

# 杏果实风味形成及调控机制研究进展

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**摘要:** 杏果实风味独特, 是北方主要落叶果树中特色最为突出的树种之一。杏果实的风味是决定果实品质好坏的重要因素, 其主要由果实中的糖、酸和挥发性芳香物质共同作用。目前, 针对杏果实风味的研究主要集中在品种间果实糖酸物质和香气物质的组成类型和含量的差异性等方面。对影响杏果实品质形成的外界因素和调控其形成的关键基因的研究较为薄弱。就近年来与杏果实可溶性糖、有机酸和香气物质合成与代谢相关文献进行了综述, 并对未来的研究进行了展望, 以期对杏果实风味品质形成研究和杏新种质的创制提供参考。

**关键词:** 杏; 风味; 可溶性糖; 有机酸; 香气

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## Research progress on the mechanism of flavor formation and regulation in apricot

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**Abstract:** Apricot is a notable deciduous fruit tree in northern China. The flavor of apricot consists of soluble sugars, organic acids and aroma, which is pivotal to determine the quality of apricot fruit. Sugars, mainly including sucrose, glucose, fructose and sorbitol, are considered as essential primary metabolite in apricot fruit. The dominant sugar in most apricot cultivars is sucrose. The flavor of apricot is also affected by the contents and types of organic acids. The primary organic acids are malic acid and citric acid in apricot. The more malic acid or citric acid in apricot, the more the fruit tasted acidic or better. Aroma plays a vital role in the sensory quality of apricot. More than 200 volatile substances have been identified in apricot fruits, including esters, alcohols, aldehydes, ketones and terpenes. The main esters include ethyl acetate, butyl acetate and  $\gamma$ -decalactone. The major components of alcohols are *trans*-3-hexenol, *cis*-3-hexenol and isobutanol. Nonal, hexal and hexenal are dominant aldehydes in apricot. Geographical factors and varietal differences are critical to the flavor of apricot. The apricots cultivated in India and Xinjiang of China have higher total sugar contents than those cultivated in Turkey and Shanxi of China, respectively. In line with sugars, the contents of organic acids in China are higher than those of Oceanian and European varieties. The sugar degree in south-central China were significantly higher than those in the rest regions. Compared with the soluble sugars and organic acids, the aroma level of apricots which cultivated in North China ecologic group were stronger than those of European eco-

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logic group. Furthermore, the diversity of volatile substances in northwest China was higher than those of in North China, Northeast China and Southwest China. In addition, the composition of sugars, organic acids and volatiles was diversified among genotypes. The synthesis and metabolism of flavor substances in apricot exhibit the spatiotemporal specificity. For temporal specificity, fructose and glucose are mainly synthesized during early development stage. At the later stage of fruit development, the sucrose and sorbitol become the main components accumulated. Different from sugars, most organic acids increase in the early stage and decrease rapidly during fruit maturation. The main aroma differs in different ripening stages. For spatial specificity, there are no significant differences in the contents of total sugars and sucrose between pulp and peel except the fructose. Fructose in the pulp is higher than in the peel. Similar to the condition of sugars, the total amount and composition of organic acids in the pulp and the peel are the same in most apricot cultivars, but the content of various organic acids in the fruit is different. The contents and types of aroma substances in the pericarp are significantly different from those in the pulp. The nutrient elements, endogenous hormones and environmental conditions affect the accumulation of soluble sugars, organic acids and aroma. The contents of total sugars in fruit are affected by the ratio of nitrogen in different forms in the soil. Meanwhile, rational application of fertilizer improves the flavor quality and yield of apricot and reduces environmental pollution. Plant hormones are involved in the formation of fruit flavor quality by influencing plant growth, regulating enzyme activity and controlling gene expression. Abscisic acid promotes the sugar contents by regulating transport of the photosynthetic products to fruits and the expression of sucrose synthase genes. 1-methylcyclopropane, an ethylene inhibitor, is involved in reduction of sugars and organic acids in fruits via reducing the activity of enzymes involved in sugar synthesis and metabolism. In addition, methyl salicylate and cytokinin have been proved to maintain and improve fruit acidity. Environmental factors, bioactive molecules and plant resistance inducers are involved in the formation of fruit quality. Appropriate temperatures may prolong the shelf life, maintain the contents of soluble solids, delay the decline in organic acids, and affect the formation of aroma substances. It is a complex process that the synthesis, transport and metabolism of flavor substances in apricot fruit. A large number of enzyme genes, transporters and transcription factors are involved. In the aspect of enzyme genes, *ParSuSys* and *PaSPSs* are involved in the synthesis of sucrose. *PaPEPC*, *PaMDH*, *PaME* and *PaCS* have been identified to participate in the biosynthesis of malic acid and citric acid. *PaFADs*, *PaLOXs*, *PaAAT1* and *PaCCDs* take part in the synthesis of esters and apocarotenoid. In the aspect of transporters, the transcript levels of *PaSTP3*, *5.1*, *5.2*, *PaSUC4* and *PaSWEET10* are up regulated with fruit ripening. It is suggested that these genes involved in sucrose transport over the tissues and cells in apricot. The transport of organic acids in apricot is mediated by vacuole transporters, carrier proteins (proton pumps) and ion channels, such as *PaALMTCs*, *PaSFCs* and *PaVPP*. In the aspect of transcription factors, *ERF* transcription factors regulate the formation of volatile substances in fruit by regulating the genes which respond to the biosynthesis of ethylene and aroma. At present, most studies focus on the differences in composition types, contents and spatio-temporal variation of the sugar, acid and aroma substances among the apricot varieties. However, the researches on apricot fruit quality which effected by external factors and key genes are weak. Here, the synthesis and metabolism of soluble sugars, organic acids and aroma substances in apricot fruits are reviewed, and the future studies are prospected in order to provide references for the flavor quality formation and new germplasm creation of apricot fruit.

**Key words:** Apricot; Flavor; Soluble sugar; Organic acid; Aroma

杏 (*Prunus armeniaca* L.) 属蔷薇科杏属, 是世界第三大广泛栽培的核果类果树<sup>[1]</sup>。目前, 全球杏产量已达 380 万吨, 主要产地为地中海地区 (占全球总产量的 40%)<sup>[2]</sup>。杏最早起源于中国, 栽培历史可追溯到距今 2600 年前<sup>[2]</sup>。杏果实味道鲜美, 气味诱人, 颜色鲜艳, 含有丰富的维生素 C、 $\beta$ -胡萝卜素和酚类等营养物质, 被认为是兼具经济价值和营养价值的果树, 深受消费者青睐<sup>[3-5]</sup>。

果实品质是由物理特征 (果实质量、硬度和颜色等)、化学特征 (可溶性固形物含量和 pH 值等)、感官特征 (外观、味道和香气等) 和营养参数 (酚含量和抗氧化能力) 等共同决定的<sup>[6-7]</sup>。消费者根据颜色和硬度等物理特征初次选购水果, 而重复购买则主要取决于果实味道和香气等感官特征。因此, 果实味道和香气对于果实至关重要。果实味道主要为甜酸味, 主要影响因子是糖分和酸度; 果实香气主要为果香型和清香型等, 主要影响因子为挥发性芳香物质。笔者从影响味道和香气两方面, 论述杏果实风味研究进展, 并对进一步研究方向进行了展望。

## 1 杏可溶性糖的合成代谢规律与调控

糖分是杏果实中必不可少的初级代谢产物, 对维持果实正常的生长发育、营养物质的合成和风味物质的积累具有重要作用。果实中可溶性糖主要包括蔗糖、果糖和葡萄糖, 其组分和含量的差异能够直接影响消费者对水果的满意度<sup>[8]</sup>。

### 1.1 杏果实可溶性糖成分及其遗传变异

果实中各类糖的含量以及优势糖的类型在果实风味形成中扮演重要角色。杏果实中可溶性糖主要包括蔗糖、葡萄糖、果糖和山梨醇等, 其中蔗糖被认为是杏果实中的优势糖组分<sup>[9]</sup>。

杏树的种植地、品种和基因型的差异影响果实风味和加工品质。杏树广泛栽培于世界各地, 栽培地区条件的变化, 影响杏果实的糖分含量。种植在土耳其和印度的杏, 虽然果实中的主要糖分物质均为蔗糖、葡萄糖和果糖, 但是印度野生杏中的糖含量显著高于土耳其东部杏品种<sup>[2]</sup>。种植在新疆和山西的杏, 虽蔗糖和果糖是决定其果实甜味的主要因素, 但新疆杏的总糖及各糖分含量显著高于山西杏<sup>[10]</sup>。近年来育种技术的进步加速了杏新品种的多样性发展, 但品种间生长习性和用途的差异导致果实含糖量不同。张君萍等<sup>[11]</sup>研究表明, 产地均为新疆的洪代克杏的总糖含量

(12.73%) 约为黑叶杏总糖含量 (4.81%) 的 3 倍。鲜食杏品种 (骆驼黄、凯里大杏和早仙居) 的含糖量显著高于仁用杏品种 (一窝蜂和大山杏)<sup>[12]</sup>。杏杂合度高, 遗传背景复杂, 栽培杏杂交后代各基因型间以及不同基因型野生杏间的含糖量差距较大<sup>[2, 13]</sup>。以上研究表明, 栽培地区生态条件的变化、品种间生长习性的变化以及基因型间遗传性状的变异直接影响果实含糖量。目前, 杏果实中糖含量的研究多集中在利用生理生化手段比较国内外不同栽培地区、种/品种和杂交后代不同类型糖分含量。但造成杏果实糖分含量差异化明显的原因、糖分含量与栽植地区生态条件之间的关系以及调控杂交后代糖分合成的机制尚不明确。因此, 应结合表型生物学、全基因组关联分析 (genome-wide association study, GWAS) 和重测序技术对世界范围内不同的杏群体和杂交后代进行研究, 明确杏果实糖分合成机制以及差异变化规律。

### 1.2 杏果实可溶性糖合成代谢的时空变化

杏果实生长发育呈典型“快-慢-快”的双 S 型。在植物体光合作用和糖分代谢的共同作用下, 发育期杏果实的蔗糖、果糖、葡萄糖和山梨醇等成分的含量呈动态变化。华北杏品种 (新世纪)、新疆杏 (苏联 2 号、库尔勒托拥和阿克牙勒克) 和欧洲生态群杏品种 (金太阳) 等的果实均在发育前期以积累果糖和葡萄糖为主; 果实发育后期, 糖代谢由分解代谢转为合成代谢, 激活了蔗糖合成酶和琥珀酸脱氢酶, 促进了果实中蔗糖和山梨醇等成分的积累, 提高了成熟期杏果实总糖和蔗糖含量<sup>[14-16]</sup>。

在果实发育的过程中, 杏果肉中的果糖含量以及占总糖的比例较果皮高, 使得杏果肉中的甜味较果皮强<sup>[15]</sup>。与果糖含量呈现的空间差异性相比, 杏果肉和果皮的总糖和蔗糖含量差异不明显<sup>[15]</sup>。

### 1.3 氮素和生长调节剂对杏果实可溶性糖合成的作用

土壤中氮素 (nitrogen, N) 水平和生长调节剂等外界因素通过调节糖代谢关键酶的活性和基因表达水平参与杏果实中糖分合成和积累。N 作为果树生长发育的必需元素, 其存在形态和含量影响树体生长、果实产量和品质形成。N 主要以硝态氮和铵态氮两种形式存在。Khasawneh 等<sup>[7]</sup>研究发现, 与单独施用  $\text{NH}_4^+$  相比, 对杏树施加  $\text{NH}_4^+/\text{NO}_3^-$  (4/6) 能够调节种植地土壤中硝态氮和铵态氮含量, 提高果实总糖含量约 34%。在杏生产过程中, 过量施加氮肥, 导

致土壤N过剩,N利用率下降,果实含糖量降低,进而影响杏果实品质<sup>[17-19]</sup>。土壤N不足,抑制杏果实中氨基酸和叶绿素合成,造成植株叶面积减少和果实减产<sup>[20]</sup>。因此,应合理施N,控制土壤N含量。已有研究表明,合理施用氮肥,能够调节土壤中N含量,提高杏果实糖分等风味品质和产量,减少环境污染<sup>[20]</sup>。目前,除氮肥之外的其他肥料影响杏果实糖分合成和积累的研究较少。在氮肥的基础上,应加强对磷、钾肥以及复合肥施用量对杏果实含糖量影响的研究,筛选适宜的氮磷钾肥搭配比例。除大量元素外,微量元素同样参与调节果实糖积累。镁和铁元素通过介导叶绿素的形成,参与果树光合作用,影响“源-库”关系调节果实糖类积累<sup>[21]</sup>。因此,应加强对镁、铁、锌和硒等微量元素肥料对果实品质影响的研究。

脱落酸(abscisic acid, ABA)和乙烯(ethylene, ETH)等植物生长调节剂在果实糖分积累与代谢的各环节中具有重要作用。ABA主要通过促进植株光合产物向果实卸载,进而提高杏果实中可溶性糖含量<sup>[22]</sup>。同时,外源ABA能够诱导杏果实蔗糖合成酶基因表达水平上调,激活蔗糖合成酶,提高果实中总糖和蔗糖的含量<sup>[23]</sup>。杏果实属于呼吸跃变型果实,对乙烯极为敏感<sup>[24]</sup>。1-甲基环丙烯(1-Methylcyclopropene, 1-MCP)为乙烯抑制剂,通过降低糖分合成和代谢相关酶的活性,减少果实中蔗糖、葡萄糖、果糖和总糖含量,抑制采后杏果实可溶性糖的积累与转化<sup>[25]</sup>。其他生长调节剂(水杨酸甲酯、赤霉素和2,4-表油菜素内酯)也参与杏果实中可溶性糖的合成<sup>[23,26-27]</sup>。

#### 1.4 杏可溶性糖合成、转运和代谢的基因调控机制

杏果实可溶性糖组分主要以蔗糖为主,参与蔗糖合成和代谢的主要酶是蔗糖合酶(sucrose synthase, SUS)和蔗糖磷酸合酶(sucrose phosphate synthase, SPS)。SUS被认为是杏果实中蔗糖积累的关键酶,能够催化果糖、葡萄糖和蔗糖之间的合成和分解反应<sup>[28-29]</sup>。SPS是一种蔗糖合成的限速酶,其活性与蔗糖积累呈正相关<sup>[30-31]</sup>。目前,借助高通量测序和生物技术手段,已在杏果实中鉴定出多个与蔗糖合成和代谢相关的酶基因<sup>[32-33]</sup>。在总糖和蔗糖积累阶段,高浓度的蔗糖诱导杏蔗糖合酶基因*PaSUS1*、*PaSUS3*、*ParSuSy5*、*ParSuSy6*和*ParSuSy7*的表达量显著上调,推测其参与蔗糖合成酶合成方向蛋白的合

成<sup>[23]</sup>。Zhang等<sup>[33]</sup>研究发现,杏蔗糖磷酸合酶基因*PaSPS2*的表达量随果实成熟呈现显著上调趋势,认为*PaSPS2*介导杏果实蔗糖生物合成和积累。

蔗糖主要在叶片(源)中合成,经韧皮部装载、长距离运输、卸载到果实(库)中,这些过程中蔗糖在细胞间的运输主要通过细胞器上糖转运蛋白完成。因此,糖分转运蛋白是调控植物体内糖分卸载、分配和积累的关键因子,也是“源-库”代谢之间信号转导的重要组成部分<sup>[34]</sup>。植物中存在三大糖分转运蛋白家族:单糖转运蛋白(monosaccharide transporter, MST)、蔗糖转运蛋白(sucrose transporter, SUT/SUC)和糖转运蛋白(sugars will eventually be exported transporter, SWEET)<sup>[35-36]</sup>。己糖转运蛋白(sugar transporter proteins, STPs)是MST超家族下的亚族<sup>[37]</sup>。在果实成熟过程中,果实糖分逐渐积累,诱导杏*STP3*、*STP5.1*和*STP5.2*表达水平上调<sup>[33]</sup>。蔗糖转运蛋白属于主要协同转运蛋白超家族(major facilitator super family, MFS)。康爽等<sup>[38]</sup>研究发现,杏*PaSUC4*主要在成熟叶中表达,具有组织表达特异性,并推测其参与“源-库”之间的蔗糖运输。SWEET糖转运蛋白是高等植物中一类全新的介导糖转运的蛋白家族<sup>[34]</sup>。Zhang等<sup>[33]</sup>以佳娜丽杏不同发育阶段的果皮为材料,利用转录组测序发现了8个杏*PaSWEET*基因响应果实成熟。值得注意的是,以上基因中仅有*PaSWEET10*表达上调,提出杏*PaSWEET10*促进胞质中糖分进入液泡或邻近受体细胞<sup>[33]</sup>。QTL(quantitative trait locus)定位是一种明确控制性状功能位点和基因的有效手段,对研究杏果实可溶性糖性状具有重要意义<sup>[39]</sup>。Zhang等<sup>[40]</sup>利用较耐贮藏杏品种串枝红与高糖低酸杏品种赛买提为双亲建立杂交群体。通过对双亲及其F<sub>1</sub>子代进行测序,构建了高密度遗传连锁图谱,并以此对杏果实品质性状进行QTL定位。该研究在杏基因组上共鉴定出3个调控果实可溶性固形物含量的候选区域,包含372个相关基因。这些基因涉及了光合电子传递、糖合成与转运、调控基因、转录因子和植物激素等,如:编码苹果酸脱氢酶的*PARG17513*、编码光系统I反应中心的*PARG15534*和*PARG17684*以及调节跨膜转运蛋白活性的*PARG17899*等<sup>[40]</sup>。Garcia-Gomez等<sup>[41]</sup>以糖酸中等的杏Bergeron(B)和高酸杏Goldrich(G)分别为母本,与具有高糖低酸性状的杏Currot(C)进行杂交,利用简单重复序列标记(sim-

ple sequence repeats, SSR)和单核苷酸多态性(single nucleotide polymorphism, SNP)标记获得的“B×C”和“G×C”F1代的表型数据和遗传连锁图谱进行QTL分析,发现调控可溶性固形物含量的QTL定位在LG4中,并在该区域内鉴定出*ppa001122m*, *ppa000854m*和*ppb001660m*等参与D-葡萄糖和D-甘露糖相关的基因。上述研究通过多组学联合分析、实时荧光定量以及正向遗传学等方法,推测出可能参与杏果实优势糖合成、转运和代谢的基因,为下一步进行基因功能验证,精准创制杏新种质奠定基础。目前,已有的研究多利用高通量测序技术探究在果实糖分积累过程中基因的表达水平的变化,缺乏证明表达量显著变化的基因参与糖分合成、转运和积累的直接证据。同时,转录因子和表观遗传修饰调控基因表达水平,但具体的转录调控和表观遗传机制尚不明确。因此,多组学分析应结合现代生物学技术,深入探究参与糖分合成、转运和积累等过程的关键基因的功能以及调控机制,进而构建清晰的调控网络。

## 2 杏有机酸的合成代谢规律与调控

酸度是果实品质的重要组成部分。杏果实酸度取决于有机酸的种类和含量。果实中有机酸主要通过糖酵解作用产生,糖异生作用降解,并通过三羧酸循环进行代谢<sup>[42]</sup>。杏果实有机酸的合成和代谢过程受遗传因素和环境因子调控<sup>[10,43]</sup>。

### 2.1 杏果实有机酸成分及其遗传变异

杏果实中含量最丰富的有机酸是苹果酸、柠檬酸、奎尼酸和琥珀酸。果实优势有机酸含量直接影响果实风味和口感。小白杏和树上干杏的优势酸是苹果酸;柠檬酸是印度CITH-A-1、CITH-A-2、CITH-A-3杏(占果实总有机酸的50%以上)和欧洲的Roxana、Gold Cot、Shakarpara杏的优势有机酸<sup>[1,43-44]</sup>。苹果酸作为优势酸的杏品种,果实酸味较强;而柠檬酸作为优势酸,能够加强酸味的融合,使果实口感更佳。

杏果实有机酸因种植区地理特征和环境条件的差异,呈现不同水平。具体表现为原产于我国中南地区果实中总酸和苹果酸的平均含量显著高于西北、东北和华北等其他地区,南疆杏虽与华北杏的总酸含量相近,但南疆杏属于苹果酸/柠檬酸优势型,华北杏属于柠檬酸/苹果酸优势型<sup>[45]</sup>。在西北地区,

新疆产区种植的杏果实中的总有机酸含量普遍高于山西产区<sup>[10,46]</sup>。同时,野生杏果实比栽培杏品种的酸度高<sup>[2]</sup>。品种间物候期、生长结果习性以及栽培适应性的差异影响果实酸度。Fan等<sup>[10]</sup>对新疆地区种植的小白杏、树上干杏和李光杏果实中有机酸含量进行测定,发现小白杏果实中的苹果酸和奎宁酸含量显著高于其他两个品种,而柠檬酸含量则远低于其他两个品种。北美杏栽培品种Goldrich(G)和西班牙栽培杏品种Currot(C)的杂交后代不同基因型中,GC 3-7的有机酸含量显著高于GC 2-11<sup>[13]</sup>。以上研究表明种植环境和自身遗传因素对杏有机酸的成分组成与含量均有影响。

### 2.2 杏果实有机酸合成代谢的时空变化

在杏果实发育过程中,几乎所有有机酸含量在发育早期(幼果期至膨大期)增加,在果实成熟期(转熟期至全熟期)迅速下降<sup>[15]</sup>。Cui等<sup>[44]</sup>和翁金洋等<sup>[16]</sup>研究发现,苹果酸含量在金太阳杏和树上干杏果实发育初期不断升高,其中树上干杏苹果酸含量上升至转色期后下降,而金太阳杏仅上升至硬核期便下降。与苹果酸含量变化趋势相比,柠檬酸含量在金太阳杏整个发育过程中呈上升趋势,表现为发育初期低,硬核期后快速增加<sup>[16]</sup>。与之相反,树上干杏中柠檬酸、异柠檬酸含量从果实发育初期到转色期迅速增加,自转色期开始到成熟期便呈迅速下降趋势<sup>[44]</sup>。杏果肉和果皮的有机酸总量和组成基本一致<sup>[47]</sup>。有意思的是,Xi等<sup>[28]</sup>研究发现,黑叶杏和小白杏果皮中苹果酸和酒石酸含量显著高于果肉,而奎尼酸和草酸在果肉中含量高于果皮。由此说明,不同种类的有机酸在果实中的主要分布存在明显差异。以上研究以多种杏品种为材料,针对有机酸在各个时期积累的情况以及在果肉/皮分布做了大量研究,为揭示杏果实有机酸的时空积累和分布的机制奠定了理论基础。在此基础上,笔者认为应深度探讨杏果实成熟过程中苹果酸和柠檬酸的合成与果实发育时期的关系。利用时空转录组和分子生物学等技术,明确不同发育时期果皮和果肉中有机酸含量的变化规律,阐明杏果肉/皮在有机酸代谢过程中的底物选择性以及不同有机酸之间的平衡机制。

### 2.3 外界因子和生长调节剂对杏果实有机酸合成的作用

杏果实的酸积累受到外界因子和生长调节剂等因子调控。外界因子包括环境因子和生物活性因子

等;生长调节剂包括水杨酸(salicylic acid, SA)和乙烯等。在外界因子方面,温度参与果实贮藏期间有机酸的合成。短时低温冷激延长小白杏的货架期,延缓有机酸含量下降<sup>[48]</sup>。贮藏前短时非致死高温可降低库买提杏果实呼吸强度和乙烯释放量,保持了果实的可溶性固形物含量和有机酸含量,改善了杏果实的贮藏品质<sup>[49]</sup>。生物活性分子和植物抗病性化学诱导制剂已经被证明可以减缓果实采后品质劣变。一氧化氮(nitric oxide, NO)作为一种生物活性分子,外源施加能够诱导杏苹果酸脱氢酶(malate dehydrogenase, MDH)基因 *PaMDH* 的表达量升高,杏苹果酸酶(malic enzyme, ME)基因 *PaME* 的表达水平下降,提高绿熟期小白杏果实的柠檬酸合酶(citrate synthase, CS)、磷酸烯醇式丙酮酸羧化酶(phosphoenolpyruvate carboxylase, PEPC)和 MDH 的活性,降低异柠檬酸脱氢酶和细胞质乌头酸酶活性,进而延缓小白杏果实中苹果酸和柠檬酸的流失,降低有机酸代谢速度<sup>[50]</sup>。苯丙噻重氮[Benzo(1,2,3) thiadiazole-7-carbothioic acid S-methylester, BTH]是一种人工合成的植物抗病性化学诱导制剂。在低温条件下,BTH 诱导杏果实中 NAD-苹果酸脱氢酶、PEPC 和 CS 等有机酸代谢关键酶活性升高,提高杏果实中苹果酸和柠檬酸含量,减缓因低温造成的果实酸流失<sup>[51]</sup>。在生长调节剂方面,ETH 和水杨酸甲酯(methyl salicylate, MeSA)对果实色、香、味和质地等一系列变化起非常重要的作用。1-MCP 作为乙烯受体抑制剂对采后杏果实进行处理,能够有效地促进贮藏末期有机酸的降解,降低杏果实内有机酸含量,阻止或延迟果实软化,提高果实贮藏品质<sup>[24-25, 52]</sup>。MeSA 可用来保持果实质量和延长贮存时间<sup>[53]</sup>。采前施用 MeSA,能够降低杏果实的腐烂率和冷害指数,并保持较高的有机酸含量<sup>[26]</sup>。细胞分裂素(cytokinin, CTK),具有促进细胞分裂、调节营养物质运输、改善果实品质、促进坐果等功能。Nafsika 杏果实受 CTK 诱导,果实中柠檬酸、抗坏血酸和总酸含量升高,并发现 CTK 和生长素结合使用能够极大程度提高杏果实酸味指数<sup>[54]</sup>。以上研究揭示了不同外界因子和植物生长调节剂对果实酸度的作用,为阐明采后贮藏期间外界因子参与杏果实有机酸积累的机制奠定前期理论基础,为明确生产实践过程中生长调节剂的选用原则提供指导。

## 2.4 杏有机酸合成、转运和代谢的基因调控机制

果实中酸的合成、转运和代谢是一个复杂的过程,其中有机酸的合成和代谢取决于糖酵解和三羧酸循环等多种途径中酶基因的参与,而转运则由液泡转运蛋白、载体蛋白(质子泵)和离子通道蛋白介导。编码杏果实有机酸的合成和代谢的酶基因表达丰度随果实成熟呈现动态变化。从硬核后期到成熟期,金太阳杏果实中 *PaPEPC* 和 *PaMDH* 的表达水平持续降低,苹果酸酶基因 *PaME* 表达水平逐渐增高,加速了苹果酸的降解速度,造成果实中苹果酸合成与积累能力下降<sup>[16]</sup>。与苹果酸合成的趋势相比,金太阳杏中介导柠檬酸合成的 *PaCS* 基因在果实发育前期呈“上升-下降”趋势,在果实发育后期不断下降<sup>[16]</sup>。相比于金太阳杏,张秋云等<sup>[55]</sup>对来自新疆的8个杏品种进行研究发现,果实中编码柠檬酸合成酶基因 *PaCS* 的表达水平在整个果实成熟期内呈“下降-上升”的趋势。由此表明,杏果实中有机酸合成和代谢的能力具有时间动态差异性以及品种差异性。果实中大部分的苹果酸和柠檬酸积累在液泡中,其转运过程可通过液泡膜上的转运蛋白实现。截至目前,在杏中已鉴定出多个参与有机酸转运的蛋白,包括铝激活苹果酸转运蛋白(aluminum-activated malate transporter, ALMT): *PaALMT1*、*PaALMT4*、*PaALMT8* 和 *PaALMT9*; 线粒体琥珀酸-富马酸转运蛋白(mitochondrial succinate fumarate transporter, SFC): *PaSFC1*<sup>[13, 33, 55]</sup>。随后,通过对上述基因在杏成熟期表达丰度和有机酸含量联合分析,提出转录后和翻译后调控可能通过介导基因表达并参与体内有机酸转运<sup>[33, 55]</sup>。除转运体以外,质子泵(V-ATPase 和 V-PPase)对有机酸进入液泡起重要作用,杏 *PaVPP* 作为首个在杏中鉴定出来的质子泵蛋白,其表达模式受发育时期的控制<sup>[55]</sup>。利用正向遗传学手段能够加速杏果实有机酸含量遗传调控的研究。Garcia-Gomez 等<sup>[41]</sup>研究发现,调控 Goldrich×Currot 和 Bergeron×Currot 杂交杏群体苹果酸含量相关的 QTL 定位在 LG2 和 LG8。Dondini 等<sup>[56]</sup>选用 Lito 杏×BO81604311 杏(L×B)杂交 F<sub>1</sub> 子代为材料进行群体定位,将苹果酸和柠檬酸定位在 LG8 号连锁群,并结合杏基因组序列,挖掘出 *PruarS.8G052800.t1*、*PruarS.8G247000.t1* 和 *PruarS.7G231300.t1* 等可能参与调控杏果实有机酸含量的基因<sup>[56]</sup>。上述研究鉴定了多种参与杏果实苹果酸和柠檬酸等有机酸合成、转

运和代谢的基因,为日后进一步进行功能研究提供理论基础。

### 3 香气物质合成代谢规律与调控

杏果实以味道和风味而闻名,其完美平衡了果实糖酸含量,并结合了强烈而丰富的香气,受到消费者的高度赞赏<sup>[57]</sup>。味道和香气的结合对果实整体风味具有重大贡献,但通常认为香气起着主导作用<sup>[43]</sup>。目前,已在桃、番茄和草莓等果实中对香气物质进行了研究<sup>[58-62]</sup>。在杏中,已针对不同品种和香气类型的果实,鉴定出果实特征香气成分为 $\gamma$ -癸内酯和 $\gamma$ -辛内酯;主要“绿色”香气成分为己醛、(Z)-3-己烯-1-醇、(Z)-2-己烯-1-醇和(Z)-2-己醛;主要“果味”香气成分为己酸乙酯、3-己烯酸乙酯和(Z)-3-己烯基乙酸酯<sup>[63]</sup>。

#### 3.1 杏果实香气物质成分及其遗传变异

果实香味是多种挥发性物质通过融合、叠加和掩盖等方式相互作用形成的。1967年,科学家首次对Blenheim variety杏中的挥发性物质进行分离和鉴别<sup>[64]</sup>。截至目前,杏果实已鉴定出的挥发性物质约200种,主要由酯类、醇类、醛类、酮类和萜烯类物质组成<sup>[65-66]</sup>。酯类物质中主要有乙酸乙酯、乙酸丁酯和 $\gamma$ -癸内酯等,醇类物质中主要包括反式-3-己烯醇、顺式-3-己烯醇和异丁醇等,醛类物质中主要有壬醛、己醛和己烯醛等。

杏果实香气物质的种类和含量具有地域差异性。商熟期的华北生态群杏果实较欧洲生态群香气浓郁,其原因是华北生态群的杏果实香气物质种类多,含量高,主要的挥发性成分是乙酸丁酯、顺式-3-乙酸己酯和反式-2-乙酸己酯等酯类与萜烯类物质;欧洲生态群香气物质种类少、含量低、香气淡,主要挥发性成分是C6醇类、C6醛类、内酯类、萜烯醇类和酮类<sup>[67]</sup>。我国西北地区杏品种果实的挥发性物质种类多样性丰富,含量最高,而华北、东北和西南地区品种物质种类多样性逐渐减少。卢娟芳等<sup>[68]</sup>和王端等<sup>[69]</sup>研究发现,新疆主栽杏品种果实中的香气物质约154种,而华北地区杏品种果实中仅有约114种。表明杏品种的挥发性物质成分与生态地理群密切相关<sup>[67]</sup>。

杏品种间果实香气物质组成不同。新世纪杏和红丰杏分别检测出74和72种香气物质,虽然主要香气成分相似(多为酮类、醇类、醛类和内酯类化合

物),但是新世纪杏的紫罗酮、芳樟醇和内酯类等成分的含量较红丰杏高<sup>[70]</sup>。与上述两个品种不同,在金凯特杏中仅检测到46种香气物质,主要香气成分为酯类、醇类和醛类<sup>[71]</sup>。远缘杂交技术可以将亲缘种属的优良基因资源导入,是进行品种遗传改良的重要方法<sup>[72]</sup>。果树种/品种间杂交F<sub>1</sub>代香味成分的遗传研究是品质育种的重要基础。武晓红等<sup>[73]</sup>研究发现,子代Z10-1-78、Z10-1-60新品系与父本丰园红杏不同的成熟期香气物质成分和特征香气一致,与母本串枝红杏差异较大,子代果实中典型玫瑰香味均来源于父本,且香气物质含量和香味浓度均高于父本。上述研究阐述了生态地理因素和品种的差异对杏果实香气合成的影响,并对杂交后代杏果实香气物质遗传规律进行初探,为进一步选择优良品种进行精准育种奠定了基础。但外界环境因素和自身遗传如何调控香气合成的机制尚不明确;不同的品种之间杂交,子代的香气遗传规律是否一致尚未报道。因此,在此基础上应广泛收集国内外杏种质资源,并从香气物质的进化、演化、合成和代谢等方面深入挖掘果实香气差异的原因。

#### 3.2 杏果实香气物质合成代谢的时空变化

在绿熟期、商熟期和完熟期等不同的成熟阶段,杏果实的主要香气物质的变化具有时间性。尹燕雷等<sup>[74]</sup>研究发现,绿熟期的凯特杏果实大量合成醇类物质,而在商熟期和完熟期以酯类为主。有趣的是,作为凯特杏实生后代的金凯特杏在整个成熟期内均以合成酯类物质为主<sup>[71,74]</sup>。与凯特杏和金凯特杏相比,绿熟期的新世纪杏主要合成C6醛类和醇类,在商熟期则大量合成萜烯醇类物质<sup>[75]</sup>。同时,通过对新疆主栽杏品种的果皮/肉中香气物质含量进行研究,发现果皮中萜烯类、醇类、醛类和内酯类含量均显著高于果肉,而酮类物质含量远低于果肉<sup>[68]</sup>。由此说明,杏果实香气物质合成代谢具有空间特异性。

#### 3.3 温度和外源处理对杏果实香气物质合成的作用

采收贮藏期温度通过调控果实体内脂氧合酶(lipoxygenase, LOX)和醇酰基转移酶(alcohol acyl transferase, AAT)活性的变化、甲基化水平的动态变化以及脂氧合酶基因LOX、过氧化氢裂解酶(hydroperoxide lyase, HPL)基因和醇酰基转移酶基因AAT等的表达水平变化直接影响水果的风味品质<sup>[60,76-77]</sup>。Cai等<sup>[78]</sup>研究发现,杏果实采后长时间低温冷藏,能够降低体内HPL、乙醇脱氢酶(alcohol dehydrogenase,

ADH)和AAT的活性,抑制香气合成途径中的支链醇、短链醛和短链醇等中间代谢产物合成,减少最终芳香物质的种类和含量,进而导致果实风味恶化。外源处理影响采后杏果实香气的存留。Ortiz等<sup>[79]</sup>和Lv等<sup>[80]</sup>发现,外源ETH或1-MCP处理,分别通过影响果实体内的LOX酶活性或乙烯释放量,促进/抑制大部分杏果实香气物质的合成。近年来,生物或非生物诱抗剂被认为不仅能够提高果实的抗病性,而且对果实品质具有一定影响。对杏分别进行草酸、苹果酸和硅酸钠处理,发现果实挥发性物质的总量显著降低,杏果香型物质(酯类物质)的释放受到显著抑制<sup>[81-82]</sup>。目前对于采后贮藏期温度和外源物质处理对杏果实香气物质的基础研究较为薄弱,应着重对采后杏果实最适贮藏温度进行筛选,加强低温介导杏果实香味变淡的遗传修饰和转录调控等方面机制的研究。加快杏保鲜剂和诱抗剂的研发和选择,保证杏的果实品质 and 市场经济价值。

### 3.4 杏香气物质合成和代谢的基因调控机制

果实香气物质的合成受到脂肪酸途径、氨基酸途径和萜类合成等途径调控。杏果实香气物质的合成以脂肪酸途径为主,其以亚油酸、亚麻酸为底物,通过LOX酶催化形成氢过氧化物,并经HPL酶和ADH酶的催化作用合成C6醛类及醇类物质,最后在AAT酶的催化下合成酯类、醇类、醛类和内酯类等。在此过程中参与前体物质合成的基因在杏果实香气过程中扮演重要角色。在脂肪酸途径中,脂肪酸去饱和酶(fatty acid desaturase, FAD)催化脂肪酸途径中前体物质不饱和脂肪酸(亚麻酸和亚油酸)的合成,影响着果实香气。目前,基于转录组测序共在杏中鉴定出36个FAD基因,并明确了5个转录水平上调的PaFADs基因可能响应内酯类物质合成<sup>[33]</sup>。LOX酶能够催化亚油酸和亚麻酸在C9和C13进行加氧,生成9/13-脂氢过氧化物,并以此为底物生成醛类、醇类和酯类等物质<sup>[83]</sup>。杏中共鉴定出13个LOX基因,其中4个PaLOXs的表达丰度下调,推测其可能是形成酯类物质的关键基因<sup>[55]</sup>。同时,吴忠红等<sup>[84]</sup>对小白杏PaLOX基因(KM067451)进行了克隆和序列分析,为进一步的功能验证奠定了前期基础。AAT酶是酯类物质合成最后一步的关键酶,过量表达杏PaAAT1基因促进果实中酯类合成,同时降低体内己烯醇、(E)-2-己烯醇和(Z)-3-己

烯醇水平<sup>[85]</sup>。除脂肪酸途径之外,在萜类合成途径中鉴定出杏中类胡萝卜素裂解酶(carotenoid cleavage dioxygenases, CCD)基因PaCCD1和PaCCD4可能参与脱辅基类胡萝卜素香气挥发物的生物合成,并验证PaCCD1是控制杏果实脱辅基类胡萝卜素类香气物质形成的关键基因<sup>[86]</sup>。随着研究的不断深入,芳香物质合成的转录调控研究已成新热点,并在多个物种中鉴定出转录因子参与调控形成,其中包括乙烯响应转录因子(ethylene response factor, ERF)、NAC和MYB等<sup>[87-89]</sup>。ERF转录因子通过调控乙烯响应基因和果实香气生物合成基因调节果实成熟和果实中挥发物的形成<sup>[90]</sup>。张丽娜等<sup>[91]</sup>研究发现,ERF转录因子(PaERF4、PaERF12和PaERF26)参与调控杏果实萜类途径中芳香味脱辅基类胡萝卜素的形成,但因品种不同而具有不同的调控效应,其中PaERF4起负向调控作用。转录因子通过结合下游基因启动子区顺式作用元件调控基因的表达,参与果实香气物质合成<sup>[92-93]</sup>。杏AP2/ERFs与CCDs之间可能存在相互作用,但具体的转录调控机制尚不清楚,仍需后期进一步验证。通过以上不同香气物质合成途径中基因的共同作用,促进杏果实中酯、内酯和脱辅基类胡萝卜素类香气成分的含量迅速提升,萜类和C6化合物含量降低。上述研究基于多组学联合分析对参与杏果实香气物质合成的多种途径中的关键基因进行初步鉴定,为进一步利用基因工程技术改良果实香气品质提供基础。截至目前,针对杏果实香气的研究尚处于初级阶段,品种间的特征香气物质鲜有报道,调控各类香气物质合成的基因尚不明确。因此,应该针对不同生态群分布的杏,选择经济价值高、风味各异的代表性品种,加强对其组学数据的挖掘和利用,鉴定介导特征香气物质合成和代谢的基因。果实香气是由多种挥发性物质复合合成,应加强对来自多条合成途径中的挥发性物质是如何通过协同/拮抗作用造成果实芳香类型多样化进行探究,明确杏果实呈现不同香气类型的原因。在杏果实成熟过程中,香气物质含量变化与关键基因表达丰度具有显著相关性。基因表达水平的变化受上游转录因子、小RNA以及DNA甲基化修饰等因素影响。因此,应借助分子生物学技术和生物信息学手段,深入探究转录调控和表观遗传修饰对杏果实香气形成的作用。



## 4 展 望

基于市场上消费者以及杏种植户对杏果实风味品质的需求,围绕杏果实风味形成及调控机制,笔者提出以下展望。

杏资源收集、筛选、评价和引种方面。应结合育种目标,加强对果实糖酸适宜、香气诱人的杏资源进行收集。分子标记辅助育种技术的应用对提升杏育种效率具有促进作用。但在杏育种的过程中多使用通量低、分辨率较差的SSR分子标记技术。鉴于杏已获得高质量基因组,故应着眼于利用“基因组+GWAS+果实性状”的模式进行分析,科学、高效地开发并筛选出果实品质性状紧密连锁的分子标记。目前在桃、甘蔗和黄瓜等植物中已经开发出糖、酸和香气相关的标记,但分子标记在杏中的研究多集中在经济性状和遗传多样性方面<sup>[94-95]</sup>。因此,加强杏风味品质相关分子标记的开发势在必行。在此基础上,应结合杏表型性状、经济性状和风味品质指标建立科学的果实风味品质优劣评价体系,将筛选优良品种进行引进或作为亲本进行选配,推动了杏育种的科学性。

杏果实风味形成及调控机制等基础研究方面。目前,针对杏果实风味物质合成和代谢研究较少,关键基因的功能鉴定研究较为薄弱。但在其他水果中已进行了大量且深入的研究,并鉴定出参与其形成的功能基因。因此,应根据表型和育种目标,在杏中利用正向遗传学和组学等手段,深度挖掘调控果实中糖类、有机酸和特征香气物质等单一性状以及多性状组合的关键转录因子和功能基因,并利用转基因技术和体内/外互作实验,明确关键基因对果实风味品质的作用功能,揭示杏果实风味物质合成、代谢的通路,为创制出品质优良的杏果实提供基础理论支撑。

果实糖酸平衡是决定水果风味的关键。首先,应深入研究调控杏糖酸平衡的基因:一方面通过构建杏果实风味代谢转录调控网络,筛选和鉴定杏果实参与糖酸平衡的基因;另一方面,应用反向遗传学手段,以已报道的其他植物果实中调节糖、有机酸和香气之间平衡的基因为基础,对其在杏中的同源基因进行验证,探究已有基因对杏果实糖酸调节的保守性。其次,加强施肥管理,通过施用不同肥料改善果实糖酸比,提升果实品质。最后,积极探索外源生

长激素对果实糖酸含量的影响。

成熟、稳定的遗传转化体系对果树的基础科学研究至关重要。在苹果、草莓和柑橘中已经建立起稳定转化体系<sup>[96-98]</sup>。杏树缺乏高效稳定的遗传转化体系,这导致基础研究的发展被严重制约<sup>[99]</sup>。转化材料是开发稳定遗传转化体系的关键基础。优质的砧木或长势好、抗性强的杏种质被认为是优良的转化材料。针对以上材料,建立无性繁殖技术,进一步研发转基因技术和基因编辑技术,对讲好杏果实风味品质形成的故事起推动性作用。

杏树高效田间栽培配套技术方面。科学的栽培繁育技术,助力杏果实品质提升。应加强对露地栽培杏树的树体密度以及树形修剪的研究,大力推进设施栽培,通过改善树体所需光照和温度条件,促进杏树生长过程中营养物质积累,调节果实形成的必需营养物质的转运和分配,进而起到改善果实风味品质的作用。杏中生长调节剂的研究多集中在利用传统单一生长调节剂解决黑斑病、冷害等生物和非生物胁迫的问题<sup>[100-101]</sup>。应通过加强新型生长调节剂的使用以及不同种类之间的搭配应用,调节杏树体内激素的动态水平,进一步影响杏果实内部的糖、酸以及香气物质含量,提升杏果实风味品质。

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