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果实糖代谢及其相关酶基因研究进展

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摘要:果实的糖分种类、含量及其构成比例和形成动态是果实风味形成的重要基础之一,同时对其代谢过程中色泽的形成以及其他营养成分的代谢具有重要的影响,是决定果实品质和商品价值的主要因素,对果实生长发育过程中糖的种类、数量、代谢途径的变化、代谢相关酶的变化及基因调控研究进行了整理综述,以期为果实品质改善、提高商品价值提供一定的理论参考。在糖的生理功能上,糖类物质是果树生长发育的重要物质,其不仅作为能源物质参与果树的生长发育过程,而且作为一种信号物质参与植物成花与果实成熟控制基因的表达调节,并且能抵抗外界非生物胁迫的作用;在糖的类型上,不同物种、不同器官组织、不同果实部位间糖的主要类型、数量、出现顺序均存在差异;叶片光合作用产物经过蛋白跨膜运输和系列酶反应,最终以蔗糖、山梨醇、果糖和葡萄糖的形式分散于果实的不同部位,使得果实具有独特的风味品质,蔗糖代谢、山梨醇代谢、已糖代谢和淀粉代谢途径是目前公认的4大糖代谢途径,这几种途径均由不同类型的代谢酶参与,不同物种间糖积累机制存在较大差异,代谢酶的调控作用也存在较大的差别,目前主要代谢酶有酸性转化酶(AI)、中性转化酶(NI)、糖合成酶(SS)、蔗糖磷酸合成酶(SPS)等;在糖相关代谢酶基因上,不同果实生长发育时期,相关代谢基因的表达差异会导致其不同时期的糖分的积累量出现差异,依靠先进的科学技术水平,现已克隆出许多和糖代谢相关的基因;糖代谢受到各种因素的影响,可以分为环境因素与栽培管理因素,其中环境因素主要是光、温度、湿度、气体等,栽培管理措施主要是指套袋、铺设反光膜、胁迫、施肥等栽培技术,均会对糖代谢造成一定的影响。果实糖代谢是一个较为复杂的生理过程,内外影响因素较多,果实糖积累过程中其不同类型的糖组分动态变化及相关酶调控机制已较为清晰,但仍需进一步通过制备抗体等方式分离纯化糖代谢过程中的关键酶,以明确酶作用中心,同时应采用多组学联用的方式明确关键酶基因对果实糖分积累的直接作用方式,并探明糖积累的机理。

关键词:果实;糖代谢;酶基因

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Progress in Research on Sugar Metabolism and Related Enzyme Genes in Fruit

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Abstract: The sugar species, the contents, the proportion and the dynamic changes in the formation process of fruit are one of the important bases for the formation of fruit flavor. At the same time, it has an important effect on the color formation and metabolism of other nutrients. It can determine fruit quality and commodity value. In this paper, the changes in sugar species, quantity and metabolic pathway during fruit growth and development are concluded, and the changes in metabolic enzymes and gene regulation are summarized. It can provide some theoretical reference for improving fruit quality and increasing commodity value.In terms of the physiological function of sugar, it is an important substance in the growth and development of fruit trees.It not only participates in the growth and development process of fruit trees as an energy substance, but also participates in the expression regulation of genes controlling flowering and fruit ripening as a signal substance, and can resist the effects of abiotic stress.In terms of the types of sugar, there are differences in the main types, amounts and occurrence orders of sugar among different species, organs and tissues and fruit parts. In terms of sugar-related metabolic enzymes, the photosynthetic products of leaves are transported through protein transmembrane and a series of enzyme reactions, and finally dispersed to different parts of the fruit in the form of sucrose, sorbitol, fructose and glucose, which gives the fruit a unique flavor quality. Sucrose metabolism, sorbitol metabolism, hexose metabolism and starch metabolism pathway are the four recognized glucose metabolism pathways, which are all involved by different types of metabolic enzymes. There are great differences in the mechanism of sugar accumulation among different species, as well as in the regulatory role of metabolic enzymes. Currently, the major metabolic enzymes include acid invertase (AI), neutral invertase (NI), sugar synthase (SS), sucrose phosphate synthase (SPS), etc. In terms of sugar-related metabolic enzyme genes, the expression differences of related metabolic genes in different fruit growth and development periods will lead to differences in the amount of sugar accumulation. Relying on advanced scientific and technological levels, many sugar-related genes have been cloned. Sugar metabolism is affected by various factors, which can be divided into environmental factors and cultivation management factors, among which environmental factors are mainly light, temperature, humidity, gas, etc. Cultivation management measures mainly refer to bagging, laying of reflective film, stress, fertilization and other cultivation techniques, which will have a certain impact on sugar metabolism. Fruit sugar metabolism is a relatively complex physiological process, with many internal and external influencing factors. During the process of sugar accumulation, the dynamic changes in different types of sugar components and the regulation mechanism of related enzymes have been relatively clear. However, it is still necessary to further isolate and purify key enzymes in the process of sugar metabolism by means of preparation of antibodies, so as to clarify the action center of enzymes. At the same time, the direct effect of key enzyme genes on sugar accumulation in fruit should be determined by multiple study groups and the mechanism of sugar accumulation should be explored.

Keywords: fruit; glucose metabolism; enzyme gene

果实中的可溶性固形物含量和种类决定着果实的风味品质。可溶性固形物中最主要的成分是糖类物质，糖类物质是果实风味品质形成的决定性因素之一，可作为能源物质，保障植株的正常生理代谢活动[1-2]。之外，还是重要的信号调节物质，参与调控植物的生长发育及相关基因的表达[3-4]。不同种类和数量的糖类物质可形成果实不同的风味品质，提升果实品质需了解糖类物质的形成、运输、代谢等过程，挖掘糖类物质代谢的相关酶对其的影响，还需不断深入代谢酶的基因研究，从分子技术水平上提高果实风味品质。目前，国内外对糖代谢主要集中在苹果[5]、柑橘[6]、葡萄[7]、芒果[8]等园艺植物上，相关代谢酶则主要集中在蔗糖合成酶(SS)、转化酶、蔗糖磷酸合成酶(SPS)上，近年来国内外有关果实糖代谢及调控分子生物学研究已十分广泛。

1　糖的生理功能

果实糖代谢的生理生化过程较为复杂，是果实表现出成熟的主要标志之一[9]。糖类物质参与果实成熟过程，其不仅是果实主要风味物质，也是果实器官发育和物质代谢的物质基础，其糖的积累共有淀粉转化型、糖积累型、中间转化型3种[10]。糖浓度的高低可诱导或抑制有关基因的表达。糖类物质是果树生长发育的重要物质，其不仅作为能源物质参与果树的生长发育过程，而且作为一种信号物质参与植物成花与果实成熟控制基因的表达调节[11]，并且能抵抗外界非生物胁迫的作用[12]，在马铃薯植物微管的形成具有促进作用[13]。果实中积累的可溶性糖大部分是蔗糖、果糖和葡萄糖[14-15]。这些糖的积累与果实成熟具有重要关系。糖类物质是许多基因表达的调控信号，其中蔗糖在各种糖类中是最有效的信号分子。研究发现蔗糖可以作为信号分子参与ABA互作调控草莓果实的成熟[16]。

2　糖的种类

糖类物质是果实的重要组成成分，且是其他营养成分及芳香物质的合成原料。不同品种间糖变化趋势不一样，如在‘红阳’猕猴桃上，糖含量呈现缓慢上升的趋势，而在‘金魁’猕猴桃糖含量则呈现上下波动趋势[17]。一般情况下，果实进入成熟后期，由于淀粉的转化作用，果实的糖含量和可溶性固形物含量会迅速增加[18]。不同器官组织糖含量不同，糖的种类也存在一定的差异，如番茄花梗和果柄维管束中主要含有蔗糖，果实的其它部位中则主要含有葡萄糖和果糖；果皮组织和果实维管束中的葡萄糖、果糖含量该与果胶质和隔壁中的含量存在显著差异[19]。不同种之间含有的糖的种类也不尽相同，如葡萄以葡萄糖为主，桃、杏以蔗糖为主。这种现象的出现很大程度上决定于果实中的糖代谢类型及相关酶的活性[20]。同种植物但不同品种间，糖类型和含量也存在较大的差异，这已在9个白梨品种上的研究中得到证明[21]。在不同成熟期黄肉桃上的研究也发现，各糖组分的含量及其所占总量的比例均有差异，蔗糖含量及其所占总糖的比例表现为早熟＞中熟＞晚熟；山梨醇则正好相反，为早熟＜中熟＜晚熟；葡萄糖和果糖表现为晚熟高于早熟和中熟，早熟与中熟间差异不显著[22]。同一品种不同果实部位间糖类物质的积累也存在一定的先后顺序，枣果实果肩部位糖积累均早于果顶，且果肩可溶性糖含量均显著高于果顶[23]。

3　糖的相关代谢酶

叶片通过光合作用产生的光合产物是果实糖类物质积累的重要来源，以蔗糖和山梨醇的形式通过韧皮部长途运输后卸载到发育过程中的果实内（图1）[24]。经过蛋白跨膜运输和系列酶反应，最终以蔗

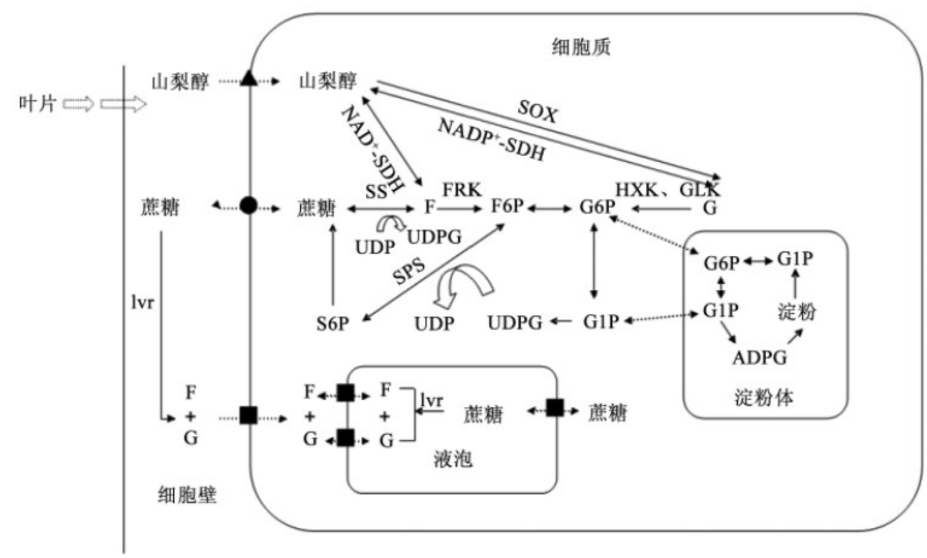

图1　果实细胞中的糖代谢途径[23]

Fig.1　Pathway of sugar metabolism in fruit cell [23]

糖、山梨醇、果糖和葡萄糖的形式分散于果实的不同部位，使得果实具有独特的风味品质[25]。蔗糖代谢、山梨醇代谢、己糖代谢和淀粉代谢途径是目前公认的4大糖代谢途径，这几种途径均由不同类型的代谢酶参与。不同物种间糖积累机制存在较大差异，代谢酶的调控作用也存在较大的差别。在西瓜上的研究则表明，酸性转化酶（AI）和中性转化酶（NI）是其主要的调控酶[26]；SS、AI和NI酶与番茄果实糖含量密切相关[27]；桃果实中的SS和SPS酶活性对糖积累起着关键性作用[28]；在草莓上，除转化酶外，己糖激酶对糖积累也起着关键作用[29]；红富士苹果果实蔗糖代谢主要受到AI和SS酶活性的调控[30]。在‘马来西亚1号’菠萝蜜上的研究发现，蔗糖的积累与AI活性呈显著负相关，与SS、SPS活性呈显著正相关[31]，与在葡萄上的研究一致[32]，并有研究认为其为菠萝蜜蔗糖合成的主要原因，AI和NI可能是导致果实甜度的主要酶[33]，在葡萄上的研究则表明AI是葡萄果实糖积累的最重要的调节因子[34]，这与枣上的研究一致[35]。在脐橙上则发现，SPS和SS是糖类物质积累的关键酶[15]；果实糖积累过程中存在蔗糖快速积累期，直接影响到果实成熟时可溶性糖含量的高低[36]。

4 糖的相关酶基因的调控

糖代谢是在相关酶基因的调节下完成的，不同果实生长发育时期，相关代谢基因的表达差异会导致其不同时期的糖分的积累量出现差异[37]。在‘南红梨’上的研究发现花后60 d时蔗糖合成酶*Pu SS1*和*Pu SS2*表达量最高，且*Pu SS2*在花后120 d及134 d也有较高的表达量；花后60 d和120 d时，蔗糖磷酸合成酶*Pu SPS2*和*Pu SPS1*分别达到最大值；在果实发育早期，蔗糖转运蛋白Pu SUT及β-葡萄糖甘酶*Pu BGLU1*、*Pu BGLU2*和*Pu BGLU4*有大量表达，在果实发育后期碱性/中性转化酶*Pu NINV1*和*Pu NINV2*有大量表达[38]。不仅在不同的果实生长发育期间其代谢酶表达会有所差异，在不同的植株部位，其糖代谢相关酶的表达也会有所差异，在桃上蔗糖合成酶的研究发现，蔗糖合成酶*Pp SS3*主要在果实和韧皮部表达，蔗糖合成酶*Pp SS1*在叶片中的表达较高[39]。在铁皮石斛上的研究表明，3个*Do Inv Inh*基因在根、茎、叶和花种都有表达，且其中*Do Inv Inh2*和*Do Inv Inh3*基因在根中表达量最低，而在花中表达量最高[40]。以桃为试验材料发现，蔗糖合成酶（*SS1*至*SS6*）在植物蔗糖代谢中起着关键作用，其外显子/内含子分析表明，*PpSS*基因含有11~13个内含子，具有高度的保守性，对6个*PpSS*基因的表达水平分析表明，*PpSS 1*的转录本在叶片和老韧皮部几乎检测不到，*PpSS 2*和*PpSS 3*在其他10个植物物种中几乎检测不到，而另外3个*PpSS*基因在所有组织中均有差异表达，并在组织发育的不同阶段被检测到[41]。在枣蔗糖合成酶*SS6*基因上表达也有类似的发现[42]。目前，在蔗糖酸性转化酶基因上的研究较多，如杨梅、柑橘、桃、甜瓜等。秦巧平等[43]以杨梅为试验材料发现，*MrIVR1*编码的蛋白质属于细胞壁酸性转化酶，半定量RT-PCR表达分析显示，其在果实发育早期表达量最高，在成熟果实中表达水平较低；安新民等[44]以柑橘基因组DNA为模板，采用PCR方法分别扩增出长约740 bp和530 bp的DNA片段，分别克隆入pBS-T和pMD18-T载体，通过测序获得柑橘酸性转化酶基因家族的两个成员A和B，分别长742 bp和524 bp，在GenBank中进行同源性检索，推测酸性转化酶基因成员A和B编码的蛋白分别定位于液泡和细胞壁。

依靠先进的科学技术水平，现已克隆出许多和糖代谢相关的基因。于喜艳等[45]从甜瓜花后25 d的果实总RNA中扩增出目标cDNA片段，检测其在甜瓜果实不同发育时期的表达变化发现，该基因在甜瓜果实花后25 d开始表达，随着果实的成熟，表达量升高；王君[46]根据GenBank中登录的酸性转化酶基因序列设计特异性引物，通过RT-PCR扩增获得长度为429 bp的酸性转化酶基因片段；应用同源克隆和RACE方法从在梨果肉中克隆到内切-β-1，4-葡聚糖酶基因的一个同源基因cDNA的全长序列，命名为*PbEG*，其碱基长度为1 971 bp，*PbEG*的开放阅读框编码493个氨基酸，相对分子量为54.596 1 kDa，等电点为9.14[47]；帅良等[48]以‘石硖’龙眼为试材，采用RT-PCR结合RACE技术成功克隆了3个龙眼中性转化酶基因全长cDNA序列，研究发现3个基因在不同组织中表达量具有较大差异，其中*DlNI-1*和*DlNI-2*在叶片中都具有较高的表达量，而*DlNI-3*在果皮组织中具有最高的表达量。*SS*基因被认为与草莓果实成熟有关，Hua等[49]利用RT-PCR方法克隆了*FaSS 1*的编码cDNA序列，进行基因沉默和原核表达，证明其具有较高的蔗糖裂解活性，在草莓果实成熟过程中起着重要的调控作用；相关研究表明生长素反应因子*SLARF 4*也参与控制番茄果实发育过程中的糖代谢[50]，同时低温驯化[51-52]、植物生长调节剂[53]对糖代谢基因的表达具有一定的影响。

5　栽培管理措施对糖代谢的影响

糖代谢受到各种因素的影响，可以分为环境因素与栽培管理因素，其中环境因素主要是光、温度、湿度、气体等，栽培管理措施主要是指套袋、铺设反光膜、胁迫、施肥等栽培技术[54-55]。在龙眼上的饥饿胁迫研究表明，饥饿胁迫会加速蔗糖分解，蔗糖含量的降低使蔗糖分解代谢酶活性转而减弱，而饥饿胁迫对SPS催化的蔗糖合成代谢影响不明显[56]。在葡萄上的根域限制栽培显著提高了‘红地球’葡萄果实成熟期的葡萄糖、蔗糖和总糖含量，提高了SAI、SNI、CBAI、SSⅡ活性，同时根域限制栽培显著提高了转色期SAI和CBAI的活性和成熟期SNI和SSⅡ的活性[57]；套袋对果实糖代谢具有一定的影响，其主要是通过影响果实发育早期转化酶活性来影响果实糖分积累[58]；在枇杷上的套袋结果表明，套袋后果实中蔗糖、葡萄糖和可溶性固形物含量增加，且套袋主要是通过提高果实SS和SPS的活性来提高光合产物的[59]；在荔枝上的水胁迫也发现，在荔枝果实发育后期，分解蔗糖的AI、SS及合成蔗糖的SPS的活性都为水分胁迫的高于灌溉处理的，这将有助于增加胁迫的果实库强及糖的积累[60]；吴瑞媛等[61]对“翠冠”梨铺银色反光膜后发现，SPS的活性高于对照，而NI活性明显低于对照，明显促进了果实的糖积累；盐胁迫对糖的代谢具有一定的影响，在枸杞上的研究表明，随NaCl浓度升高和处理时间的延长，枸杞叶片多糖和可溶性糖含量显著增加($P_{0.05}$)，蔗糖含量呈上升趋势，而淀粉含量显著下降($P_{0.05}$)，还原糖含量呈下降趋势[62]；有研究也表明高温胁迫对糖代谢具有影响，温度升高果糖显著降低，葡萄糖含量不受影响或略有升高，3种己糖磷酸酯的含量、葡萄糖-6-磷酸酯(G-6-P)、葡萄糖-1-磷酸(G-1-P)和果糖-6-磷酸(F-6-P)的浓度均相应地降低，而葡萄糖-6-磷酸(G-1-P)和果糖-6-磷酸(F-6-P)的含量则下降了，蔗糖合成酶分解产生的糖核苷酸(UDP-葡萄糖)浓度在高温下也降低了[63]；此外，不同有机肥[64]、硼元素[65]、喷施沼液[66]、地膜覆盖[67]等对果实和叶片糖代谢也具有一定的影响，UV-b辐射除对植物叶片外，对茎、根、果、粒含糖量均具有影响[68]。

6　研究展望

糖类物质是生命活动的重要能源物质，可以保障植株的正常生理代谢活动，除此之外还是风味品质形成的主要决定因素之一。了解果实糖代谢的生理特性，可以有效改善果实品质，提高果实商品价值。而果实糖代谢是一个较为复杂的生理过程，受到诸多酶基因及外在环境因素的影响。目前，果实糖积累过程中其不同类型的糖组分动态变化及相关酶调控机制已较为清晰，但仍需进一步通过制备抗体等方式分离纯化糖代谢过程中的关键酶，以明确酶作用中心。科学技术的进步必将带动农业技术的革新，在果树上基因组学、蛋白组学和转录组学已经成为目前较为热门的研究领域，但代谢组学仍然是果树研究领域的重要组成部分。第三代测序技术的发展给糖代谢酶相关调控基因的研究带来契机，可明确关键酶基因对果实糖分积累的直接作用方式，并探明糖积累的机理。

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