

# 桃果实红色形成的分子机制研究进展

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**摘要:** 中国是桃的原产地, 有着丰富的桃种质资源, 尤其是果皮和果肉颜色类型多样, 为中国桃提供了优异的种质资源。桃果皮和果肉的红色多少由花色苷含量决定, 而花色苷的合成积累主要由遗传因子决定, 另一方面光照、温度、激素及糖等因子也影响其合成。总结了前人在桃果皮和果肉红色形成的遗传变异、影响因素以及花色苷合成的分子调控机制等方面的研究进展, 以期为桃果实颜色性状的精准鉴定以及红色桃种质创新提供参考。

**关键词:** 桃; 红色; 花色苷; 遗传变异; 调控机制

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## Research progress on the molecular mechanism of red color formation in peach fruit

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**Abstract:** The peach *Prunus persica* (Rosaceae) is an important deciduous fruit tree native to China, where many wild varieties provide excellent genetic resources for peach-breeding programs. Colors of these varieties vary widely including reds, yellows, greens, and whites. Of them, red color is generated mainly by accumulation of anthocyanin, a natural water-soluble pigment that occurs widely in plants. The color of anthocyanin varies depending on pH, temperature and other conditions. The pigment also has medicinal properties such as prevention of cardiovascular disease, relieving vision, and enhancing immunity. The greater the anthocyanin content, the deeper the red color. When the fruit is green, white or yellow, anthocyanin contents are low. The common anthocyanin pigments in peach are primarily cyanidin and elargonidin, and secondarily delphinidin, peonidin, petunidin, and malvidin. Anthocyanin synthesis is mainly affected by genetics, with *PpMYB10.1* serving as the key transcription factor in peach. However, synthesis is also affected by light, temperature, hormones, sugar, and mineral elements. Anthocyanin plays an important role in people's health, and studies on red color production in peach fruit benefits breeding programs. While China's first early maturity and low-acid red-fleshed peach variety Jinling xuepan has taken China's peach-breeding research to a new level. However, further enriching the diversity of peach fruit color should also be considered in breeding programs. In this paper, we review the studies on genetic variation and regulatory mechanisms related to formation of red color in peach pericarp and pulp to improve the identification of genotypes affecting peach fruit color,

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and innovation in peach-red-germplasm in breeding programs.

**Key words:** Peach; Red color; Anthocyanin; Genetic variation; Regulation mechanism

桃 [*Prunus persica* (L.) Batsch] 为蔷薇科 (Rosaceae) 李属 (*Prunus*) 桃亚属 (*Persica*) 植物, 原产于中国<sup>[1]</sup>, 有众多野生资源、地方品种及育成品种<sup>[2-3]</sup>。据统计, 2021年中国桃种植面积和产量为82.50万hm<sup>2</sup>、1 601.65万t, 分别占全球比重的54.83%、64.08%。在品种结构上, 近年中国培育出“果个大、产量高、耐贮运、风味浓郁”等类型多样的优良品种, 基本满足了消费者对桃果品的多样性需求。根据着红色部位, 可分为果皮红色与果肉红色, 二者均因积累花色苷而呈现不同程度的红色<sup>[4]</sup>。花色苷是植物中广泛存在的一类水溶性黄酮类色素, 在不同pH、温度等条件下, 呈现出不同的颜色<sup>[5]</sup>。另外, 花色苷还具有清除体内自由基、预防心血管疾病、抗肿瘤等保健功效<sup>[6]</sup>。以此特点, 红肉桃被众多消费者所青睐, 亦被越来越多的育种家作为重点选育对象。

花色苷合成通路上结构基因或调控转录因子的变异直接决定了花色苷的积累。例如, *PpMYB10.1* 启动子上5243 bp转座子插入导致桃果皮不能合成花色苷<sup>[7]</sup>; *PpBL* 启动子上6688 bp转座子是形成红肉桃的关键<sup>[8]</sup>。另外, 转录因子 *PpNAC1*、*PpSPL1*、*PpHYH* 和 *PpHY5* 可直接激活或作用于 *PpMYB10.1*, 进而影响下游花色苷合成途径结构基因的表达, 促进或抑制花色苷的合成<sup>[9-11]</sup>。环境因素如光照、温度、激素等对花色苷合成同样有较大影响。本文基于前人的报道, 对桃果皮和果肉红色形成的遗传变

异、变异前后作用机制差异以及环境因素影响的分子调控机制等进行了总结, 为利用和开发分子标记进行桃亲本选配和杂种后代的早期选择提供帮助。

## 1 桃果实颜色多样性及与花色苷含量的关系

桃亚属在中国分布有6个种, 包括普通桃 [*P. persica* (L.) Batsch]、甘肃桃 (*P. kansuensis* Rehd.)、山桃 [*P. davidiana* (Carr.) Franch]、陕甘山桃 (*P. potanini* Rehd.)、光核桃 (*P. mira* Koehne) 和新疆桃 [*P. ferganensis* (Kost. et Kiab) Kov. et Kost]<sup>[11]</sup>。其中, 普通桃在中国被广泛栽培, 在果皮颜色和果肉颜色多样性及遗传变异方面存在较大差异<sup>[12]</sup>。在《桃种质资源描述规范和数据标准》一书中, 王力荣等<sup>[13]</sup>将果肉颜色分为红肉、白肉、黄肉, 根据花色苷含量分为多、中、少、无(图1-A); 将果皮底色分为乳白、绿、乳黄、黄等, 根据着色面积分为多、中、少、无(图1-B)。徐子媛<sup>[13]</sup>调查了73份桃种质资源品质性状, 发现果皮底色为乳白色的占比最高, 为45.2%, 果皮不同程度红色的有66份, 占90.4%, 仅7份材料果皮不着红色; 果肉红色的种质资源有12份, 占16.4%。这也从侧面反映了中国桃种质资源多样性的丰富程度。

为探究果实红色与花色苷含量的关系, 查阅了前人对桃果实花色苷含量测定的相关文献。白肉桃果皮和果肉花色苷分布范围在0.65~37.21 mg·100 g<sup>-1</sup>和



红肉桃照片来自王蛟等<sup>[14]</sup>; 果肉照片和果皮照片是独立的, 并非上下对应。

Photos of red-fleshed peaches were provided by Wang Jiao et al<sup>[14]</sup>. Photos of the fruit flesh and skin are independent and do not correspond to the top and bottom.

图1 桃果肉和果皮颜色类型  
Fig. 1 Peach flesh and skin color types

0.07~25.20 mg·100 g<sup>-1</sup>,黄肉桃为0.61~32.33 mg·100 g<sup>-1</sup>和 0.17~18.59 mg·100 g<sup>-1</sup>,而红肉桃为 1.04~113.11 mg·100 g<sup>-1</sup>和 0.73~129.06 mg·100 g<sup>-1</sup>,值得注意的是红肉桃中果皮和果肉总酚含量是白肉桃和黄肉桃的2~3倍<sup>[16-17]</sup>。丁体玉等<sup>[18]</sup>根据桃果肉着色面积和花色苷含量的动态变化,将红肉桃分为两类:(1)“成熟积累型”在果实成熟期果肉花色苷含量达到最大值(170~320 mg·kg<sup>-1</sup>);(2)“发育中期积累型”在盛花后70~80 d果肉花色苷含量达到峰值(150~800 mg·kg<sup>-1</sup>),随着果实成熟花色苷含量逐渐下降。章秋平等<sup>[19]</sup>比较了12份不同果肉颜色品种中花色苷含量,红肉桃品种花色苷平均含量显著高于白肉和黄肉品种,红肉桃中果肉花色苷含量1.249~19.503 mg·g<sup>-1</sup>,白肉桃中0.393~2.264 mg·g<sup>-1</sup>,黄肉桃中0.552~1.465 mg·g<sup>-1</sup>。而红肉桃品种间花色苷含量也有很大差异,有的红肉品种花色苷含量甚至显著低于白肉品种,这可能是由于红肉桃果肉中存在大量的多酚物质从而干扰了花色苷含量的测定,而且花色苷含量与栽培环境、试验取样等也存在一定关系。

## 2 桃果实主要花色苷组分及合成途径

花色苷是类黄酮物质中含量和分布最为广泛的一类色素物质,普遍存在于植物的花、果实、叶片等

组织中<sup>[20]</sup>,对植物器官的色泽、风味和香气等都有一定影响<sup>[21]</sup>。常见的花色苷有矢车菊色素(cyanidin, Cy)、天竺葵色素(pelargonidin, Pg)、飞燕草色素(delphinidin, Dp)、芍药色素(peonidin, Pn)、牵牛色素(petunidin, Pt)和锦葵色素(malvidin, Mv)6种<sup>[22]</sup>。花色苷糖基化的糖分子也具有多样性,多数为葡萄糖(glucose),少数为半乳糖、木糖、鼠李糖和阿拉伯糖,以及由这些单糖所构成的二糖或者多糖<sup>[5]</sup>。不同色素结合糖基而形成不同的颜色,矢车菊色素和天竺葵色素呈红色,飞燕草色素及甲基化的衍生物牵牛色素和锦葵色素呈现蓝紫色。

花色苷在植物体内的合成主要由一系列结构基因(*CHS*、*CHI*、*F3H*、*DFR*、*ANS*、*UFGT*等)所调控,这些结构基因通过编码不同功能的酶来参与花色苷的合成,同时这些结构基因受上游转录因子(*PpMYB10.1*、*PpbHLH*、*PpWD40*及*PpBL*等)的转录调控。苯丙氨酸是花色苷生物合成的直接前体物质,由苯丙氨酸到花色苷大致有3个阶段。桃果实中花色苷的生物合成途径已基本明晰<sup>[23-24]</sup>,如图2所示。第一阶段:苯丙氨酸在苯丙氨酸解氨酶(PAL)催化作用下,形成肉桂酸;肉桂酸经肉桂酸-4-羟化酶(C4H)和4-香豆酰-CoA连接酶(4CL)形成4-香豆酰-CoA;再经查尔酮合成酶(CHS)催化合成黄色的查尔酮。第二阶段:在查尔酮异构酶(CHI)以

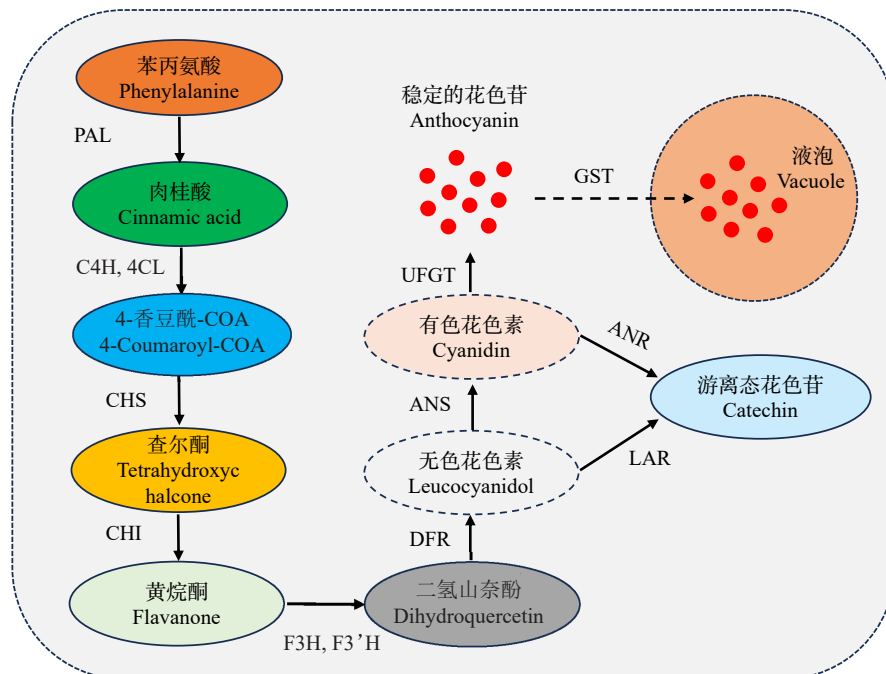


图2 桃果实花色苷生物合成途径

Fig. 2 Anthocyanin biosynthesis pathway in peach fruit



查尔酮为底物,异构化合成黄烷酮;在黄烷酮-3-羟化酶(F3H)催化下形成二氢山柰酚。第三阶段:二氢山柰酚经二氢黄酮醇-4-还原酶(DFR)合成无色花色苷;无色花色苷由花青素苷合成酶(ANS)催化形成彩色的花色苷;最后通过类黄酮-3-O-糖基转移酶(UFGT)的作用,游离的有色花色苷形成能够稳定存在于植物中的花色苷,使植物呈现出鲜艳的颜色;花色苷在细胞质中合成后,经谷胱甘肽-S-转移酶(GST)将其转移运输到液泡中,是花色苷显色的关键代谢途径;未修饰的花色苷由无色花色苷还原酶(LAR)或者花色苷还原酶(ANR)的作用产生。

### 3 桃果实红色形成的遗传变异及调控机制

#### 3.1 桃果皮红色形成的遗传变异及调控机制

桃果皮颜色由底色和盖色(或红晕)共同决定,在果实成熟过程中,果皮底色由绿色转为白色或黄色。在此阶段,因不同品种基因型差异,果皮底色上有不同类型(斑点、条纹、红晕)且深浅不同的红色沉积<sup>[12]</sup>。研究表明,果皮红晕由多个基因控制<sup>[25-27]</sup>,但同时也取决于环境因素<sup>[28]</sup>。2003年,Beckman等<sup>[29]</sup>将整个果面红色性状描述为“全红”,基因型为FR,果面无或极少红色性状被描述为“高亮”,基因型为frfr。2004年,Dirlewanger等<sup>[30]</sup>发现,位于基因组第3连锁群上的3个MYB10基因,*PpMYB10.1* (ppa026640m), *PpMYB10.2* (ppa016711m)和*PpMYB10.3* (ppa021385m)与颜色性状的*Anther color* (*Ag*)标记关联。2005年,Beckman等<sup>[31]</sup>进一步将果皮颜色描述为红与非红,红色对非红为显性(*H/h*)。

对桃果皮花色苷合成通路研究发现,*PpMYB10.1*和*PpMYB10.3*可调控花色苷合成通路上结构基因的表达,促进花色苷积累,进而使果皮呈红色<sup>[23,32]</sup>。Tuan等<sup>[7]</sup>分析非红品种Mochizuki中*PpMYB10*基因簇3个基因(*PpMYB10.1*、*PpMYB10.2*、*PpMYB10.3*)的表达,表明桃果皮花色苷含量与*PpMYB10.1*表达量密切相关,进一步分析其序列发现*PpMYB10.1*启动子-1173 nt处存在5243 bp的转座子插入,导致*PpMYB10.1*丧失功能,下游结构基因不能被激活转录,使得Mochizuki果皮不能合成积累花色苷(图3-A)。对63份桃野生资源、地方品

种和育成品种进行*PpMYB10.1*启动子上变异鉴定,发现育成品种表型和基因型完全吻合,而部分地方品种果皮颜色表型与基因型不匹配,猜测可能存在其他调控机制或变异,还有待继续研究<sup>[33]</sup>。而*PpMYB10.1*启动子上483 bp的缺失会增强其驱动活性,有利于*PpMYB10.1*对下游结构基因的转录调控<sup>[18]</sup>。Zhao等<sup>[9]</sup>研究光照对桃果皮着色分子机制发现,在光照条件下,光响应基因*PpPHYH*与伴侣蛋白*PpBBX*互作形成异源二聚体激活*PpMYB10.1*,促进果皮着红色;然而在黑暗条件下,光信号抑制因子*PpCOPI*在细胞核大量积累,引起*PpPHYH*蛋白降解,导致花色苷积累受阻(图3-B)。

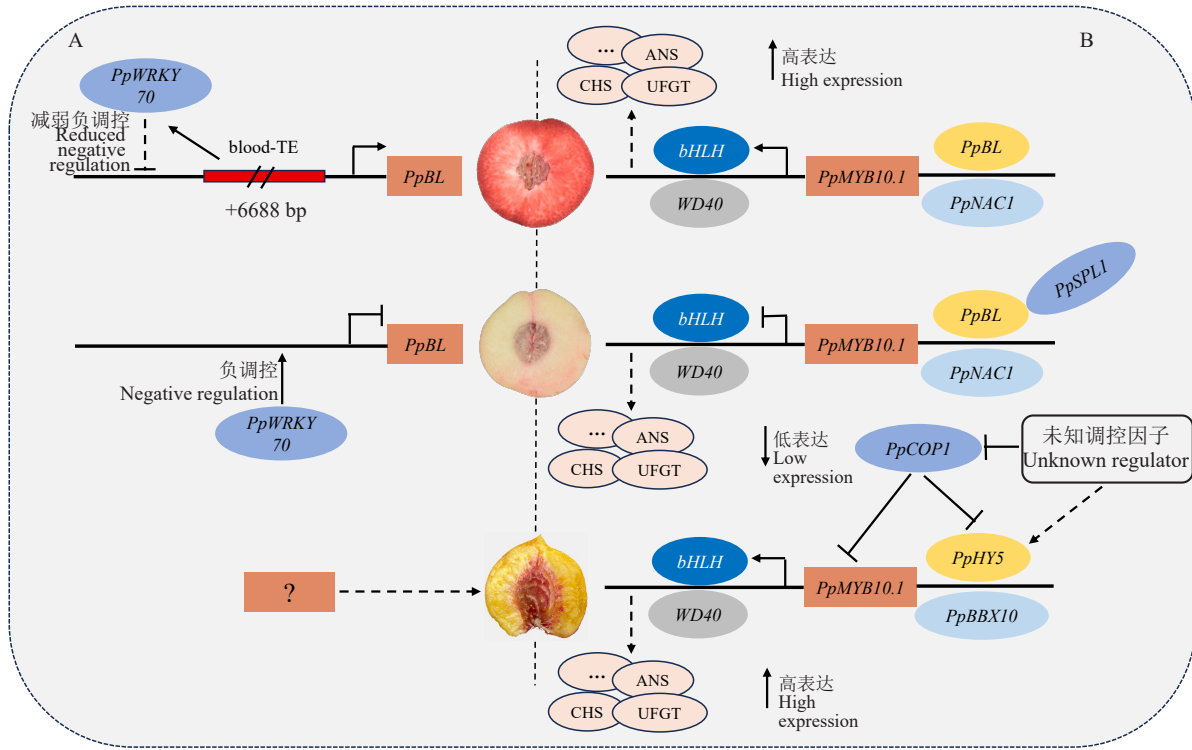
另外,表观遗传修饰也能影响桃果实花色苷的合成。Zhu等<sup>[34]</sup>研究表明,当贮藏温度升高到16℃时,随着DNA去甲基化程度增加,白肉桃果肉中会积累大量花色苷;Cheng等<sup>[35]</sup>研究发现,桃果实花色苷合成与*PpUGT78A1*和*PpUGT78A2*糖基化有关。

#### 3.2 桃果肉红色形成的遗传变异及调控机制

研究表明,桃红肉性状存在两种类型,由多个基因或者QTL位点调控。第一种类型以加拿大红肉品种Harrow Blood为代表,从硬核前期就开始大量积累花色苷,且叶片背面叶脉变红<sup>[36]</sup>。Werner等<sup>[37]</sup>分析了Harrow Blood×Rutgers Red Leaf 2n的F<sub>2</sub>后代中果肉颜色分离情况,发现红肉桃和普通桃的比例符合1:3,提出红肉性状是由一个隐形基因*bf*控制;Gil等<sup>[38]</sup>进一步将*bf*基因定位到第4连锁群的顶端,但没有候选基因被报道。章秋平<sup>[39]</sup>研究了2个杂交群体组合,发现后代果肉均为红色,但红色深浅不同,推断红肉性状并非单一的隐性性状,而是受多个基因控制的数量性状。第二种是血桃类型,果实进入成熟期果肉才开始积累花色苷而变红,且叶脉不变红。Shen等<sup>[40]</sup>对中国血桃品种五月鲜进行研究,提出这类血桃是由一对显性基因*DBF*控制的,利用SSR标记将此位点定位到第5连锁群的顶端。周晖<sup>[41]</sup>在大红袍×曙光杂交群体中鉴定发现,大红袍血桃性状为显性遗传,与Harrow Blood的隐性红肉性状不同。

Zhou等<sup>[11]</sup>在5号染色体上发现一个NAC家族转录因子,*BLOOD* (*BL*)与红肉性状密切相关,*PpBL*与*PpNAC1*形成二聚体促进*PpMYB10.1*表达,进而促进果肉花色苷合成;同时鉴定到*PpSPL1*蛋白可以





该图根据 Miyuki 等<sup>[8]</sup>、Zhou 等<sup>[11]</sup>、Wang 等<sup>[42]</sup>和 Zhao 等<sup>[43]</sup>的研究结果绘制。

The figure is drawn according to the results of Miyuki et al., Zhou et al., Wang et.al. and Zhao et al.

图 4 桃果肉花色苷合成调控模型

Fig. 4 Regulation model of anthocyanin synthesis in peach flesh

对桃果皮和果肉花色苷积累的影响试验表明,桃果肉花色苷积累不完全依赖于光照,即在黑暗条件下,果肉花色苷可以正常合成。综上,光照可以提高相关酶活性或基因表达量,促进花色苷合成,而这种作用只是在桃果皮上。

### 4.2 温度

温度对果实花色苷合成也具有重要影响。昼夜温差大和夜间温度低的地区果实着色更好,可能是由于低温减弱了呼吸速率,促进糖分积累,从而有利于花色苷积累<sup>[53]</sup>。Zhou 等<sup>[54]</sup>研究表明,高温和遮光处理显著降低了桃红色叶片中花色苷合成基因的表达,导致花色苷积累减少。研究者提出,高温条件下花色苷合成速率减慢,降解加快,其稳定性差,降低了花色苷的积累,又称“高温褪色”反应<sup>[55]</sup>。在苹果<sup>[56]</sup>、葡萄<sup>[57]</sup>研究中表明,适当低温处理可使花色苷合成相关基因高表达,促进花色苷的积累。Yin 等<sup>[58]</sup>研究表明,高海拔地区不同光质和低温有利于葡萄果皮花色苷合成。

### 4.3 激素

外源激素处理有利于果实着色。Zhang 等<sup>[59]</sup>研

究表明,乙烯通过抑制花色苷合成上游转录因子的活性,抑制桃果皮花色苷合成,而1-甲基环丙烯(1-MCP)有着与乙烯相反的作用。果实采后用不同激素处理研究表明,茉莉酸酯类、苯丙氨酸、L-谷氨酸和油菜素内酯均可以增加桃果皮花色苷含量,促进果实着色<sup>[60-62]</sup>。另外,在苹果、梨、葡萄中,激素促进或抑制花色苷合成的研究较为深入。例如,在苹果中乙烯和茉莉酸通过 *MdERF1B-MdMYC2* 基因模块协同正调控苹果花色苷合成<sup>[63]</sup>;Li 等<sup>[64]</sup>鉴定发现,乙烯和生长素响应因子之间相互作用来调节苹果果皮花青素积累。在梨中,乙烯单独或者与茉莉酸共同作用,抑制梨果皮花色苷形成<sup>[65-66]</sup>;乙烯通过 *PpERF9-PpTPL1* 共抑制复合体介导的组蛋白去乙酰化效应抑制 *PpRAP2.4* 和 *PpMYB114* 的表达,从而抑制梨果皮花色苷合成的分子机制<sup>[67]</sup>。孙玉帅等<sup>[68]</sup>对葡萄外施 ABA 和乙烯的研究表明,ABA 能通过 *VIMyba1* 直接调控着色,也可间接通过乙烯促进 *VIMyba2* 的表达来调控葡萄着色。

### 4.4 糖、矿质元素

Wang 等<sup>[69]</sup>试验表明,葡萄糖、蔗糖、果糖及山梨



醇均能诱导桃果肉中花色苷的积累,且 *PpDFR* 及 *PpUGT* 表达量显著升高。Zhou 等<sup>[70]</sup>用热空气和 UV-C 处理桃果实发现,两种处理通过调节蔗糖、苹果酸和柠檬酸含量增强花色苷积累,同时上调了相关酶活性和基因表达。外源蔗糖处理显著增加了桃果皮花色苷含量,促进着色<sup>[71]</sup>。Maatallah 等<sup>[72]</sup>研究 N-P-K 施肥对桃果实品质的影响,认为 N 和 K 在增加产量和品质的同时,增加了花色苷含量进而改善桃果实颜色。

## 5 展 望

桃基因组数据公布<sup>[73]</sup>和测序技术的进步,直接加速了对目标性状候选基因的定位,实现了对表型性状的精准鉴定,为桃分子辅助育种和果树遗传改良奠定了良好的基础<sup>[74]</sup>。分子标记辅助育种主要有两种方法:(1)在控制目的性状的基因序列上开发分子标记,直接完成表型鉴定;(2)首先鉴定亲本基因型,在目标性状位点两侧开发分子标记,进而完成表型鉴定<sup>[75]</sup>。例如,桃果皮红色与纯色性状,直接取决于 *PpMYB10.1* 启动子上的等位变异,开发出分子标记 *MYB10.1-1/MYB10.1-1* (全红)、*MYB10.1-1/MYB10.1-2* (半红) 以及 *MYB10.1-2/MYB10.1-2* (纯色),在苗期即可对果实颜色进行鉴定<sup>[7]</sup>。另外中国特有的一些地方品种抗逆性强,且果皮纯色(绿色、浅黄、白色),分子标记 *MYB10.1-2/MYB10.1-2* 并不能 100% 预测<sup>[33]</sup>。因此,找到新目的基因、新等位变异对目的基因的精准鉴定,并开发出标记被育种家所利用,是目前桃树上快速从杂交后代中筛选符合育种目标优株的主要手段。

根据桃果肉颜色分为白肉、黄肉和红肉。红肉桃富含花色苷等抗氧化成分,有益于人体健康,但大多红肉桃品种风味偏酸且早熟,阻碍了红肉桃的育种进程和新品种推广。由于桃尚未形成成熟的遗传转化体系,基因编辑技术尚不能被高效利用,所以分子标记快速鉴定表型成为当前育种中最直接有效的改良性状的手段。例如,选择高糖低酸且综合性状优良的桃品种作为亲本,与红肉桃品种杂交获得果肉性状分离的群体,同时利用红肉性状分子标记和酸味性状分子标记可快速筛选到低酸且红肉的桃优株,加快了育种进程。中国早熟且风味甜的红肉蟠桃金陵血蟠品种<sup>[76]</sup>的选育,也标志着中国桃育种工作在颜色多样性方面迈向新的台阶。另外,桃近核

处果肉红色且伴有苦味受多个基因协同调控,不受光环境诱导,存在的遗传机制尚不清楚,可利用中国丰富的种质资源优势,发掘候选基因以及可能存在的遗传变异,解析果肉近核处泛红的分子机制,开发分子标记为桃育种服务。

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