果 树 学 报 2017,34(5):534-540
Journal of Fruit Science

DOI:10.13925/j.cnki.gsxb.20160305

‘南果梨’及其芽变‘南红梨’果实中糖分积累与相关基因表达差异分析

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摘 要:**【目的】**对‘南果梨’及其芽变‘南红梨’果实发育期间的可溶性糖含量及糖代谢相关基因的表达量进行分析,探索‘南果梨’及‘南红梨’糖积累差异的分子机制。**【方法】**以‘南果梨’及‘南红梨’果实为试材,利用高效液相色谱对2者可溶性糖含量进行测定,qRT-PCR对蔗糖代谢关键基因中性转化酶(NI)、蔗糖磷酸合成酶(SPS)及蔗糖合成酶(SS)的表达差异进行分析。**【结果】**‘南果梨’与‘南红梨’中的果糖含量均在果实发育后期(8月21日)达到最大值,而‘南果梨’与‘南红梨’果实中葡萄糖与山梨醇含量差异不明显。果实发育初期,2者蔗糖含量差异不明显,采收期(9月14日)‘南红梨’果实中蔗糖含量约为‘南果梨’果实的2倍。*PuNI*与*PuSS3*在‘南果梨’中的表达量显著高于‘南红梨’,而*PuSPS1*、*PuSS1*和*PuSS2*在‘南红梨’中的表达量则高于‘南果梨’。**【结论】**‘南果梨’及‘南红梨’果实发育过程中糖代谢相关基因的差异表达会导致不同糖分的积累量出现差异。

关键词:‘南果梨’;‘南红梨’;蔗糖;中性转化酶;蔗糖合成酶;蔗糖磷酸合成酶

中图分类号:S661.2 **文献标志码**:A **文章编号**:1009-9980(2017)05-0534-07

Differences in sugar accumulation and the related gene expression in fruit development between ‘Nanguo’and its mutant ‘Nanhong’pears

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Abstract:【Objective】‘Nanhong’pear is a bud mutation of the ‘Nanguo’pear and has been released as a new pear cultivar. The soluble sugars, especially sucrose, play important roles in many physiological pathways, such as fruit ripening and resistance. Here we aim to analyze the contents of soluble solids and major soluble sugars in ‘Nanguo’and ‘Nanhong’pear (*Pyrus ussuriensis* Maxim.) fruits and the expression profiles of sugar metabolism-related genes during fruit development. By doing this, we hope to clarify the relationship between soluble sugars and their related genes, providing some additional evidence for explaining the mechanism of why ‘Nanguo’and ‘Nanhong’pears show sugar accumulation mechanisms.【Methods】We measured the soluble sugar content by utilizing HPLC (High Performance Liquid Chromatography). By using the NCBI (National Center for Biotechnology Information) database and pear genome, we obtained the sequences of key genes involved in sugar metabolism. Then we designed specific primers and analyzed the expression profiles of these key genes in the ‘Nanguo’and ‘Nanhong’pears utilizing qRT-PCR (Quantitative real time polymerase chain reaction).【Results】The ‘Nanhong’pear is a bud mutation of the ‘Nanguo’pear. The pericarp of the ‘Nanhong’pear fruits turn red at the late development stage, which is very popular in the marketplace and can be sold quickly. As a bud mutation of the ‘Nanguo’pear, most of the main characteristics of the ‘Nanhong’pear, such as the phonological period and

收稿日期:2016-09-02 接受日期:2017-02-16

基金项目:辽宁省科技厅梨创新团队项目(2014204004);辽宁省农业领域青年科技创新人才培养计划(2014047)

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the adaptability, are similar to the ‘Nanguo’ pear. Here we analyzed the soluble sugar contents of the ‘Nanguo’ and ‘Nanhong’ pear and observed the expression profiles of the genes involved in sugar metabolism. The soluble solid contents of the ‘Nanhong’ pear are different from the ‘Nanguo’ pear during fruit development: the contents of the ‘Nanguo’ pear reached its highest point before harvest (15.33%) and then declined a little on the harvest day; while the ‘Nanhong’ pear reached the highest point at its harvest day (16.06), which is higher than the ‘Nanguo’ pear. The contents of fructose, glucose, sucrose and sorbitol also showed different trends during the ‘Nanguo’ and ‘Nanhong’ pear fruit development. Both the fructose contents of the ‘Nanguo’ and ‘Nanhong’ pears reached the highest point at day 8.21, which were 62.87 and 76.85 $mg \cdot g^{-1}$, respectively. But what is different is that the fructose content of the ‘Nanguo’ pear remained basically unchanged after day 8.21, but the ‘Nanhong’ pear then declined after day 8.21 and then increased at the harvest day. The glucose change trend of the ‘Nanhong’ pear is basically the same as the ‘Nanguo’ pear, reaching the highest point at day 7.22, which were 22.21 and 21.18 $mg \cdot g^{-1}$, respectively and then started to decrease a little. What is different is that before day 8.6, the glucose content of the ‘Nanhong’ pear is higher than the ‘Nanguo’ pear, but after that date, the glucose content is higher in the ‘Nanguo’ pear. The sorbitol change trend of the ‘Nanhong’ pear is also basically the same as the ‘Nanguo’ pear: with fruit development, the sorbitol content increased gradually and reached its highest point at day 7.22, 43.65 and 45.18 $mg \cdot g^{-1}$, respectively, then started to decrease a little. But the ‘Nanhong’ pear showed an increase at day 9.14. During the early stage of fruit development, there existed no obvious differences between the sucrose contents of the ‘Nanguo’ and ‘Nanhong’ pears. But at the harvest day, the sucrose content of the ‘Nanhong’ pear is dramatically higher than the ‘Nanguo’ pear, almost double when compared to the ‘Nanguo’ pear, which were 29.82 and 16.06 $mg \cdot g^{-1}$, respectively. This is the first time that anyone has compared the differences between soluble sugars of the ‘Nanguo’ pear and its bud mutation, the ‘Nanhong’ pear. From our results, we found that the sucrose content of the ‘Nanhong’ pear is higher than that of the ‘Nanguo’ pear, especially at the harvest day. In order to understand why the sucrose content is different between these two pears, we analyzed the expression profile of several sucrose related genes. We performed a blast search by using the NCBI database and pear genome, finally we obtained one NI (Neutral Invertase), two SPS (Sucrose-phosphate Synthase) and three SS (Sucrose Synthase). Based on these gene sequences, we designed specific primers and analyzed their expression profiles during the ‘Nanguo’ and ‘Nanhong’ pear’s fruit development. The *PuNI* showed a higher expression level in the ‘Nanguo’ pear than in the ‘Nanhong’ pear, especially at days 6.22 and 8.21, showing a double to fourfold change. At the early development stage, the expression level of *PuSPS1* was higher in the ‘Nanguo’ pear than in the ‘Nanhong’ pear, but at the other development stage, the *PuSPS1*showed a higher expression level in the ‘Nanhong’ pear. The expression of *PuSPS2* showed no expression regularity, sometimes higher in the ‘Nanguo’ pear, while sometimes higher in the ‘Nanhong’ pear. SS is one type of glycosyltransferase and it can catalyze the sucrose synthesis and decomposition, primarily catalyzing decomposition. *PuSS1* and *PuSS2* showed higher expression levels in the ‘Nanhong’ pear, while *PuSS3* was expressed higher in the ‘Nanguo’ pear.【Conclusion】The expression differences of these three types of key genes may explain why the ‘Nanhong’ pear has a higher content of sucrose than the ‘Nanguo’ pear.

Key words: ‘Nanguo’ pear; ‘Nanhong’ pear; Sucrose; Neutral invertase; Sucrose synthase; Sucrose-phosphate synthase

‘南果梨’是辽宁省的一个极具地方特色的秋子梨(*Pyrus ussuriensis* Maxim)品种,其果实色泽鲜艳,果肉细腻多汁、芳香味浓,深受消费者的喜爱。其芽变品种‘南红梨’[1]因成熟后果皮黄里透红,市场销售

价比‘南果梨’高2~3倍，具有更好的经济价值。‘南红梨’与‘南果梨’的可溶性固形物含量差异不明显，但蔗糖含量‘南红梨’明显高于‘南果梨’。

糖是果实品质和风味物质的主要成分，也是色素和芳香物质等其他营养成分合成的基础原料[2]。葡萄果实花青苷合成受糖分诱导[3-4]。蔗糖作为一种典型的可溶性糖，同样发挥重要作用。拟南芥花及种子中的花青苷含量受蔗糖调控[4-7]。‘南果梨’果实糖积累和转化的生理机制受蔗糖代谢相关酶和淀粉酶的调控[8]。蔗糖代谢相关酶主要包括酸性转化酶（acid invertase，AI），中性转化酶（neutral invertase，NI），蔗糖合成酶（sucrose synthase，SS）和蔗糖磷酸合成酶（sucrose-phosphate synthase，SPS）[8]。AI、NI活性降低是‘南果梨’果实蔗糖积累的必要前提，蔗糖的积累是多种酶共同作用的结果[9]。在苹果果实发育初期，转化酶及蔗糖合成酶的活性较高，果实中蔗糖积累量少；在果实发育后期，蔗糖磷酸合成酶的活性逐渐升高，果实中蔗糖的含量逐渐增多[10]。蔗糖合成酶是一种糖基转移酶，具有催化合成和分解的双重作用，但主要是以分解作用为主[11]。不同梨品种果实中蔗糖含量存在差异，而这种蔗糖含量的差异主要是由蔗糖合成酶（合成方向）活性引起的[12]。

目前针对‘南红梨’的研究主要集中在栽培技术、生物学特性等方面，色泽突变机制还尚不清楚。糖分积累与花青苷的合成有一定的相关性，因此对‘南果梨’及‘南红梨’糖分含量及相关基因的表达进行分析，对明确2者之间的着色差异具有一定的指导意义。

笔者以‘南果梨’及‘南红梨’为试材，对2者果实发育过程中糖含量以及糖代谢相关酶基因的表达特性进行比较分析，旨在探索‘南果梨’与‘南红梨’果实糖积累和转化的生理机制的差异，为阐明2者之间着色差异产生的原因提供一定的理论基础。

1 材料和方法

1.1 材料

‘南果梨’及其芽变‘南红梨’果实样品于2014年采摘于辽宁省海城市王石镇小女寨村。盛花后30 d第1次采样，以后每30 d采1次样（8月和9月每15 d采1次样），直至花后144 d果实成熟，每个时期各取4~10个果。去除果皮，将所取果实果肉切碎，整体充分混合后放入-80 ℃冰箱备用。

1.2 可溶性固形物含量的测定

可溶性固形物含量利用折光仪（Atago，PAL-1，日本）测定。用匀浆仪将整个果实打成匀浆，之后用滤纸滤去果汁，取0.3 mL检测。每个果测量设3次重复，每组测量3个果实。

1.3 糖含量测定

果实果糖、葡萄糖、蔗糖以及山梨醇含量的测定采用高效液相色谱法（High Performance Liquid Chromatography，HPLC，Waters 600E）。测定步骤参照许传强等[13]发表的方法并略有改动。分别取各时期的样品3 g置于50 mL离心管中，每个时期3次重复。向每个离心管中加入25 mL 80%乙醇（浸没样品），将离心管放到80 ℃水浴锅内水浴30 min，冷却至室温，10 000 r·min^{-1}离心5 min，取上清液移至200 mL烧杯中，重复上述步骤3次。用加热的方法将烧杯中的溶液浓缩，之后用10 mL超纯水溶解。用0.45 μm滤膜过滤上清液后，进行HPLC测定。色谱条件为：碳水化合物柱，柱温35 ℃，蒸发光检测器，流动相成分为75%乙腈和25%超纯水，流速为1.0 mL·min^{-1}。用Waters Millennium软件控制及处理数据。

1.4 实时荧光定量PCR分析

用改良的CTAB法提取‘南红梨’及‘南果梨’不同发育时期的果肉总RNA，并根据反转录试剂盒（PrimeScriptTM RT reagent Kit with gDNA Eraser，TaKaRa）提供的方法进行cDNA合成。荧光定量反应在定量PCR仪IQ5（Bio-Rad，USA）上进行。利用荧光定量试剂盒（DRR041A，Takara）检测各个基因的表达量，步骤参照试剂盒说明。PCR反应程序为：95 ℃ 3 min；95 ℃ 10 s，54~60 ℃ 30 s，72 ℃ 30 s，40个循环，收集荧光信号；50~60 ℃ 30 s，生成溶解曲线。各引物序列及退火温度见表1。每个样品做3次重复，获得3组Ct值带入公式$2^{-\Delta\Delta Ct}$计算各个基因的相对表达量，结果用GraphPad Prism5软件分析。

2 结果与分析

2.1 ‘南果梨’及‘南红梨’果实发育过程中可溶性固形物含量的动态变化

可溶性固形物含量测定结果显示‘南果梨’与‘南红梨’果实可溶性固形物含量的变化趋势略有不同。‘南果梨’果实可溶性固形物含量在果实发育过程中呈现上升-下降-上升-下降的趋势，在花后134 d达

到最高值(15.33%),花后144 d略有下降;而‘南红梨’果实可溶性固形物含量在果实发育过程中呈现上升-下降-上升的趋势,果实发育初期(花后30 d至花后90 d)可溶性固形物含量基本保持上升趋势,并达到一个高峰,之后呈缓慢下降趋势,直到采收前(花后134 d)可溶性固形物含量呈上升趋势,采收时达到整个发育期的最高峰(16.06%)(图1)。

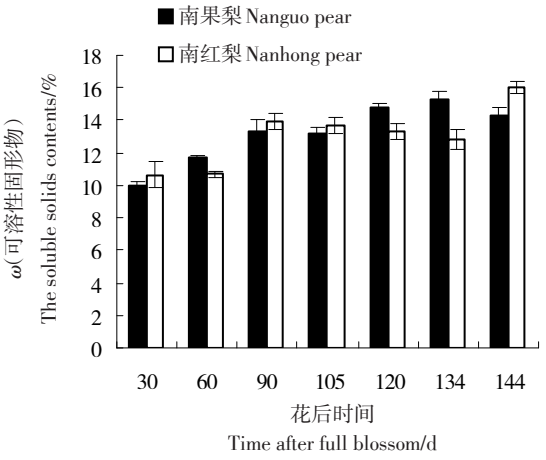

图1　‘南果梨’及‘南红梨’果实发育过程中可溶性固形物含量的变化

Fig. 1 The soluble solid contents of the ‘Nanguo’ pear and ‘Nanhong’ pear during fruit development

2.2　‘南果梨’及‘南红梨’果实发育过程中可溶性糖的变化规律

梨中主要的可溶性糖包括果糖、葡萄糖、蔗糖和山梨醇,因此笔者对以上4种糖在‘南果梨’及‘南红梨’果实发育过程中的动态变化进行了分析(图2)。

果糖含量的变化趋势在‘南果梨’及‘南红梨’中基本一致,在花后30 d果实发育初期果糖含量很低,之后果糖含量持续上升。2者之间不同的是,‘南果梨’中果糖含量在花后120 d达到高峰,为62.87 mg·g^{-1},之后直到花后144 d采收期含量基本不变;而‘南红梨’在花后120 d达到最大值,为76.85 mg·g^{-1},之后出现下降,花后144 d采收时果糖含量又稍微出现上升(图2-A)。

‘南果梨’与‘南红梨’葡萄糖含量的变化趋势基本一致,都是在花后90 d达到最大值,分别为21.19 mg·g^{-1}和22.22 mg·g^{-1},‘南红梨’略高于‘南果梨’,后期呈现略微下降的趋势。不同的是,在花后105 d之前,‘南红梨’的果糖含量略高于‘南果梨’,而从花后120 d直至花后144 d采收期‘南果梨’葡萄糖含量略高于‘南红梨’(图2-B)。

在果实发育前期,‘南果梨’与‘南红梨’蔗糖含量都比较低,并且从花后30 d直到花后105 d以相同的幅度呈现上升趋势;直到花后120 d,‘南红梨’果实中的蔗糖含量上升幅度逐渐大于‘南果梨’,到花后144 d采收期时,‘南红梨’和‘南果梨’果实中蔗糖

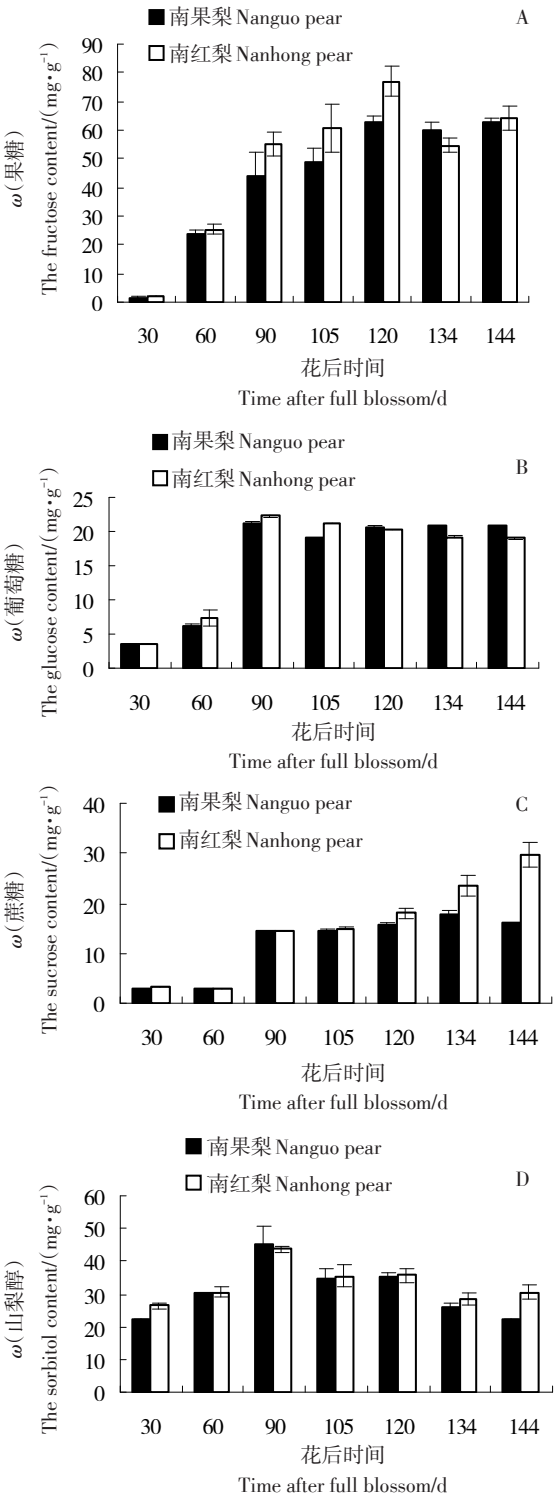

图2　‘南果梨’及‘南红梨’果实发育过程中可溶性糖含量的变化

Fig. 2 The content changes of sugar of ‘Nanguo’ and ‘Nanhong’ pears during fruit development

含量分别为29.82 mg·g^{-1}和16.06 mg·g^{-1}，‘南红梨’中蔗糖含量约为‘南果梨’的2倍(图2-C)。

‘南果梨’与‘南红梨’中山梨醇含量变化基本一致，随着果实的发育山梨醇含量逐渐上升，并在花后90 d达到整个发育期的高峰，‘南果梨’和‘南红梨’中分别为45.18 mg·g^{-1}和43.65 mg·g^{-1}，而后略微出现下降(图2-D)。不同的是，‘南红梨’在花后144 d采收期时山梨醇含量呈现小幅度的上升。

2.3 ‘南果梨’及‘南红梨’果实发育过程中糖代谢相关基因的表达量变化

生理数据检测结果显示，‘南果梨’及‘南红梨’可溶性糖含量存在一定的差异，尤其是蔗糖含量2者差异非常明显。

为了初步解析导致这种差异的分子机制，笔者对糖积累与代谢相关基因的表达特性进行了分析。从NCBI(National Center for Biotechnology Information)数据库(https://www.ncbi.nlm.nih.gov/)以及梨基因组数据库(https://www.rosaceae.org/node/1)中得到1个中性转化酶(NI)、2个蔗糖磷酸合成酶(SPS)和3个蔗糖合成酶(SS)，设计特异引物(表1)，并对以上基因在‘南果梨’及‘南红梨’果实发育过程中的表达特性进行分析。

表1 所用引物序列

Table 1 The primers used in this research

引物名称 Primer name	引物序列 Primer sequence	退火温度 Annealing temperature/℃
PuNI-RT-F	GCGAGTAGCCGTGTTGGTTG	58
PuNI-RT-R	CACGATCCGTCTCGATCCTCT	
PuSPS1-RT-F	GCTCACGGCTTACCTATTGTTG	55
PuSPS1-RT-R	GTCCATTCTGCCTGCATCTT	
PuSPS2-RT-F	CGTCGGATAGAGGCAGAGGA	60
PuSPS2-RT-R	ATCACCATCATGCGGAACAA	
PuSS1-RT-F	TCTCCGTGTTCACTGCTACGA	54
PuSS1-RT-R	GGTGCCTCAAGAAGGTCCAA	
PuSS2-RT-F	GAGGACACTCTCTCCGACCA	60
PuSS2-RT-R	GACGAACTGCTAAGGCCACA	
PuSS3-RT-F	CCGACCACCGCAACTAACTC	60
PuSS3-RT-R	CGGCAGAATAATGGCTTCCT	

2.3.1 中性转化酶基因在‘南果梨’及‘南红梨’发育过程中的表达特性 中性转化酶是一种蔗糖专一性的酶，催化蔗糖水解为六碳糖[14]。检测结果显示，‘南果梨’发育过程中*PuNI*的表达量普遍高于‘南红梨’，尤其在花后60 d和花后120 d‘南果梨’中的表达量是‘南红梨’的2~4倍(图3)。

2.3.2 蔗糖磷酸合成酶在‘南果梨’及‘南红梨’发育过程中的表达特性 蔗糖磷酸合成酶是蔗糖合成途径中的一个重要控制点，它的活性及表达量反映蔗糖生物合成途径的能力[15]。对得到的2个蔗糖磷酸合成酶基因在‘南果梨’及‘南红梨’果实发育过程中的表达特性进行了分析(图4)。结果显示，在果实发育初期(花后30 d)，虽然*PuSPS1*在‘南果梨’中的

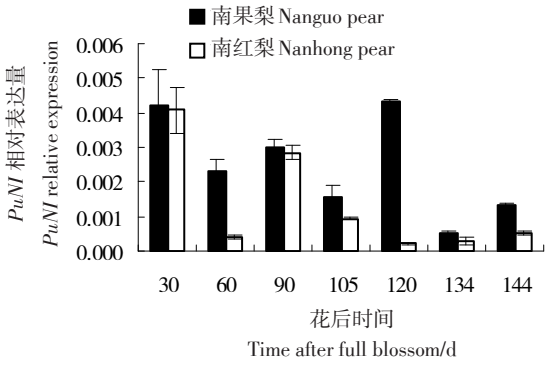

图3 ‘南果梨’及‘南红梨’果实发育过程中中性转化酶表达量变化

Fig. 3 The expression of *PuNI* of ‘Nanguo’ and ‘Nanhong’ pears during fruit development

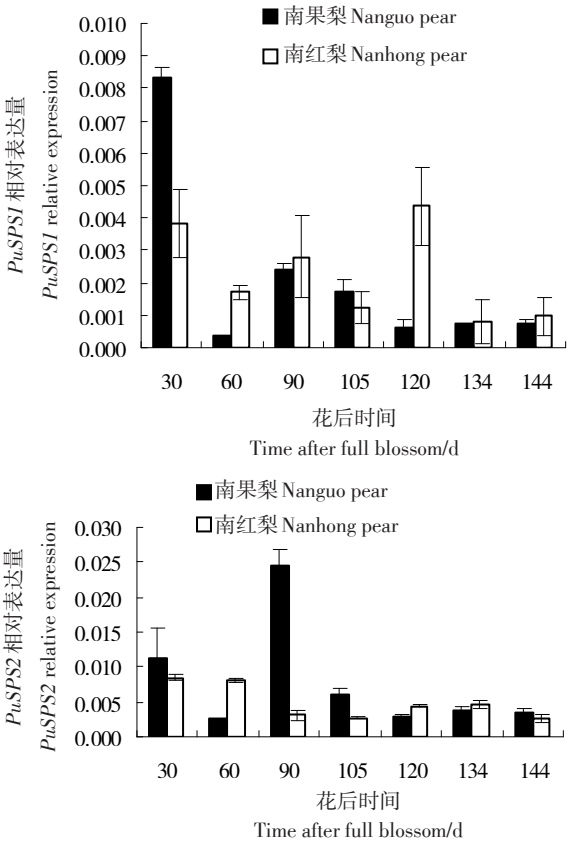

图4 ‘南果梨’及‘南红梨’果实发育过程中蔗糖磷酸合成酶表达量变化

Fig. 4 The expression of *PuSPS* in the ‘Nanguo’ and ‘Nanhong’ pears during fruit development

表达量显著高于‘南红梨’(约为2倍),但在其余的发育时期中,‘南红梨’中的表达量几乎都高于‘南果梨’,尤其是在花后120 d,表达量为‘南果梨’的6倍(图4-A)。*PuSPS2*的表达没有明显变化规律(图4-B)。

2.3.3　蔗糖合成酶在‘南果梨’及‘南红梨’发育过程中的表达特性　对3个蔗糖合成酶基因的表达特性进行分析,结果表明*PuSS1*和*PuSS2*在‘南红梨’果实发育过程中的表达量普遍高于‘南果梨’(图5-A和5-B);而*PuSS3*在‘南果梨’发育时期的表达量高于‘南红梨’(图5-C)。

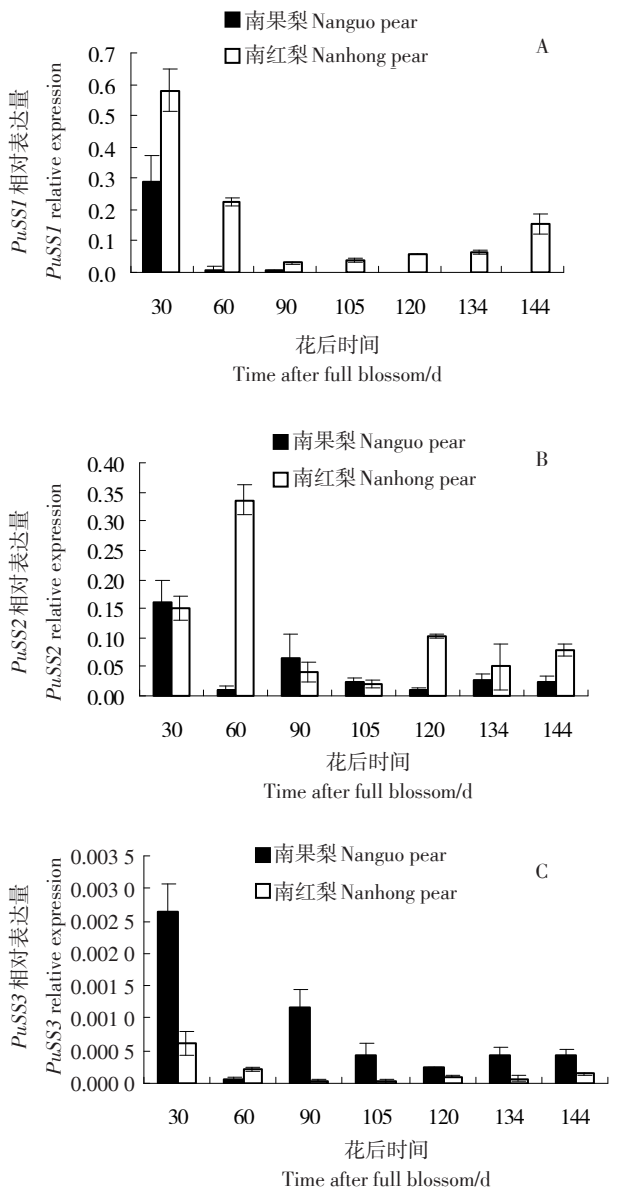

图5　‘南果梨’及‘南红梨’果实发育过程中蔗糖合成酶表达量变化

Fig. 5 The expression of *PuSS* in the ‘Nanguo’ and ‘Nanhong’ pears during fruit development

3　讨　论

蔗糖是光合作用的主要产物,除了为植物提供必要的能源物质以外,也是一种必要的信号分子,能够参与植物的生长发育、细胞周期、基因表达等生命过程[16]。蔗糖能够调节草莓果实成熟以及拟南芥花青苷合成等生命过程[5,17]。‘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’,尤其是在采收期(花后144 d)。‘南红梨’果实成熟后果皮颜色明显着红色,而且‘南红梨’果实中蔗糖含量明显高于‘南果梨’。由此笔者推测梨果实中的蔗糖可能作为一种信号分子影响果皮中色泽代谢通路相关基因的功能,进而导致‘南果梨’与‘南红梨’的着色差异。

为了阐释导致‘南果梨’及‘南红梨’蔗糖差异的机制,笔者对3种蔗糖代谢关键酶基因在‘南果梨’及‘南红梨’中的表达特性进行了分析。

NI能够不可逆地催化蔗糖分解为果糖和葡萄糖,在甜瓜中NI活性的降低是甜瓜果实蔗糖积累的必要前提[9]。‘南红梨’果实中*NI*的表达量明显低于‘南果梨’,说明蔗糖含量与中性转化酶基因的表达量呈负相关,与苹果、葡萄等果实发育早期蔗糖含量与转化酶活性呈负相关的结果一致[18]。‘南果梨’中*PuNI*的表达量高于‘南红梨’,这可能是‘南红梨’中蔗糖含量高于‘南果梨’的一个原因。

SPS在蔗糖代谢中起着重要作用。网纹甜瓜在花后5~25 d内,SPS活性较低,甜瓜中没有或几乎没有蔗糖的积累;花后30 d之后,随着SPS活性的升高,甜瓜中才开始出现蔗糖的积累[19],由此可见SPS对蔗糖积累发挥重要作用[20]。*PuSPS1*在‘南红梨’果实中的表达量高于‘南果梨’果实,尤其是在花后120 d。花后120 d刚好是‘南红梨’果实中蔗糖含量开始迅速上升的时期,这一点与Lester等[19]的研究结果一致。

SS是一个大的基因家族,柑橘中存在2个蔗糖合成酶,SuSy1和SuSy2,SuSy1主要在未成熟果实中起分解蔗糖的作用;而随着果实成熟,SuSy2则对蔗糖迅速积累起作用[7]。*PuSS1*和*PuSS2*在‘南红梨’果实中的表达量高于‘南果梨’,与王德孚等[12]SS合成方向的活性差异导致‘鸭梨’‘茌梨’和‘八里香’不同品种间蔗糖含量不同的研究结果一致。结合‘南果梨’及‘南红梨’果实发育过程中蔗糖含量的变化趋

势，笔者推测PuSS3可能主要负责分解蔗糖，其高表达可能是导致‘南果梨’果实蔗糖含量低的一个原因。

蔗糖不仅是果实品质形成的重要因子，同时也是细胞代谢的调节因子。蔗糖的调控是一个复杂的网络，并不是由一种单一的酶来调控，而是多种酶共同协作的结果。为了系统地阐述‘南红梨’果实中蔗糖含量高于‘南果梨’的分子机制，仍需要对各种关键酶基因的作用进行深入的研究。

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