RONEN G, CARMEL-GOREN L, ZAMIR D, et al. An alternative pathway to  $\beta$ -carotene formation in plant chromoplasts discovered by map-based cloning of beta and old-gold color mutations in tomato[J]. *PNAS*, 2000, 97: 11102-11107.
- [58] NEUMAN H, GALPAZ N, ZAMIR D, et al. The tomato mutation *nxd1* reveals a gene necessary for neoxanthin biosynthesis and demonstrates that violaxanthin is a sufficient precursor for abscisic acid biosynthesis[J]. *Plant journal*, 2014, 78: 80-93.
- [59] MARCO A, PAOLO F, FEDERICA B, et al. Identifying a carotenoid cleavage dioxygenase (*CCD4*) gene controlling yellow/white fruit flesh color of peach[J]. *Plant molecular biology reporter*, 2013, 31 (5): 1166-1175.
- [60] ZHANG J, YUAN H, FEI Z, et al. Molecular characterization and transcriptome analysis of orange head Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*) [J]. *Planta*, 2015, 241: 1381-1394.
- [61] ZHANG B, LIU C, WANG Y, et al. Disruption of a carotenoid cleavage dioxygenase 4 gene converts flower colour from white to yellow in *Brassica* species [J]. *New phytologist*, 2015, 206: 1513-1526.
- [62] HAN F Q, CUI H L, ZHANG B, et al. Map-based cloning and characterization of *BoCCD4*, a gene responsible for white/yellow petal color in *B. oleracea* [J/OL]. *BMC genomics*, 2019, 20: 242 [2022-03-15]. <https://doi.org/10.1186/s12864-019-5596-2>.
- [63] YAN C H, HUANG Y, LIU Z X, et al. Rapid identification of yellow-flowered gene *Bofc* in cauliflower (*Brassica oleracea* var. *botrytis*) by bulked segregant analysis and whole-genome resequencing [J/OL]. *Euphytica*, 2020, 216: 26 [2022-03-15]. <https://doi.org/10.1007/s10681-020-2560-9>.
- [64] RACHELE F, ELISA V, LAURA Z, et al. Three distinct mutational mechanism acting a single gene underpin the origin of yellow flesh in peach[J]. *Plant journal*, 2013, 76: 175-187.
- [65] YOSUKE F, TAKAYUKU T, SEISUKE H, et al. Mutations in the *CCD4* carotenoid cleavage dioxygenase gene of yellow-flesh peaches[J]. *Bioscience biotechnology and biochemistry*, 2013, 77 (12): 2514-2516.
- [66] MA J J, LI J, ZHAO J B, et al. Inactivation of a gene encoding carotenoid cleavage dioxygenase (*CCD4*) leads to carotenoid-



- based yellow coloration of fruit flesh and leaf midvein in peach [J]. *Plant molecular biology reporter*, 2014, 32(1): 246-257.
- [67] 范家琪, 吴金龙, 李勇, 等. 桃类胡萝卜素合成关键基因 *PpCCD4* 的表达与启动子活性分析[J]. *果树学报*, 2020, 37(9): 1271-1280. FAN J Q, WU J L, LI Y, et al. Expression and promoter activity analysis of *PpCCD4* closely related to carotenoid synthesis in peach[J]. *Journal of fruit science*, 2020, 37(9): 1271-1280(in Chinese with English abstract).
- [68] DEVITT L C, FANNING K, DIETZGEN R G, et al. Isolation and functional characterization of a lycopene beta-cyclase gene that controls fruit colour of papaya (*Carica papaya* L.) [J]. *Journal of experimental botany*, 2010, 61: 33-39.
- [69] XU X M, LUO W L, GUO J X, et al. Fine mapping and candidate gene analysis of the yellow petal gene *ckpc* in Chinese kale (*Brassica oleracea* L. var. *alboglabra* Bailey) by whole-genome resequencing[J/OL]. *Molecular breeding*, 2019, 39: 96 [2022-03-15]. <https://doi.org/10.1007/s11032-019-1011-6>.
- [70] ZHANG B, HAN F Q, CUI H L, et al. Insertion of a CACTA-like transposable element disrupts the function of the *BoCCD4* gene in yellow-petal Chinese kale [J/OL]. *Molecular breeding*, 2019, 39: 130 [2022-03-15]. <https://doi.org/10.1007/s11032-019-1008-1>.
- [71] HUH J, KANG B, NAHM S, et al. A candidate gene approach identified phytoene synthase as the locus for mature fruit color in red pepper (*Capsicum* spp.) [J]. *Theoretical and applied genetics*, 2001, 102: 524-530.
- [72] ARANGO J, JOURDAN M, GEOFFRIAU E, et al. Carotene hydroxylase activity determines the levels of both alpha-carotene and total carotenoids in orange carrots [J]. *Plant cell*, 2014, 26: 2223-2233.
- [73] WELSCH R, ARANGO J, BAR C, et al. Provitamin A accumulation in cassava (*Manihot esculenta*) roots driven by a single nucleotide polymorphism in a phytoene synthase gene [J]. *Plant cell*, 2010, 22(10): 3348-3356.
- [74] ARIIZUMI T, KISIMOTO S, KAKAMI R, et al. Identification of the carotenoid modifying gene *PALE YELLOW PETAL 1* as an essential factor in xanthophyll esterification and yellow flower pigmentation in tomato (*Solanum lycopersicum*) [J]. *The plant journal*, 2014, 79: 453-465.
- [75] HARJES C E, ROCHEFORD T R, BAI L, et al. Natural genetic variation in *lycopene epsilon cyclase* tapped for maize biofortification[J]. *Science*, 2008, 319: 330-333.
- [76] BODIN P, KEIICHI W, SHINJI M, et al. Expression of *CCD4* gene involved in carotenoid degradation in yellow-flowered *Petunia × hybrida*[J]. *Scientia horticulturae*, 2020, 261: 8-18.
- [77] SUMITOMO K, SHIRASAWA K, ISOBE S, et al. Genome-wide association study overcomes the genome complexity in auto-hexaploid chrysanthemum and tags SNP markers onto the flower color genes [J/OL]. *Scientific reports*, 2019, 9: 13947 [2022-03-15]. <https://doi.org/10.1038/s41598-019-50028-z>.
- [78] GONZALEZ-JORGE S, HA S H, MAGALLANES-LUNDBACK M, et al. Carotenoid cleavage dioxygenase 4 is a negative regulator of beta-carotene content in *Arabidopsis* seeds [J]. *Plant cell*, 2013, 25: 4812-4826.
- [79] GONZALEZ-JORGE S, MEHRSHAHI P, MAGALLANES-LUNDBACK M, et al. Zeaxanthin epoxidase activity potentiates carotenoid degradation in maturing *Arabidopsis* seed [J]. *Plant physiology*, 2016, 171: 187-1851.
- [80] LU S, YE J, ZHU K, et al. A fruit ripening-associated transcription factor CsMADS5 positively regulates carotenoid biosynthesis in citrus [J]. *Journal of experimental botany*, 2021, 72(8): 3028-3043.
- [81] ZHU K, SUN Q, CHEN H, et al. Ethylene activation of carotenoid biosynthesis by a novel transcription factor CsERF061 [J]. *Journal of experimental botany*, 2021, 72(8): 3137-3154.
- [82] XIONG C, LUO D, LIN A, et al. A tomato B-box protein *S/B-BX20* modulates carotenoid biosynthesis by directly activating *PHYTOENE SYNTHASE 1*, and is targeted for 26S proteasome-mediated degradation [J]. *New phytologist*, 2019, 221(1): 279-294.
- [83] WU M, XU X, HU X, et al. *S/MYB72* regulates the metabolism of chlorophylls, carotenoids, and flavonoids in tomato fruit [J]. *Plant physiology*, 2020, 183(3): 854-868.
- [84] AMPOMAH-DWAMENA C, THRIMAWITHANA A H, DENOPRAT S, et al. A kiwifruit (*Actinidia deliciosa*) R2R3-MYB transcription factor modulates chlorophyll and carotenoid accumulation [J]. *New phytologist*, 2019, 221(1): 309-325.
- [85] FU C, CHEN H, GAO H, et al. Two papaya MYB proteins function in fruit ripening by regulating some genes involved in cell-wall degradation and carotenoid biosynthesis [J]. *Journal of the science of food and agriculture*, 2020, 100(12): 4442-4448.
- [86] HAN Y, WANG H, WANG X, et al. Mechanism of floral scent production in *Osmanthus fragrans* and the production and regulation of its key floral constituents,  $\beta$ -ionone and linalool [J/OL]. *Horticulture research*, 2019, 6: 106 [2022-03-15]. <https://doi.org/10.1038/s41438-019-0189-4>.
- [87] HAN Y, WU M, CAO L, et al. Characterization of *OfWRKY3*, a transcription factor that positively regulates the carotenoid cleavage dioxygenase gene *OfCCD4* in *Osmanthus fragrans* [J]. *Plant molecular biology*, 2016, 91(4/5): 485-496.
- [88] MENG N, WEI Y, GAO Y, et al. Characterization of transcriptional expression and regulation of carotenoid cleavage dioxygenase 4b in grapes [J/OL]. *Frontiers in plant science*, 2020, 11: 483 [2022-03-15]. <https://doi.org/10.3389/fpls.2020.00483>.
- [89] SLUGINA M A, EFREMOV G I, SHCHENNIKOVA A V, et al. Characterization of *RIN* isoforms and their expression in tomato fruit ripening [J/OL]. *Cells*, 2021, 10(7): 1739 [2022-03-15]. <https://doi.org/10.3390/cells10071739>.

## Progress on studying color difference of horticultural plants caused by gene variation of carotenoid metabolic pathway

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**Abstract** Carotenoids are secondary metabolites and pigments widely existed in horticultural plants. They play an important role in the growth and development of plants and ornamental value. It is also a natural active substance with high-value, which is beneficial to human health. Therefore, the metabolic regulation of carotenoids has always been a research hotspot in horticultural plants. The differences in the components and contents of carotenoid are one of the important reasons for the diversity of color and nutritional value of horticultural plants. Analyzing the molecular mechanism of the formation of high-quality traits is the premise and basis for directional improvement. To date, the metabolic pathway of plant carotenoids has been clarified. A large number of studies have shown that mutations of promoters and coding regions in metabolic pathways are the key factors causing the diversity of carotenoid metabolism. This article reviewed the strategies of studying the genetic mechanism of carotenoid variation in horticultural plants, the types of variation in promoters and coding regions, and the effects of variation on carotenoid metabolism. It will provide a theoretical basis for the directional improvement of carotenoids in horticultural plants.

**Keywords** carotenoid; plant color; genetic variation; transcription regulation; molecular marker assisted breeding

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