

## 梨果实糖酸研究进展

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**摘要:**可溶性糖酸含量是影响梨果品质的经济性状,是人类长期驯化选择的重要性状。在梨果实生长发育、成熟与衰老过程中,糖酸代谢发生一系列生理生化反应,果实中的糖酸含量以及组分变化存在一些规律性。梨果肉主要可溶性糖包括蔗糖、果糖、葡萄糖、山梨醇等,主要可溶性酸包括苹果酸、柠檬酸等,糖酸含量及组分和糖酸比显著影响果实风味。影响梨果肉糖酸含量及组分的因素主要包括品种、光照、激素、肥料、采后技术及砧木等。果实糖酸代谢是十分复杂的生理生化代谢网络的一部分,糖酸是一个由多个基因控制的数量性状,许多关键的功能基因已被验证。目前梨果糖酸研究已在相关酶、糖转运体、转录因子、QTLs分子标记、基因组学、蛋白组学等方面取得重要的研究进展。围绕上述研究,综述了糖酸的主要研究进展,并进行总结和展望,以期为梨果糖酸含量及组分评价、功能基因挖掘和指导梨育种提供参考。

**关键词:**梨;糖;酸;基因

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### Research progress in sugar and acid in pear fruit

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**Abstract:** Pears are the third temperate fruit crop in the world and are widely popular due to their unique taste. The contents of soluble sugars and organic acids in pear fruits are very important to fruit quality. The differences in the content and composition of soluble sugars and organic acids in the fruit contribute to the different flavors of different pear varieties. During the growth, development, maturation and aging of pear fruits, a series of physiological and biochemical reactions occur through sugar and acid metabolism, and there are some patterns in the sugar and acid content and component changes in the fruit. Research on the contents of soluble sugars and organic acids in pear fruits has emerged endlessly, and a significant progress has been made. This article will provide an overview of the research on the sugar and acid contents in pear fruits. It mainly consists of four aspects: research progress in sugar and acid contents during fruit growth and development, sugar and acid content in post harvest pear fruits, factors affecting sugar and acid content and molecular mechanisms of sugar and acid change. During fruit growth and development, organic acids are formed in the early stages of fruit development and gradually decrease as the fruits mature. The organic acid components in pear fruits mainly include malic acid, citric acid, quinic acid, oxalic acid, shikimic acid and tartaric acid. Pear varieties are divided into malic acid dominant and citric acid dominant varieties based on the content of each organic acid component in the fruit. With Asian pear varieties, the main organic acid found in most pear varieties is

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malic acid, while with European pear varieties, the main organic acid found in most pear varieties is citric acid. Malic acid shows a first increasing and then decreasing trend throughout the entire growth and development process, while citric acid dominant varieties will undergo a transition of malic acid decreasing and citric acid increasing in the middle stage of fruit development. Malic acid is the main factor causing significant differences between varieties. The total soluble sugar content is relatively low in the early stage of fruit development and gradually increases with fruit maturity. The soluble sugar components present in pear fruits mainly include sorbitol, fructose, glucose and sucrose. Most pear varieties have sorbitol as the main sugar in the young fruit, while fructose is the main sugar in the mature fruit. There are significant differences in the proportion of sugar components at different developmental stages, with an increase in fructose content and a significant decrease in sorbitol content during maturity. Sucrose is an important factor causing differences among varieties. Pears belong to the respiratory climacteric type of fruit. During storage, fructose and glucose contents in the fruit gradually increase, sorbitol and malic acid contents gradually decrease, and sucrose first increase and then decrease. Under low temperature storage conditions, the contents of fructose, glucose and sucrose increase until they gradually decrease after 90 days. The organic acid contents show a trend of first decreasing and then stabilizing. Although the total soluble sugar content of refrigerated fruits is higher than that of unfrozen fruits, long-term refrigeration can lead to a deterioration and decrease in sucrose content in the fruits. Bagging treatment could reduce the content of total soluble sugar and reduce the content of malic acid. The application of different plant hormones or growth regulators could affect the sugar and acid contents in pear fruits. Ethylene treatment could increase the soluble sugar content and reduce the titratable acid content. GA treatment could increase the contents of sucrose and malic acid. IAA and ABA treatment could promote the accumulation of sorbitol, while MT treatment could increase the content of sucrose and sorbitol. Applying potassium and calcium fertilizers could increase the accumulation of glucose, fructose, sorbitol and sucrose in fruits. 1-MCP treatment could delay and inhibit the downward trend of organic acids, but also delay the increase of total soluble sugar content. The sugar and acid contents in pear fruits are a quantitative trait controlled by multiple genes. With the rapid development of genomics, many key gene functions have been verified. *PbCPK28* promotes the phosphorylation of *PbTST4* and *PbVHA-A1*, promoting sugar transport and storage in vacuoles. *PbrAc-Inv1* and *PbrII5* are involved in the degradation of sucrose. Overexpression of *PbPH5* can significantly increase the malic acid content. The sugar transporter family genes involved in sugar transport in pear fruits include *PbSWEETs*, *PbSOTs*, *PbTMTs*, *PbSUTs*, *PbPLTs* and *PbTSTs*. Overexpression of *PuSWEET15* increases sucrose content, while silencing *PuSWEET15* reduces sucrose content. *PbTMT4* is an important contributor to the accumulation of fructose, glucose and sucrose in pear fruits. By developing sugar related QTL markers, two individual sugar content regions associated with acid invertase genes have been identified in linkage groups LG1 and LG7. This article has mainly summarized and reviewed the research papers related to the sugar and acid contents of pear fruit in recent years around these four parts, in order to provide reference for the study on sugar and acid contents in the pear fruit, component evaluation, functional gene mining and new variety breeding, and to propose prospects for future research directions.

**Key words:** Pear; Sugar; Acid; Gene

梨(*Pyrus L.*)是世界第三大温带水果,有着悠久的栽培历史,是广受欢迎的水果。梨栽培品种果实性状与野生种果实性状的差异是人类选择的结

果<sup>[1]</sup>,梨品种果实糖酸含量是长期驯化的性状<sup>[2-3]</sup>。可溶性糖在梨果的生长、发育和果实品质中起着重要的作用<sup>[4]</sup>,果实糖酸比的差异严重影响梨果实风

味<sup>[1]</sup>。梨果中可溶性糖酸种类较多,在库尔勒香梨果肉初生代谢中共检测到蔗糖、果糖、葡萄糖、山梨醇等共 17 种糖以及苹果酸、柠檬酸等共 8 种有机酸,总糖酸比为 71.49<sup>[5]</sup>。在比较可溶性糖组分含量时,栽培梨和野生梨成熟时果糖含量差异最大<sup>[4]</sup>。总糖和个别糖含量是形成果肉甜味的原因,果肉的单个糖含量代表了风味方面的重要信息<sup>[6]</sup>。果实中糖酸含量和糖酸比是影响梨果实风味品质的重要因素,也是梨新品种选育的重要评价指标<sup>[7]</sup>。在梨的杂交育种实践中,多数个体因表现出低糖高酸的特征而被淘汰。日本梨品种成熟果实中的个体含糖量有很大的差异,提高总糖含量和甜度高的糖组分含量是日本梨育种计划的主要目标<sup>[8]</sup>。

高等植物中的果实糖积累是一个复杂的过程,涉及酶对糖代谢的调节,这些酶受激素的调节;已知酶和激素调节因环境因素和基因型而异<sup>[9]</sup>。山梨醇属于糖醇类,是梨属植物主要的光合产物,也是梨糖运输的主要形式,由叶片转运到果实的山梨醇大部分转化成为果糖和葡萄糖,可溶性糖的转运由糖转运体蛋白介导<sup>[10-11]</sup>。三羧酸(TCA)循环和糖酵解为果实中有机酸提供了所必需的成分,几种酶参与 TCA 循环,包括磷酸烯醇式丙酮酸羧化酶(PEPC)、苹果酸脱氢酶(MDH)、苹果酸酶(NADP-ME)、鸟头酸酶(ACO)、NAD 依赖型异柠檬酸脱氢酶(NAD-IDH)和琥珀酸脱氢酶(SDH)等<sup>[3]</sup>。梨果中的有机酸主要储存在液泡中,有机酸的转运由许多蛋白质介导<sup>[12]</sup>。糖酸含量是由多个基因控制的数量性状,是一个复杂的代谢网络的一部分<sup>[3-4]</sup>。梨品种果实糖酸组分含量形成的差异,以及与野生种间的差异,仍需要更深入的分子机制研究去解释。

随着现代化仪器的快速发展,研究人员利用高效液相色谱(HPLC)等精准测定果实可溶性糖酸组分,加之分子生物学和基因组测序等技术的迅速更新,对果实糖酸表型和基因型的精准评价成为可能。近年来关于梨果实糖酸的相关研究已经取得重要成果,主要涉及梨果实发育过程中糖酸含量研究、梨果采后室温和低温糖酸含量研究、影响梨果糖酸含量的因素研究,以及相关基因组、转录组、蛋白组、基因和分子标记开发等分子机制研究。笔者在本文中围绕以上所述的几个方面进行综述分析,并进行总结和展望,以期为未来梨果实糖酸研究和梨新品种选育提供参考。

## 1 梨果实生长发育过程中糖酸含量研究

大多数研究表明,在梨果实生长发育过程中,果实中的有机酸通常在果实发育早期形成,随着果实成熟逐渐减少;而可溶性总糖含量在果实发育前期较少,发育后期呈增加趋势。在玉露香梨果实生长发育过程中,总糖含量呈现出“慢-快-慢-快”的上升趋势<sup>[10]</sup>。大部分梨品种幼果期果实中的糖以山梨醇为主,成熟果实中的糖以果糖为主<sup>[10, 13-16]</sup>,而成熟的云红梨 1 号果实中山梨糖醇仍是含量最多的糖,其次为果糖、蔗糖和葡萄糖<sup>[13]</sup>。杨志军等<sup>[17]</sup>研究鸭梨×京白梨杂交后代高糖个体和低糖个体的果实糖动态变化,发现发育前期总糖含量逐渐升高,其中果糖含量最高,山梨醇含量次之,蔗糖含量相对较低。成熟时,高糖个体的果糖含量显著低于低糖个体,并且蔗糖、葡萄糖、山梨醇乃至总糖含量均显著高于低糖个体。潘俨等<sup>[18]</sup>研究库尔勒香梨果实发育过程中糖含量变化,分别测定果心、果肉和果皮的 4 种可溶性糖组分含量,发现不同发育阶段糖组分比例有明显差异,成熟期均表现为果糖含量比例升高,山梨醇含量比例明显下降。南红梨是南果梨的一个红色芽变品种,南红梨果实发育过程中蔗糖含量普遍高于南果梨,采收期南红梨果实中蔗糖含量约为南果梨果实的 2 倍<sup>[14]</sup>。采用黄冠梨和鸭梨对比发现,黄冠梨果实中的糖代谢过程为典型的“山梨醇-淀粉-可溶性糖”中间模式,鸭梨果实中糖代谢过程为典型的“山梨醇-蔗糖-淀粉-可溶性糖”中间模式<sup>[19]</sup>。

在梨果实发育过程中有机酸含量呈先上升后逐渐下降的趋势<sup>[10, 20-22]</sup>。霍月青等<sup>[23]</sup>研究 4 个砂梨(*P. pyrifolia* Nakai)品种有机酸含量,总有机酸含量随果实增长呈下降趋势,主要是奎尼酸下降幅度很大,苹果酸呈先上升后下降的抛物线变化趋势,而以柠檬酸占优势型的品种,在果实发育的中期会发生苹果酸下降而柠檬酸升高的转变。库尔勒香梨果实 在不同阶段的有机酸含量变化差异明显,在 5 月份时苹果酸含量( $\rho$ )最高,达到  $1.198 \text{ g} \cdot \text{L}^{-1}$ ,柠檬酸含量达到  $0.476 \text{ g} \cdot \text{L}^{-1}$ ,酒石酸达到  $0.382 \text{ g} \cdot \text{L}^{-1}$ <sup>[22]</sup>。李甲明等<sup>[24]</sup>研究鸭梨×京白梨杂交后代高酸个体和低酸个体的果实有机酸动态变化,高酸个体属于苹果酸优势型,低酸个体属于柠檬酸优势型,且成熟时两者在总酸含量上表现出的差异主要是苹果酸含量的差异

所致。刘清鹤等<sup>[25]</sup>研究鲁秀梨果实的有机酸动态变化,果心、果肉、果皮不同部位有机酸组分含量不同,有机酸含量随着果实成熟逐渐下降,果皮部位有机酸含量低于果肉和近果心部位,后二者相似。Wu等<sup>[26]</sup>对193种梨成熟果实进行研究,发现各有机酸组分在梨果实中含量从高到低依次为苹果酸>柠檬酸>奎尼酸>草酸>莽草酸,总酸含量分别与苹果酸、柠檬酸含量存在显著的正相关性。果实中糖酸含量之间呈显著的负相关性<sup>[1]</sup>。

## 2 采后梨果实糖酸含量研究

### 2.1 室温贮藏

果实在贮藏过程中的成熟与衰老以及糖酸含量变化是一系列生理生化反应所共同调控的结果。梨是呼吸跃变型果实,采后贮藏期间的糖损失是果实自身呼吸消耗和蔗糖酶活性变化的结果<sup>[27]</sup>。Wang等<sup>[28]</sup>研究早红考密斯成熟梨果实采后糖含量,采后果实中果糖是主要的糖,其次是葡萄糖、蔗糖和山梨醇;随着后熟过程推进,果实中果糖和葡萄糖含量逐渐增加,山梨醇含量逐渐减少,蔗糖含量先升高后降低。Wang等<sup>[29]</sup>研究丰水梨亦发现,苹果酸含量在贮藏期间下降。丰水梨在室温贮藏过程中,果糖和葡萄糖逐渐积累;蔗糖、山梨醇和苹果酸含量呈下降趋势<sup>[30]</sup>。Xu等<sup>[31]</sup>研究早熟山梨(*P. ussuriensis*)在室温下0~8 d后熟过程中的代谢产物,认为可溶性糖类含量的变化不是影响梨果实后熟的原因,果胶、脂质代谢物和一些激素如脱落酸(ABA)等变化影响梨果实的后熟和软化。

### 2.2 低温贮藏

低温环境有利于延缓水果各种生理代谢,延缓果实品质变化,从而延长水果的保质期。Zhao等<sup>[27]</sup>研究冷藏中7个梨品种果实糖代谢发现,果糖是主要的糖,占总糖的60%以上,其次是葡萄糖和蔗糖;在冷藏过程中,果糖、葡萄糖、蔗糖和可溶性固形物含量增加,至90 d后逐渐下降。Lwin等<sup>[32]</sup>比较圆黄梨大果(550~950 g)和小果(250~350 g)的糖含量,在冷藏和货架期,大果的葡萄糖和果糖含量高于小果,而蔗糖和山梨醇含量低于小果。Dias等<sup>[33]</sup>比较Rocha梨果实低温贮藏1周和1个月后的糖酸含量,两批果实之间的蔗糖和果糖存在显著差异,第2批的可溶性糖含量较高,葡萄糖和山梨醇含量几乎没有随时间的变化;第2批样品中的苹果酸含量显著

升高,且在货架期的开始和结束之间略有增加。黄丽等<sup>[34]</sup>以玉露香梨、红香酥梨和酥梨为试材,研究冷藏期(0~240 d)糖酸含量变化,3种梨的可溶性糖含量均表现为先升高后降低趋于稳定的趋势,红香酥梨和酥梨60 d达到最高,玉露香梨于180 d达到最高,不同糖组分含量变化不同;玉露香梨和酥梨总有机酸含量变化动态一致,均先下降后趋于稳定,红香酥梨总有机酸含量先上升后下降,苹果酸是3种梨果实中含量最高的有机酸,其变化动态与总有机酸相似。在低温贮藏期(0~180 d)鲁秀梨果实可溶性总糖含量整体呈先上升后下降趋势,在贮藏30 d时可溶性总糖含量最高,不同糖组分含量的变化不同<sup>[25]</sup>。在低温(1 °C)贮藏时鲁秀梨果实有机酸含量呈先下降后稳定趋势,有机酸组分含量变化有所不同;在贮藏60 d时,有机酸含量最低,之后随着贮藏期延长,有机酸含量轻微上升后趋于稳定<sup>[25]</sup>。Wang等<sup>[35]</sup>研究发现,(0±0.5) °C、85%~90% RH低温贮藏可有效延长南果梨采后贮藏期,冷藏果实的可溶性总糖含量高于未冷藏果实,但长期冷藏会导致果实中的蔗糖含量下降。

## 3 影响梨果糖酸含量的因素

### 3.1 品种

梨果实中糖酸含量及其组分的不均匀分布,造就了不同品种果实的风味差异。不同栽培品种梨果实中总糖和总酸及其组分含量不同<sup>[25,36-38]</sup>,根据苹果酸和柠檬酸比值可将不同品种划分为苹果酸优势型和柠檬酸优势型<sup>[8,10,39]</sup>。霍月青等<sup>[23]</sup>研究70个砂梨成熟果实的有机酸含量,将砂梨品种分为苹果酸优势型和柠檬酸优势型两类,其中选育品种基本上是苹果酸型的,柠檬酸型的基本是地方品种;选育品种的苹果酸含量与比率变化幅度较地方品种小,且含量显著高于地方品种,选育品种的柠檬酸含量与比率都显著低于地方品种。姚改芳等<sup>[40]</sup>对10个不同栽培种的梨果进行糖酸分析,发现白梨(*P. bretschneideri* Rehd.)和砂梨的总糖和总酸含量都较低,秋子梨(*P. ussuriensis* Maxim)的总糖和总酸含量都较高,新疆梨(*P. sinkiangensis* Yu)的总糖含量相对较高,总酸含量居中,西洋梨(*P. communis* L.)的总糖含量较高,总酸含量最高。姚改芳等<sup>[41]</sup>分析5个栽培种的98个梨品种果实糖酸含量,发现西洋梨的总酸含量最高,其次是秋子梨、白梨和砂梨,含量最低

的是新疆梨,大部分西洋梨品种是柠檬酸优势型。李甲明等<sup>[20]</sup>将茌梨、鸭梨和八里香这3个品种进行对比,发现在果实成熟时,茌梨的总酸含量最高,鸭梨居中,八里香最低,苹果酸是引起品种间显著差异的主要因素。Akagić等<sup>[6]</sup>测定10个西洋梨品种成熟果实可溶性糖含量,结果表明果糖含量最高,其次是山梨醇和葡萄糖含量,蔗糖含量最低。Gao等<sup>[42]</sup>以翠冠梨为试材,发现含有较高的柠檬酸是造成果实核心酸的原因。张莹等<sup>[15]</sup>研究发现,秋子梨栽培品种南果梨和野生资源东宁山梨1果实之间糖和淀粉的积累规律存在差异。安景舒等<sup>[43]</sup>研究发现,不同品种间,果糖和葡萄糖的含量相对稳定,蔗糖和山梨醇含量变化较大。

### 3.2 光照

光照是影响梨树光合作用的重要因素,果实套袋可改变果实生长发育的微环境,影响果实糖酸代谢<sup>[44-45]</sup>。柯凡君等<sup>[46]</sup>研究套纸袋对翠冠梨和黄金梨果实的糖组分含量变化,两个品种的套袋果实在发育过程中糖组分变化趋势与对照基本一致,套袋果实可溶性糖含量均低于对照但差异不显著,对不同糖组分影响有差异。李芳芳等<sup>[44]</sup>研究两种果袋对库尔勒香梨可溶性糖含量的影响,套袋降低了库尔勒香梨果实可溶性糖含量,但不影响其变化规律,在果实成熟时,套紫色膜袋对蔗糖、葡萄糖和山梨醇含量的影响比套纸袋大。李芳芳等<sup>[47]</sup>研究表明,库尔勒香梨果实套紫色塑料膜袋后,各可溶性糖及总糖含量均无显著变化,总酸和苹果酸含量显著减少,其他有机酸含量变化差异不显著;果实套纸袋后,蔗糖和山梨醇含量显著减少,柠檬酸含量显著增加,其他酸含量变化差异不显著。孔佳君等<sup>[48]</sup>利用红、橙、绿、蓝、紫色滤光膜单层果袋处理砀山酥梨,套袋果实可溶性糖含量均显著低于对照,红色套袋果实可溶性糖含量最低,相比对照减少31.27%,且紫色和橙色果袋内果实的可溶性糖含量较高。李刚波等<sup>[49-50]</sup>对苏翠1号研究发现,不同时期套袋,果实中可溶性固形物含量和糖酸比明显低于对照,套袋果实的山梨醇含量并没有显著差异,但蔗糖、葡萄糖、果糖含量明显降低,同时对苹果酸、奎尼酸和总酸含量影响较大,对柠檬酸含量影响不大<sup>[51]</sup>。不同果袋的效果亦有差别,套黄白纸袋果实的可溶性固形物含量、糖酸比和总糖含量都高于复合纸袋果实,果实综合品质更好<sup>[49-51]</sup>。徐锴等<sup>[52]</sup>以红色梨为试材,研究发现套袋后果实中的可

溶性固形物含量增加,褐色和蓝色果袋处理降低了果实糖酸比。Wang等<sup>[45]</sup>对茌梨研究发现,与未套袋果实相比,聚乙烯袋和无纺布袋处理都不利于可溶性糖积累。吴瑞媛等<sup>[53]</sup>研究表明,铺设反光膜可以提高翠冠梨果实单果质量,促进果实糖积累。

### 3.3 激素

梨果实中糖酸代谢是一个复杂的过程,植物激素参与相关的调控<sup>[54]</sup>,外用激素可以调节果实糖酸含量<sup>[55-57]</sup>。韩彦肖等<sup>[55]</sup>利用不同生长调节剂处理黄冠梨,果实成熟时,赤霉素( $GA_3$ 和 $GA_{4+7}$ )处理果实的蔗糖含量显著高于对照; $GA_3$ 处理果实的苹果酸和有机酸含量显著高于对照,萘乙酸(NAA)、生长素(IAA)和 $GA_{4+7}$ 处理果实与对照无显著差异,不同类型生长调节剂处理对果实中莽草酸含量无显著影响。李节法等<sup>[58]</sup>用2.7%  $GA_{3+4}$ 处理花后25 d的翠冠梨,果实膨大前期,果实以山梨糖醇为主,显著高于对照;后期果糖含量上升,山梨糖醇含量下降, $GA$ 处理果实的总糖含量显著高于对照。施春晖等<sup>[56]</sup>对翠冠梨喷施适宜浓度的NAA、NAA-Na两种调节剂,与对照相比,具有高效疏果作用,提高了果实中蔗糖含量,但是NAA与NAA-Na调节剂之间差异不显著。Gu等<sup>[54]</sup>对翠冠梨施用10 mg·L<sup>-1</sup> IAA或1 mg·L<sup>-1</sup> ABA,促进梨果实中山梨醇积累。Tian等<sup>[59]</sup>研究库尔勒香梨和其芽变早美香梨的激素、糖含量与果实大小的关系,发育过程中葡萄糖和山梨糖醇的差异较大,早美香梨在整个细胞分裂过程中积累了大量的山梨糖醇,葡萄糖、山糖醇含量与细胞数呈正相关,葡萄糖、山梨醇、玉米素、脱落酸及内源激素的比例可能与库尔勒香梨和早美香梨的细胞分裂有关。Liu等<sup>[9]</sup>利用100 μmol·L<sup>-1</sup> 褪黑素(MT)处理早酥梨,发现在果实成熟期间,MT增加了可溶性糖含量,特别是蔗糖和山梨糖醇含量,而MT对果实的有机酸含量没有影响。Wang等<sup>[60]</sup>利用100 μmol·L<sup>-1</sup> MT处理接种轮纹病菌(*Botryosphaeria dothidea*)的翠冠梨,外源褪黑素处理能提高梨果实中可溶性糖和有机酸含量,增强轮纹病抗性。Wang等<sup>[61]</sup>利用10 mmol·L<sup>-1</sup> 甜菜碱(GB)处理南果梨,与对照相比,低温贮藏后果实蔗糖含量升高,果糖和葡萄糖含量降低。邵白俊杰等<sup>[62]</sup>在大蕾期用300 mg·L<sup>-1</sup> 乙烯利处理库尔勒香梨对果实品质影响最大,使脱萼果的可溶性固形物和可溶性糖含量与对照相比分别显著提高12.03%和10.22%,可滴定酸含量则显著降低

19.75%。韩春红等<sup>[57]</sup>对3个红皮梨品种叶面喷施0.5、1.0、2.0 mmol·L<sup>-1</sup>的茉莉酸甲酯(MeJA)和二氢茉莉酸内酯(PDJ),结果表明成熟期果实果糖、葡萄糖、山梨醇、总糖含量及糖酸比上升,但果实总酸含量下降。

### 3.4 肥料

在梨树上施用有机肥和矿质营养能显著提高果实品质和产量,有助于改善糖酸含量比例<sup>[63-64]</sup>。Shen等<sup>[63]</sup>利用不同浓度梯度氧化钾(K<sub>2</sub>O)肥处理黄冠梨,连续两年与对照相比,增加钾的施用量促进了葡萄糖、果糖、山梨醇和蔗糖在果实中积累。高钾促进光合作用,增加果实中山梨醇、蔗糖、果糖含量。果实成熟时,低钾会抑制蔗糖和有机酸代谢,但能促进果糖和葡萄糖积累<sup>[65]</sup>。周君等<sup>[66-67]</sup>在黄金梨幼果期进行喷钙处理,与对照相比,氨基酸钙和硝酸钙[Ca(NO<sub>3</sub>)<sub>2</sub>]处理的果实均能提高可溶性固形物含量和糖酸比,氨基酸钙效果更好。魏树伟等<sup>[68]</sup>利用4%氯化钙(CaCl<sub>2</sub>)处理南果梨,结果显示,钙处理提高了南果梨果实中可溶性糖含量,其中商熟期前5 d时钙处理总糖含量较对照提高了4.68%,果实中有机酸含量较对照提高了49.93%;商熟期可溶性糖含量较对照提高了8.43%,后熟5 d时可溶性糖含量较对照提高了10.97%,而果实中的有机酸含量低于对照。Pessoa等<sup>[69]</sup>以不同浓度Ca(NO<sub>3</sub>)<sub>2</sub>和CaCl<sub>2</sub>喷施Rocha梨,与对照相比,采收时钙处理梨果中蔗糖、葡萄糖、果糖和山梨醇含量不受影响,贮藏后钙处理果实中可溶性糖含量保持较高水平。Xu等<sup>[70]</sup>以爱甘水梨为试材,研究发现,与普通复合肥料相比,缓释肥增加了果实可溶性固形物含量,袋控缓释肥显著提高了糖酸比。Wang等<sup>[64]</sup>以砂梨新品种初夏绿为试材,发现与普通化肥相比,生物有机肥和有机肥处理均可以增加梨果实中蔗糖含量,降低果糖和葡萄糖含量,并促进柠檬酸的降解。刘松忠等<sup>[71]</sup>研究表明,施用堆肥+叶片喷施氨基酸肥或腐熟动物废弃料,可显著提高黄金梨果实总糖、蔗糖、果糖和葡萄糖含量。邵微等<sup>[72]</sup>利用不同有机酸+氮磷钾肥配施处理红宝石梨,以单独用氮磷钾肥为对照处理,结果表明,不同浓度苹果酸、柠檬酸及草酸与氮磷钾肥配施处理的可溶性糖含量显著高于对照,其中5%苹果酸+氮磷钾肥配施显著提高了梨的可溶性固形物含量与糖酸比,果实品质的提升效果最佳。丁易飞等<sup>[73]</sup>设置4个氮素水平(165、330、660和990 kg·hm<sup>-2</sup>)

处理寿新水梨,梨果实可溶性固形物、可溶性糖含量及糖酸比随施氮量提高呈先增加后降低的趋势,最大值均出现在330 kg·hm<sup>-2</sup>处理,果实中山梨醇含量比对照分别提高了25.3%和90.9%。张海棠等<sup>[74]</sup>研究不同钾镁配比对早酥梨果实糖酸组分含量的影响,钾镁配比为10.76时,糖酸比最高,早酥梨果实中果糖含量最高,占总糖含量的52.52%,为果糖积累型;早酥梨为柠檬酸优势型,随钾镁配比的提高,苹果酸含量先增加后降低,柠檬酸含量的变化趋势与苹果酸完全相反。

### 3.5 1-MCP处理

1-甲基环丙烯(1-MCP)是一种有效的乙烯拮抗剂,在贮藏过程中具有保持果实质量的潜力,已被用于维持许多呼吸跃变果实的储存质量和延长其保质期<sup>[75-76]</sup>。1-MCP处理南果梨延缓了可溶性固形物和可滴定酸的损失,并显著抑制可滴定酸含量的下降,但也延缓了总可溶性固形物含量的增加<sup>[76]</sup>。Lwin等<sup>[77]</sup>采前1周用1-MCP处理圆黄梨,与对照相比,采收时蔗糖含量上升,山梨醇含量降低,冷藏3个月后果实可溶性固形物含量高于未处理的对照,不同糖组分含量变化不一致。Lwin等<sup>[78]</sup>利用1-MCP采前处理Chuhwangbae梨,1-MCP处理的果实的蔗糖水平高于未处理的果实,冷藏后及货架期果实可溶性固形物含量高于未处理对照。Lwin等<sup>[79]</sup>利用1-MCP采后处理圆黄梨,冷藏6个月后与未处理的对照组相比,果糖、葡萄糖和苹果酸含量降低,但在储存的后半段保持了更高的蔗糖和山梨醇含量。Tokala等<sup>[75]</sup>以1-MCP处理Gold Rush梨果实,冷藏后发现,1-MCP处理的果实可溶性固形物含量较高,并且果糖和山梨醇含量高,而蔗糖含量低;有机酸含量没有明显变化。Latt等<sup>[80]</sup>利用1-MCP处理新品种Greensis梨,发现与对照相比果实中果糖、葡萄糖含量减少,而果实中蔗糖含量的提高。Wang等<sup>[29]</sup>利用1-MCP处理成熟丰水梨,与对照相比,熏蒸显著抑制了丰水梨的质量恶化,保持了较高的苹果酸含量。Bai等<sup>[76]</sup>用1-MCP处理成熟南果梨,室温货架期1-MCP处理果实柠檬酸含量高于对照,两者均呈降低趋势。

### 3.6 其他

矮化砧木影响接穗的生长,对提高果实质量和产量很重要<sup>[81]</sup>。Wang等<sup>[82]</sup>研究发现,嫁接云南榅桲(*Cydonia oblonga* Mill.)的成熟早酥梨果实含糖量

高于嫁接杜梨(*P. betulifolia*)。徐文清等<sup>[83]</sup>利用川梨(*P. pashia*)、豆梨(*P. calleryana*)和杜梨为砧木嫁接丰水梨,结果表明不同砧木对接穗品种丰水梨果实中有机酸代谢具有调控作用,杜梨可以降低丰水梨果实中柠檬酸的含量,导致苹果酸含量与柠檬酸含量的比值升高。Liu 等<sup>[7]</sup>连续 2 a(年)测定砀山酥梨与丰水梨正反交后代群体果实糖酸含量,大部分个体的酸和糖含量、总酸含量和总糖含量均高于砀山酥梨,而低于丰水梨,趋于平均水平;母系亲本的选择对酸的含量有重要影响,父母本对糖组分含量和总糖含量没有显著影响。Duan 等<sup>[84]</sup>研究发现,0.8 mmol·L<sup>-1</sup>ATP 处理可以抑制南果梨果实中可溶性总糖含量的下降。Wang 等<sup>[85]</sup>以 10% CO<sub>2</sub> 处理鲜切翠冠梨,发现可以促进可溶性固形物的积累,加速贮藏末期葡萄糖、果糖、山梨醇和蔗糖的积累,分别比对照提高 12.58%、13.86%、24.7% 和 13.9%。

## 4 梨果糖酸分子机制研究

### 4.1 基因研究

糖含量是一个由多个基因控制的数量性状,许多关键的基因功能已被验证。李节法等<sup>[58]</sup>研究表明,外源赤霉素(GA)处理翠冠梨后,GA 处理显著提高梨果肉和果心组织中的可溶性糖含量,GA 诱导糖代谢相关酶基因的表达,如促进 *S6PDH*、*SS*、*SI* 和 *SPS* 基因表达上调,而前期抑制 NAD 依赖型山梨醇脱氢酶基因(*NAD-SDH*)的表达,并在果心和果肉中存在空间表达差异。丁易飞等<sup>[73]</sup>研究表明,成熟期 330 kg·hm<sup>-2</sup> 氮素水平处理显著上调果实中 *NAD-SDH3* 基因的表达,有利于山梨醇的分解,提高成熟期果实糖含量。Liu 等<sup>[9]</sup>研究表明,转化酶基因 *Pbinvertase1/2* 在 MT 处理的果实中的表达水平较低,导致酶活性较低, *PbSPS1/2/3* 表达提高促进蔗糖磷酸合成酶(*SPS*)的活性提高。Wang 等<sup>[45]</sup>研究表明,在梨果实套袋处理降低了光照度,*SPS* 基因表达水平降低,抑制蔗糖的合成。Abdullah 等<sup>[86]</sup>报道了 30 个蔗糖合酶(*SS*)基因,其中 *PbSS30*、*PbSS24* 和 *PbSS15* 在梨果实发育阶段具有潜在的作用。Li 等<sup>[4]</sup>研究钙依赖性蛋白激酶(*PbCPK28*),*PbCPK28* 表达量的升高导致了梨果实中果糖水平的显著升高。Ma 等<sup>[30]</sup>研究发现,酸性转化酶 1(*PbrAc-Inv1*)和转化酶抑制剂 5(*PbrII5*)参与蔗糖降解,*PbrII5* 可以与液泡中的 *PbrAc-Inv1* 相互作用,调节液泡转化酶活性,从而改

变梨果实的糖组成。Shen 等<sup>[65]</sup>研究表明,高浓度钾肥能提高叶片的光合效率,而低浓度钾肥诱导参与山梨醇代谢的 3 个 *SDH* 和 2 个 *S6PDH* 基因表达上调,促进果糖的积累。

糖转运体(ST)有不同类型,梨相关的糖转运家族基因如 *PbSOTS*<sup>[87]</sup>、*PbSWEETs*<sup>[11, 88-89]</sup>、*PbTMTs*<sup>[90-91]</sup>、*PbSUTs*<sup>[92]</sup>、*PbPLTs*<sup>[93]</sup>、*PbTSTS*<sup>[4]</sup> 等。Li 等<sup>[88]</sup>研究表明, *PbSWEET5* 表达下调,与蔗糖水平呈负相关,说明 *PbSWEET5* 可能对蔗糖外排和调节果实糖含量起关键作用。Ni 等<sup>[89]</sup>研究表明, *PbSWEET4* 可以促进糖从叶片流向其他器官,过表达 *PbSWEET4* 可显著降低叶片中蔗糖的含量。Li 等<sup>[94]</sup>发现 *PuSWEET15* 在梨果实中运输蔗糖,过表达 *PuSWEET15* 会增加蔗糖含量,而沉默 *PuSWEET15* 则会降低蔗糖含量。Qin 等<sup>[95]</sup>研究证实了液泡质体单糖转运体相关基因 *PbrTMT1* 的功能,该基因负责促进梨果实中果糖的积累。Yu 等<sup>[11]</sup>研究表明, *PbSOT6/20* 的表达模式与梨果实中山梨醇积累模式的相关性更强,低质量分数(100 mg·g<sup>-1</sup>)的外源山梨醇诱导了 *PbSOT6/20* 的表达,而在叶片中不表达。Li 等<sup>[93]</sup>研究表明 5 个糖转运体基因(*PbTMT2*、*PbTMT3*、*PbTMT4*、*PbPLT9* 和 *PbPLT22*)与梨果实发育和成熟过程中的糖积累水平密切相关,可能比其他基因发挥更重要的作用。Cheng 等<sup>[90]</sup>研究表明, *PbTMT4* 被认为是梨果中果糖、葡萄糖和蔗糖积累的重要贡献者,转此基因的成熟番茄的葡萄糖和果糖含量比对照植株增加了约 32% 和 21%。Wang 等<sup>[64]</sup>研究表明,施用有机肥和生物有机肥后,糖转运体基因的转录丰度均显著增加,如 *SOT*、*SUT14*、*UDP-GLUT4*、*UDP-SUT*、*SUC4*、*SUT7*、*SWEET10* 和 *SWEET15*,促进糖的运输,两种肥料均促进果实中蔗糖积累和柠檬酸降解。Wang 等<sup>[82]</sup>研究发现,嫁接榅桲的早酥梨基因 *PbSWEET6* 表达量高于嫁接杜梨的,过表达基因 *PbSWEET6* 的转基因番茄果实和梨果实愈伤组织中蔗糖和葡萄糖含量增加。

大多数梨品种果实中主要的有机酸是苹果酸和柠檬酸,目前相关功能基因的研究明显少于糖的研究。Wang 等<sup>[29]</sup>研究发现,1-MCP 熏蒸可上调基因 *cyNAD-MDH* 的表达和 *cyNAD-MDH* 活性,抑制 *cyNADP-ME* 活性,从而使储藏的丰水梨保持更高的苹果酸丰度。Song 等<sup>[12]</sup>选择 5 个梨品种研究,发现 *PbPH5* 过表达显著增加了苹果酸含量,相比之下,

通过RNA干扰沉默基因*PbPH5*则显著降低了其转录水平和梨果实中苹果酸含量。Li等<sup>[3]</sup>比较研究高酸和低酸两个梨品种,结果表明,三羧酸循环(TCA)相关通路和转运蛋白基因在有机酸积累中发挥重要作用,12个TCA相关基因和3个转运体被筛选为候选基因。

#### 4.2 转录因子研究

转录因子(TF)在调节碳水化合物的分配和糖酸的代谢中发挥重要作用,调控梨果糖酸的部分转录因子功能已被验证。Lü等<sup>[96]</sup>研究发现,高蔗糖含量参与了C<sub>2</sub>H<sub>2</sub>、BZIP、GRAS、MADS和WRKY的上调,它们与蔗糖生物合成相关的靶基因启动子上的特定结合位点相互作用。Li等<sup>[94]</sup>研究发现,转录因子*PuWRKY31*与*PuSWEET15*基因启动子结合,诱导其表达,*PuWRKY31*的高表达导致南果梨芽变品种的蔗糖含量高于南果梨。Li等<sup>[97]</sup>利用外源性蔗糖处理南果梨,蔗糖激活*PuWRKY31*表达,*PuWRKY31*的表达增强了*PuACSlα*和*PuACO1*的表达,从而导致梨果实中乙烯产量的增加,表明蔗糖调节梨果中乙烯生物合成。Li等<sup>[3]</sup>研究高酸梨果酸代谢TCA通路相关的转录因子中,8个MYB、6个bHLH和6个NAC调控作用突出。Lin等<sup>[98]</sup>从杜梨中筛选到转录调控基因*PbWRKY40*,通过超表达和沉默该基因,研究表明,*PbWRKY40*至少部分地通过调控*PbVHAB1*的表达,在耐盐性和有机酸积累方面发挥作用。

#### 4.3 基因组学研究

基因组测序和基因组学的快速发展为大规模梨基因组测序和分析提供了便利,使表型和基因型的比较分析研究取得了重要进展。Li等<sup>[93]</sup>研究ST基因家族的染色体分布和基因复制,对梨基因组的研究发现了75个糖转运体基因,其中有6个基因属于蔗糖转运体(SUT)家族,表达分析显示,大多数ST基因在果实发育过程中表达。Wu等<sup>[2]</sup>从基因组水平上分析63个亚洲梨和50个欧洲梨,发现了许多糖相关基因,对于亚洲梨,在选定的区域共鉴定出45个糖相关基因,在欧洲梨中只鉴定出11个糖相关基因;但发现参与有机酸代谢的基因较少,亚洲梨和欧洲梨中存在不同优势酸成分。Zhang等<sup>[99]</sup>对312个砂梨品种开展GWAS关联分析,获得大量与可溶性糖和有机酸等代谢相关的基因。Nishio等<sup>[8]</sup>对106个日本梨和1112个杂交后代开展基因组GWAS关联分析,基因组最佳线性无偏预测(GBLUP)对蔗

糖、果糖和葡萄糖的基因组选择的准确性相对较高(0.67~0.75),这表明选择蔗糖和果糖含量高、葡萄糖含量低的个体是可能的。

#### 4.4 其他研究

Wu等<sup>[100]</sup>研究证明,miRNAs广泛参与调控果实的发育和果实品质的形成,9个miRNAs被鉴定参与酥梨果糖和酸代谢。Reuscher等<sup>[101]</sup>基于定量蛋白质组学,为梨果实发育过程中的糖积累以及关键反应和转运步骤的候选基因提供了新的见解。Nishio等<sup>[102]</sup>利用砂梨秋月后代群体开发糖相关QTL标记,在连锁群LG1和LG7上发现了两个与个体糖含量相关的区域,认为侧翼区域的酸性转化酶基因*PPAIV3*和*PPAIV1*很可能是控制个体糖含量的候选基因。Jiang等<sup>[16]</sup>研究获得与总糖含量相关的2个QTLs标记(LG12-Chr3和LG6-Chr7),鉴定了几个与果实糖积累相关的差异表达基因,在甜梨后代中,*PpS6PDH*和*ATP-PpPFK*表达上调,蔗糖转运体*PpSUT*表达下调。

### 5 小结与展望

梨品种果实糖酸含量及组分因其不同发育阶段、不同品种、采后不同阶段而不同,不同的糖酸含量及组分差异形成了丰富多样的酸甜风味。关于糖酸含量及组分差异的研究成果已经相当丰富,各种调控糖酸含量的措施研究已经具有很强的指导性,基于采前采后的相关研究,针对具体梨品种可开展调控果实糖酸的生产实践应用。关于梨品种果实糖酸含量及组分差异的分子机制研究,在功能基因、转录调控、QTLs分子标记、基因组学和蛋白组学方面也已经取得一系列成果,但是果实糖酸代谢是十分复杂的生理生化代谢网络的一部分,依然有巨大的研究空间。现有梨果实糖酸分子生物学的研究成果已经阐释了梨果糖酸代谢的部分现象,并已在梨杂交群体后代评价中进行探索研究,这将有助于开展不同糖酸比的梨新品种选育。

梨属植物是高度杂合的物种,有着漫长的进化过程。梨栽培品种是人类长期驯化选择的产物,许多果实经济性状优于梨野生种。关于梨果实糖酸的研究,应从以下几方面加强探索:一是开展梨品种和野生型之间的比较研究,探索糖酸代谢的关键功能基因和调控因子,从而更清晰地阐释梨品种果实糖酸性状驯化的分子机制;二是开展杂交群体梨果实

糖酸遗传规律的研究,进行相关功能基因定位,以开发相关糖酸分子标记,指导梨新品种选育;三是利用基因编辑技术完善梨品种果实糖酸代谢,以期实现果实糖酸含量的精准调控,从而指导梨新品种选育。伴随人类科技的日新月异和各种高科技技术的综合应用,将使有目的地改造梨品种果实糖酸含量和精准调控梨果实酸甜风味成为可能。

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