

## 柑橘果实色素—类胡萝卜素的进展

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**摘要:**柑橘果实丰富多彩, 广受大众喜爱, 外观色泽作为消费者选择看重的果实品质之一, 其研究就显得格外重要。类胡萝卜素是柑橘果实呈色的主要贡献者, 成为近年来柑橘果实色素研究的重点。类胡萝卜素包括胡萝卜素和叶黄素两大类, 不同的色素单体呈现黄到橙红甚至紫红多种颜色, 其丰富多样的组成给与柑橘果实丰富的颜色表现。笔者概述了柑橘果实呈色色素的主要来源、内外部及其他影响因素、3条合成途径(番茄红素、胡萝卜素和含氧类胡萝卜素生物合成), 并介绍了类胡萝卜素对植物体和人体的生理活性功能, 但目前对类胡萝卜素的分解过程以及分解产物存在形式和生理功能的研究较少, 有待进一步深入开展。

**关键词:**柑橘; 果实; 色泽; 类胡萝卜素

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### Advance study of pigment-carotenoids in *Citrus* fruits

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**Abstract:** The varieties of Citrus fruits such as *Citrus sinensis* (orange), *Citrus reticulata* (mandarin), *Citrus limon* (lemon), *Citrus grandis* (pomelo) and *Citrus paradise* (grapefruit) gained massive popularity around the world. The United Nations Commodity Trade Statistics Database revealed that the international consumption of wide-skinned citrus increased from less than 9 million tons to 37 million tons from 2000 to 2016. Nevertheless, 2011, the total export of China was 6157.975 million dollars, only accounting for 5.52 percent of the international citrus market, which is extremely disproportionate to the place of China named major producer of citrus. After entering WTO, the international and domestic markets have put forward higher requirements for fresh citrus fruits quality. The commercial value of citrus fruit primarily involves external quality, including color and rind conditions, and internal quality that was determined by the content of sugar and organic acids, the ratio of sugar/acid, texture and digesting residue degree and others nutritional components. Now “beautiful” is not only a single adjective for people, but also the first factor to be considered of gourmet fruits. Especially in developed country, appearance and color are the most valued qualities by consumers, hence the research of citrus peels pigment shows great significance and urgency. The critical pigments in the peels of immature citrus fruit are caused by the presence of chlorophylls, which exhibit green color, whereas the predominant colorations of bright yellow, orange and red in the peels of mature citrus fruit which closely related with carotenoids composition and proportion. The carotenoids are terpenoids synthesized in plastids of leaves,

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endosperm, and roots, which include hydrocarbons (carotenes) and oxygenated derivatives (xanthophylls). The former consists of  $\xi$ ,  $\alpha$ ,  $\beta$ ,  $\delta$ -carotene, lycopene and their isomers, while the later include lutein, zeaxanthin, violaxanthin and  $\beta$ -cryptoxanthin and  $\beta$ -citraurin. In different growing conditions of citrus fruits, those compositions of carotenoids mixed in varying proportions that create richer color. In colored fruits, epoxy and hydroxylated carotenoids are the major components and account for up to 80% of total carotenoids. Therefore, “why accumulate?” and “what’s the function of carotenoids for plants?”. In higher plants, carotenoids are essential components of the photosynthetic apparatus, when exposed to high irradiance, it’s the supernumerary protector to dissipate excess light energy absorbed by the antenna pigments, harvest light for photosynthesis, and the colorful flower and fruits for carotenoids attract pollinators and agents of seed dispersal. Actually, many carotenoids are beneficial to human and animals, for its antioxidants, decreasing the risk of cancer, protecting vision. There is a new proof that ample dose of carotenoids applied to pregnant woman in daily foods can reduce anemia risk. However, the color of citrus fruits is not stable, there are many factors impact citrus pigments formation in maturation stages, mainly dividing into three parts: inhesion, outer and others. The inhesion related to citrus plant development stages, the structure gene expression in the pathway of carotenoids, the genes of regulation and light signal transduction expression level, the formation and number of plastids that pigments biosynthesis developed and the contents of endogenous hormones. The outer factors of carotenoids synthesis contain: light intensity, temperature, humidity, soil nutrition and infection of bacteria and fungi. And the third was expanded by people when they did different treatments on fruits in different stages to find out the influence factors or metabolization, which include proteins synthesis inhibitor applied, such as CPTA and MPTA (lycopene cyclase inhibitor), different sugar solution daubing, and different exogenous hormone spraying. Until now, more than 150 carotenoid synthase genes have been isolated from nature, which encode more than 20 key enzymes in the biosynthesis pathway, respectively. The pathway own three branches: lycopene, carotene and xanthophylls biosynthesis. The first committed step in the carotenoid pathway is the synthesis of phytoene, catalyzed by the enzyme PSY, which is the key limiting enzyme to control the synthesis speed. In the citrus plant, PSY has three transcripts and show tissue specificity, the *PSY1* mainly expressed in fruits, the *PSY2* increased expressed in green tissue, the *PSY3* only expressed in root. In the next steps, proteins PDS and ZDS catalyzed the colorless phytoene into red lycopene. The carotene formation carried out by protein cyclase *LCYb* and *LCYe*, which catalyzed precursors lycopene into  $\alpha$ ,  $\beta$ , -carotene. There is a proof that no  $\alpha$ -carotene accumulation for 14 bp nucleotides deletion of *LCYe* at DNA molecular level in Cara Cara. Well, the xanthophylls biosynthesis pathway contains three kinds of enzymes: hydroxylase (HYb, HYe), carotenoid cleavage dioxygenases (CCDs) and 9-cis-epoxycarotenoid dioxygenases (NCEDs). Those enzymes catalyzed and formed richer carotenoids together. Besides that, the biosynthesis in plants is connected with the plant regulator abscisic acid (ABA), which produced through  $C_{15}$  intermediates after oxidative cleavage of specific xanthophylls. Based on previous studies, we found these aspects will still attract our eyes, which include mutating key site of the structure genes to explore why the different citrus plants show distinct function; the interaction between transcript factors with structure genes; epigenetic regulation mechanism of carotenoids accumulation; the ligation with anthocyanin formation; and related omics of citrus fruits. Whereas, the related flavor and aroma released by carotenoids degradation products that impact fruit value in citrus are still unclear, maybe the work should be spotlighted.

**Key words:** *Citrus*; Fruits; Color and pigment; Carotenoids

## 1 柑橘果皮色泽研究的重要性

柑橘(*Citrus*)是我国南方栽培面积最广、经济地位最重要的果树之一,拥有多种深受人们喜爱的商品性水果,如:甜橙(*Citrus sinensis*)、橘(*Citrus reticulata*)、柠檬(*Citrus limon*)、柚(*Citrus grandis*)、葡萄柚(*Citrus paradisi*)等<sup>[1-2]</sup>。据国家统计局数据显示,2016—2017年我国橘、橙的出口额由1 036.79百万美元下降至835.97百万美元,出口数量由723 683 t下降至561 681 t(<http://data.stats.gov.cn/search.htm?s=橘橙>),销售单价却逐年上升,数据反应我国柑橘的出口面临很大压力<sup>[3-4]</sup>。加入WTO后,国际国内市场对柑橘品质提出了更高要求,外观品质日益受到重视,消费者会从果品的色泽,风味以及营养物质等方面综合考虑选择消费<sup>[5]</sup>。单价较高的情况下,提升果品质量是应对外在压力有效措施之一。提高果品质量需从内质和外观两个方面着手,内质主要是糖、酸含量、糖酸比、化渣程度、纤维含量、果汁多少及果汁中类胡萝卜素、维生素和其他营养物质的含量;外观品质包括果实色泽、大小、形状及整齐度等<sup>[6]</sup>。

目前,“好看”不只是针对人的形容词,美食三大基本要求之首的——“色”也是被最先考虑的因素。传统地说,消费者一方面会结合果皮的红黄程度、亮度、以及色素是否均匀来挑选;另一方面也会结合果肉的色泽和新鲜程度综合考虑。果皮由绿变黄,标志着果实完全成熟,也作为外观品质指标,直接影响柑橘商品价值,关乎价格的高低<sup>[7]</sup>,因而柑橘果实色泽的研究是目前重要的且急迫的任务。笔者从柑橘成熟期果实色素-类胡萝卜素的组成、调控呈色影响因素、以及类胡萝卜素的生理功能等方面进行综述,并对柑橘类胡萝卜素待深入研究的方面进行展望,为后期研究柑橘果实色泽相关的研究人员提供基础理论参考。

## 2 柑橘果实呈色色素概论

柑橘类果实的红色色素有两种来源:脂溶性类胡萝卜素和水溶性花青素<sup>[8]</sup>。柑橘果实发育成熟过程中,果皮因类胡萝卜素和花青素以及叶绿素分配比例的差异,表现出不同的色泽,从绿色、黄色、橙色到橙红色各不相同。自然界存在的类胡萝卜素有750多种,且平均每年都会发现20多种新的类胡

萝卜素成分<sup>[9]</sup>,其中柑橘体内至少含有115种<sup>[10]</sup>,2016年在柑橘内又分离出几十种,包括8种类胡萝卜素单体,34种单酯和33种双酯<sup>[11]</sup>。类胡萝卜素是一类镶嵌于叶绿体和有色体内的天然色素,包括胡萝卜素和叶黄素<sup>[12]</sup>。胡萝卜素是碳氢化合物,包括脱落酸(ABA)合成途径上的中间产物 $\xi$ 、 $\alpha$ 、 $\beta$ 、 $\delta$ -胡萝卜素和番茄红素以及它们的同分异构体等;叶黄素是胡萝卜素的氧化衍生物,主要包括叶黄素、 $\beta$ -隐黄质、玉米黄素、环氧玉米黄素、紫黄质和 $\beta$ -柠乌素等<sup>[13-14]</sup>。柑橘果实主要积累叶黄素,果皮是类胡萝卜素积累的主要部位,通常果皮比果肉类胡萝卜素含量高2.5~15倍<sup>[15]</sup>,王伟杰<sup>[16]</sup>通过HPLC技术测定宫内伊予柑果皮色素的组成和含量,发现宫内伊予柑果皮中以玉米黄素、 $\beta$ -隐黄质两种色素为主, $\beta$ -胡萝卜素含量不足类胡萝卜素的1%, $\alpha$ -胡萝卜素极低<sup>[17]</sup>。近期Gang等<sup>[18]</sup>在研究一种新的栽培种脐橙‘Seinan-nohikari’(*Citrus* spp.)的成熟过程果皮和汁胞类胡萝卜素合成途径中发现果皮和汁胞存在大量类胡萝卜素,尤其是 $\beta$ -隐黄质,比来自母本的温州蜜柑‘Miyagawa-wase’(*Citrus unshiu*)高2.5倍。关于紫黄质的研究,近期也有进展,Kato等<sup>[19]</sup>以紫黄质含量不同水平的柚、温州蜜柑、脐橙为材料,研究发现紫黄质含量与剪切双加氧基因(*CitCCD1*, *CitNCED2*和*CitNCED3*)的表达量具有明显的联系。 $\beta$ -柠乌素则被证实是朱红橘等果实后期呈现红色的主要贡献色素<sup>[20-21]</sup>。除了之前的红外光谱对果皮色泽的检测,随着拉曼光谱的推广,拉曼也应用到水果色泽和新鲜度检测上,检测数值对于观众的消费引导具有强烈影响<sup>[22]</sup>。

## 3 柑橘果实呈色的影响因素

在植物体内,类胡萝卜素的合成受到外部环境:光、温湿度等,内部因素:特定的细胞器官、不同的发育时期、相关结构基因表达、调控和光信号转导有关基因或转录因子、有色体的分化和形成以及数量的多少等多种因素共同调控<sup>[23]</sup>。

### 3.1 外部影响因素

光照强度对叶黄素循环(玉米黄素 $\longleftrightarrow$ 环氧玉米黄质 $\longleftrightarrow$ 紫黄质)有较大的影响,在弱光或黑暗环境下玉米黄素环氧酶(ZEP)活性较高,玉米黄素向紫黄质转化;而在强光条件下则刚好相反,紫黄质脱环氧酶(VDE)活性较高,紫黄质向玉米黄素转化,消耗

多余光能,保护光合组织不受强光伤害<sup>[24-26]</sup>。适当增加光照强度可以有效提高柑橘果实可溶性糖和类胡萝卜素的量,减少有机酸<sup>[27]</sup>。套袋遮光一段时间实验表明柑橘果肉中糖类、维生素C、以及微量元素均显著减少,而在采摘前期去套袋,橙红色色素 $\beta$ -隐黄质含量显著升高,后期光照有助于类胡萝卜素的合成,有利于改善果皮外观色泽,提高商业价值<sup>[28]</sup>。光质对植物类胡萝卜素代谢也有影响,研究表明柑橘采后用红光照射能促进果实红色色泽加深,HPLC分析表明,红光提高果实中各种类胡萝卜素组分的含量,其中有 $\beta$ -隐黄质和番茄红素峰值增加明显<sup>[29-30]</sup>。Deng等<sup>[31]</sup>发现10 h 450 nm LED蓝光照射果实,可以显著降低果实绿色,猜测蓝光诱导的柑橘增强了果实对乙烯的敏感性,进而导致颜色加深变黄。温度对柑橘类胡萝卜素的合成也起着关键作用,Ladaniya<sup>[32]</sup>研究发现,10~15 °C最有利于柑橘果实中类胡萝卜素的合成,高温使柑橘果皮类胡萝卜素严重降解,含量不断降低<sup>[33]</sup>,温度过低则易发生冷害,导致果实外观品质下降<sup>[34]</sup>。其他因素包括水肥营养、土壤结构对柑橘果皮色素的形成也有一定的影响。

### 3.2 内部影响因素

调控柑橘类胡萝卜素合成的内部因素包括:直接调控结构基因的表达,调控和光信号转导有关基因,转录因子对结构基因的间接调控、色素合成场所所有染色体的分化、形成以及数量的多少和内源激素不同水平的影响。Kato等<sup>[19]</sup>和Rodrigo等<sup>[35]</sup>研究发现:在温州蜜柑和伏令夏橙成熟过程中,和类胡萝卜素合成相关的基因:八氢番茄红素合成酶(*Psy*),八氢番茄红素脱氢酶(*Pds*), $\xi$ -胡萝卜素脱氢酶(*Zds*),番茄红素 $\beta$ -环化酶(*Lcyb*), $\beta$ -胡萝卜素羟化酶(*HYb*)和玉米黄质环化酶(*Zep*)的表达量逐渐上升,而支路的剪切双加氧酶基因(*CCD1*,*NCED2*,*NCED3*)表达水平逐渐降低<sup>[19-20,36]</sup>如图1。光照是一个重要的环境因素,其影响相关的光信号转导转录因子的表达,转录因子又影响结构基因的表达。类胡萝卜素合成酶基因由核基因编码,翻译成蛋白质后转运至质体,主要存在于质体膜上,形成色素蛋白质膜复合体,其分化和形成对类胡萝卜素的量也起到关键作用<sup>[37-38]</sup>。内源激素赤霉素(GA)和脱落酸ABA对果实转色,也有显著性影响。GA含量在果实膨大期迅速下降,并于果实转色前下降到最低值,以后维持较低水平,

ABA经过2次迅速上升,并于果实转色前达到最大,进入转色期,ABA含量迅速下降,成熟期维持较高水平<sup>[39]</sup>。

### 3.3 其他影响因素

番茄红素环化酶抑制剂(CPTA和MPTA)具有类似于除草剂的作用,可以阻断杂草类胡萝卜素的合成并干扰其正常光合作用,王永<sup>[40]</sup>就两种抑制剂对柑橘类果实类胡萝卜素代谢的影响做了深入的研究,发现CPTA和MPTA均可以诱导番茄红素的生成,低浓度的MPTA较低浓度的CPTA作用效果更明显。‘宫川’储存过程中,不同质量浓度(0.1%、0.5%、1.0%,w/v)的4种不同糖分(葡萄糖、甘露醇、果糖、蔗糖)溶液涂膜处理,结果发现,不同浓度的4种糖分均促进叶绿素褪去,并有利于类胡萝卜素显现和形成<sup>[41]</sup>。乙烯处理提前采摘的柑橘,能加速叶绿素的降解,但叶绿素降解相关基因(*Citchlase*,*CitCAB1*和*CitCAB2*)的表达量显著降低,可能主要是因为叶绿素b还原酶基因*CitNYC*表达量上升<sup>[7]</sup>。外施GA<sub>3</sub>处理除了延缓果皮叶绿素的降解,外施ABA加速叶绿素的降解,但两种处理均抑制果皮类胡萝卜素的合成<sup>[42-43]</sup>,因而外施ABA或者GA<sub>3</sub>均不利于果实色泽品质的提高。

3.3.1 柑橘果皮色素合成途径主要酶及其基因的研究进展 从自然界中分离出150多个类胡萝卜素合成酶基因,他们分别编码合成途径上20多种关键酶,柑橘成熟过程类胡萝卜素合成代谢途径见图1。

3.3.2 番茄红素生物合成 合成前体异戊烯焦磷酸(IPP)在八氢番茄红素合成酶(PSY)的催化下形成八氢番茄红素,PSY是类胡萝卜素合成上游关键的调节酶,也是一个限速酶,其是类胡萝卜素合成途径上研究的最为透彻的一个酶<sup>[44]</sup>。1991年从番茄果实中证实分离出第一条PSY基因(登录号:P08196)<sup>[45]</sup>,目前已登陆NCBI的PSY基因在拟南芥(登录号:P37271)、玉米(登录号:AY773475,AY773476,DQ356430)、辣椒(登录号:X68017)、油菜(登录号:XP013649804)和柑橘(登录号:AB114656)<sup>[46]</sup>等20多种植物中都被克隆;多基因编码使其在不同植物体内有多个转录本存在:拟南芥中有1个,烟草有2个,玉米、水稻、番茄、油菜和柑橘则含有3个转录本<sup>[47]</sup>。不同的转录本在不同的组织种特意表达,PSY1在果实特异性表达<sup>[48]</sup>,PSY2在绿色组织中大量表达<sup>[49]</sup>,PSY3则仅在根中表达<sup>[50]</sup>,PSY3在干旱等胁迫

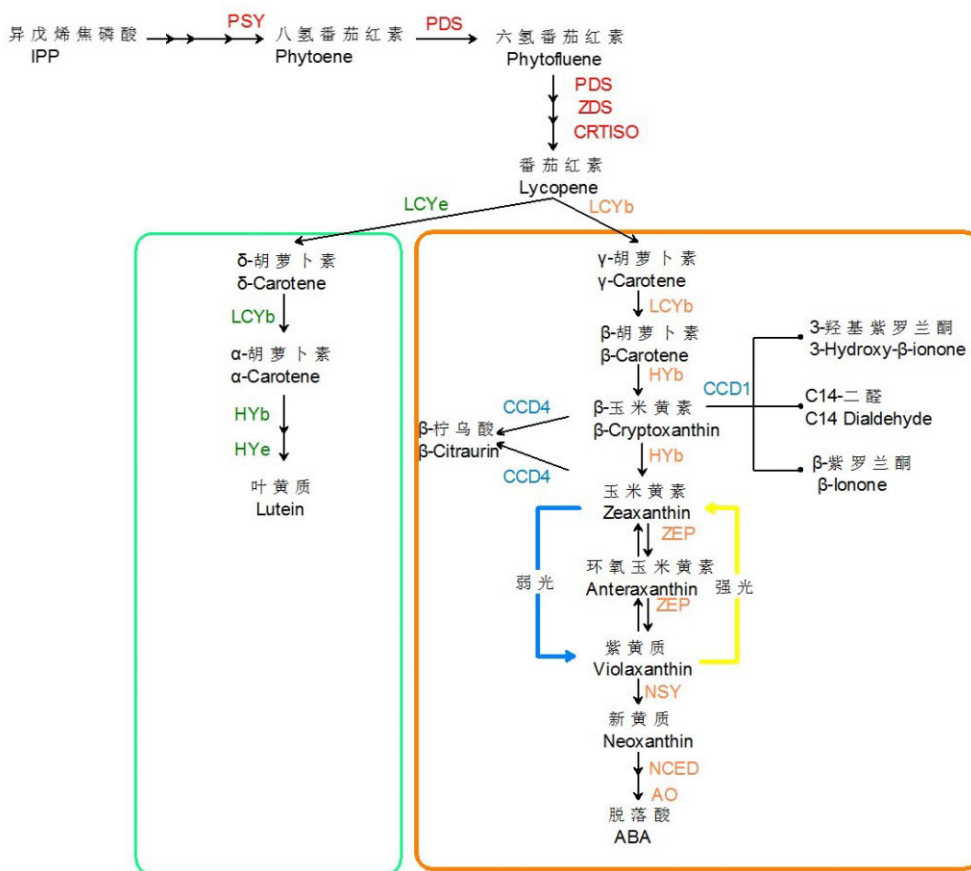


图1 高等植物类胡萝卜素合成代谢途径<sup>[40]</sup>  
 Fig. 1 Carotenoid biosynthetic pathway in higher plants<sup>[40]</sup>

迫条件下接受ABA的诱导表达,在根中生成其他类胡萝卜素代谢产物<sup>[51]</sup>。

无色八氢番茄红素经过八氢番茄红素脱氢酶PDS、 $\xi$ -胡萝卜素脱氢酶(ZDS)催化脱氢和类胡萝卜素异构酶(CRISO)催化异构形成红色番茄红素。2001年Kita首次从柑橘中分离出PDS1(登录号:AB046992)<sup>[52]</sup>,并检测了PDS1在果肉和果皮部位的表达,发现其在果皮的表达量显著高于果肉,Kato等<sup>[46]</sup>首次克隆了柑橘ZDS(登录号:NP\_001275793),发现在柑橘成熟期,ZDS表达量逐渐增加并且达到最高表达水平并保持。CRISO是催化类胡萝卜素顺反结构转化的关键酶<sup>[53]</sup>,CRTISO催化异构反应需要FAD(黄素腺嘌呤二核苷酸)的存在<sup>[50]</sup>,拟南芥叶片中的顺式异构体在光下发生异构反应,但番茄叶片CRTISO酶是必需的,光照不是异构化发生的必需因素<sup>[54-55]</sup>。近期关于柑橘CRTISO基因的研究有了新进展,利用一种导入柑橘全基因组但缺乏CRTISO基因的番茄工程植株,将CRTISO基因回补,发现回补植株果实和未敲除的果实对照颜色相

似,直接证明了柑橘CRTISO基因的功能,补充了柑橘CRTISO基因研究的空白<sup>[56]</sup>。

3.3.3 胡萝卜素生物合成 番茄红素环化是类胡萝卜素合成途径上的关键分界点,由 $\beta$ -环化酶(LCYb)和 $\epsilon$ -环化酶(LCYe)控制<sup>[57-58]</sup>。番茄红素的环化通常发生于两个 $\beta$ -环末端(如 $\beta$ -胡萝卜素)或者一个 $\epsilon$ -环和一个 $\beta$ -环末端(叶黄素)。番茄红素环化酶基因最初在拟南芥中克隆,LCYb(登录号:Z29211)和LCYe(登录号:U58919)均以单克隆的形式存在,两者具有较高的同源性(36%)。随后相继在辣椒(登录号:X86221)、番茄(登录号:X86452)、烟草(登录号:X81787)中都分离出LCYb,Ronen等<sup>[59]</sup>发现番茄LCYb存在两个拷贝,且均能调控番茄红素的合成。前人在‘红肉脐橙’和‘华盛顿脐橙’中克隆出有两个不同的 $\beta$ -环化酶,命名为Cs $\beta$ -LCY1和Cs $\beta$ -LCY2,这两个环化酶均为单拷贝<sup>[60-61]</sup>。Berta等<sup>[62]</sup>从甜橙中也克隆了两条LCY,研究发现Cs $\beta$ -LCY1在植物体内表达量始终保持在较低水平,而Cs $\beta$ -LCY2在甜橙积累类胡萝卜素时期呈现出显著的上调趋势,猜测

*Csβ-LCY2* 基因在有色体内表现特异性。Kato 等<sup>[66]</sup>在研究柑橘果实成熟时发现, *LCYb* 表达增强, *LCYe* 表达减弱,  $\beta$ -隐黄质、玉米黄素和紫黄质大量增加。Mendes 等<sup>[63]</sup>证实 *LCYb2* 的表达是导致红肉和白肉葡萄柚表型差异的关键影响因素。Tao 等<sup>[64]</sup>从不含有  $\alpha$ -胡萝卜素的脐橙突变体中分离出 *LCYe*, 基因序列分析显示该突变体的  $\epsilon$ -环化酶 *LCYe* DNA 水平上有 14 个碱基的缺失, 因此 *LCYe* 的表达被终止, 导致该脐橙中无  $\alpha$ -胡萝卜素积累。

3.3.4 含氧类胡萝卜素的生物合成 含氧类胡萝卜素统称为叶黄素(xanthophylls), 包括以  $\alpha$ -胡萝卜素为底物生成的叶黄质<sup>[65]</sup>和以  $\beta$ -胡萝卜素为底物衍生的  $\beta$ -隐黄质和玉米黄质、环氧玉米黄素、紫黄质和新黄质<sup>[66-67]</sup>。

这两个支路涉及到的主要关键酶有羟化酶(HYb 和 HYe), 玉米黄素环氧酶和裂解双氧合酶(CCDs 和 NCEDs), 如图 1 所示<sup>[19, 68]</sup>。HYb 羟化酶催化胡萝卜素  $\beta$ -环的羟化反应, 形成  $\beta, \beta$ -类胡萝卜素, 目前该基因已经在柚(登录号: DQ002893)、杂柑(登录号: AF315289)和甜橙(登录号: NP001275830)等柑橘属植物中被克隆到。Zhou 等<sup>[69]</sup>通过比对野生型和类胡萝卜素突变性马铃薯发现, 突变体马铃薯块茎内类胡萝卜素代谢途径的 BCH1/2(HYb) 的表达受可溶性糖正调控影响。在烟草中过表达柑橘羟化酶基因(*HYb*), 玉米黄素的量比对照组高出 30%, 进行 UV 和氧化处理, 发现转基因植株修复 UV 和氧化损伤的能力加强, 进而证明玉米黄素对于植物的生理生化功能<sup>[70]</sup>。

HYe 可以催化  $\epsilon$ -环羟化反应, 属于细胞 P450 加氧酶, 在柑橘中研究相对较少。CCDs 作为动植物常见的裂解双氧合酶<sup>[71]</sup>, 能够将类胡萝卜素裂解产生  $\beta$ -紫罗兰酮等挥发性萜类化合物(图 1), 参与叶、花、果颜色和香味的形成, 对植物体具有重要生理意义。目前, 已经在拟南芥(*AtCCD1*, 登录号: AEE80498)、番茄(*LeCCD1A*, 登录号: NP\_001234542 和 *LeCCD1B*, 登录号: AAT68187)、矮牵牛(*PhCCD1*, 登录号: AAT68189)等植物中分离出部分同源基因; 然而在高等植物体, ABA 作为必要的植物内源激素, *NCED* 作为关键的限速酶, 具有催化生成脱落酸前体物质的能力<sup>[72]</sup>。*NCED* 已经被广泛的克隆, 比如玉米(*VPI4*, 登录号: NP\_001105902)和大豆(*PvNCED1*, 登录号: Q9M6E8), 2006 年 Kato

克隆了柑橘的裂解双氧合酶(*CitCCD1*, 登录号: BAE92958; *CitNCED2*, 登录号: BAE92961 和 *CitNCED3*, 登录号: BAE92964), 结合基因的表达量以及化合物的含量测定给出猜测: 裂解双氧合酶(*CitNCED2* 和 *CitNCED3*) 在维持柑橘体内 ABA 和紫黄质的含量起到一个动态的平衡的效果<sup>[19]</sup>。

## 4 类胡萝卜素的生理功能

### 4.1 类胡萝卜素对植物体的生理功能

类胡萝卜素赋予植物叶片、花和果实等器官以丰富的色彩, 是许多农作物和野生植物的重要外在特征之一。类胡萝卜素的存在, 以不同的比例和不同的异构型存在, 可以呈现由黄到橙红多种颜色<sup>[73]</sup>, 柑橘果皮和果肉丰富的颜色正是因为类胡萝卜素组成比例和含量不同引起的。植物花和果实鲜艳的颜色有助于吸引传粉者和种子传播者<sup>[74]</sup>。除参与着色外, 类胡萝卜素是所有植物、藻类和蓝细菌光合作用器官中不可或缺的基本成分, 能迅速淬灭三重态叶绿素、单重态氧和超氧阴离子自由基; 在强光照射下, 可以消耗叶绿素吸收的过多光能, 在弱光照条件下收集光能以补充光合作用<sup>[75]</sup>。

### 4.2 类胡萝卜素对人体的医疗保健作用

类胡萝卜素可以在植物、细菌和真菌中合成, 但在人体内不能合成, 需要从日常饮食中获取<sup>[76]</sup>。柑橘果实中含有丰富的大量的类胡萝卜素, 是人类类胡萝卜素摄取的重要来源, 部分类胡萝卜素, 比如:  $\beta$ -胡萝卜素、 $\beta$ -隐黄素、叶黄素和虾青素作为维生素 A 的前体, 具有抵抗年龄相关的黄斑变性(AMD)、抗氧化、降低癌症发病率和抗慢性疾病的作用<sup>[77-79]</sup>。2012 年, Thornelyman 等<sup>[80]</sup>报道孕期补充充足的维生素 A 和类胡萝卜素, 可以降低孕妇贫血风险。

给体外培养 HepG2 细胞饲喂柑橘混合物, 测定柑橘混合物的生物可及性、细胞吸收率以及细胞的抗氧化能力, 结果显示饲喂柑橘混合物的细胞的抗氧化能力更强, 且细胞抗氧化能力与吸收的  $\beta$ -胡萝卜素和柚皮苷的量呈正相关<sup>[81]</sup>。这篇文章首次从动物细胞吸收上证明多食柑橘类水果有助于提高细胞抗氧化能力, 为提高柑橘经济价值提供理论支持。

## 5 展 望

近年来, 类胡萝卜素因其组成多样性和对人体重要的生理意义, 被广泛研究。柑橘作为基础消费、

流通面广、类胡萝卜素丰富存在的作物,同样引起了研究者的兴趣。而柑橘又是类胡萝卜素丰富的载体,因而柑橘色素-类胡萝卜素的研究表现出了强劲发展。

随着甜橙和其他柑橘属基因组、转录组、代谢组数据的完善,野生型柑橘资源的挖掘<sup>[82]</sup>,柑橘类胡萝卜素的研究将会更加深入和全面,不仅仅局限于关键酶基因的克隆与功能验证,化合物的测定和鉴定,外界胁迫对色素积累的影响。接下来几年,这几个方面可能会成为研究热点:基因的乙酰化和甲基化等表观调控对类胡萝卜素积累和存在形式的影响,类胡萝卜素降解产物的去向和生理功能的研究,以及面对胁迫灾害条件下,如何保证或者保护柑橘果皮颜色的一致性和均一性,增加果品价值和供应周期。除此之外,关于转录因子与关键基因之间的调控在很多植物上都有大量研究,但在柑橘色素上研究的并不多,应该展开深入研究。

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