

根蘖和嫁接灵武长枣果实可溶性糖含量变化及其差异基因筛选

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摘要:【目的】揭示根蘖繁殖与嫁接繁殖对灵武长枣果实可溶性糖代谢变化的差异, 为提高果实品质提供科学依据。【方法】以根蘖与嫁接灵武长枣在白熟期(NB vs JB)、着色期(NZ vs JZ)和成熟期(NC vs JC)的果实为材料, 测定果实葡萄糖、果糖、蔗糖及可溶性糖含量; 基于转录组数据, 从糖酵解/糖异生(ko00010)、淀粉与蔗糖代谢(ko00500)、果糖与甘露糖代谢(ko00051)以及氨基糖和核苷酸糖代谢(ko000520)4个关键糖代谢通路中, 筛选与可溶性糖合成代谢相关的差异基因; 将表型数据与转录组数据结合, 进行WGCNA分析; 利用qRT-PCR验证以确保结果的可靠性。【结果】灵武长枣在白熟期和着色期的糖分积累形式主要为果糖, 而在成熟期则以蔗糖为主要积累形式。不同繁殖方式下灵武长枣果实糖类积累呈现显著的发育阶段特异性。着色期根蘖繁殖的果糖含量比嫁接繁殖高20.25%; 成熟期根蘖繁殖的蔗糖含量比嫁接繁殖高49.32%。从上述4条通路中筛选获得了24个显著差异表达基因(DEGs)。通过GO功能富集分析发现, 这些差异基因主要富集在碳水化合物代谢过程相关功能条目中。此外, 加权基因共表达网络分析结果表明, 黑色、棕色和绿色模块与可溶性糖代谢显著关联, 其中ncbi_112492650、HERC2(ncbi_107420452)、PGMP(ncbi_107414395)基因的连通性最强。qRT-PCR分析结果表明, 所测定的差异表达基因在不同时期的表达模式存在差异, 与转录组数据中的表达趋势一致。【结论】基因ncbi_112492650、HERC2(ncbi_107420452)、PGMP(ncbi_107414395)在调控灵武长枣可溶性糖代谢方面发挥关键作用, 可作为后续关键验证基因。本研究为优化灵武长枣的繁殖方式及提高果实品质提供了重要的理论依据。

关键词: 灵武长枣; 根蘖繁殖; 嫁接繁殖; 可溶性糖; 差异基因

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Changes in soluble sugar content and differential gene screening in *Ziziphus jujuba* Mill. 'Lingwuchangzao' propagated by root tiller and grafting

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Abstract: 【Objective】*Ziziphus jujuba* Mill. 'Lingwuchangzao' belongs to Rhamnaceae Jujube. Its fruits are rich in protein, sugar and other nutrients, and have high economic value and market development potential. It usually propagated by root tillers and grafting. The study aimed to reveal the differences of soluble sugar metabolism in the fruits of Lingwuchangzao propagated by different propagation methods through studying on the changes of soluble sugar content in different developmental stages of the fruits of Lingwuchangzao propagated by root tillers and grafting in order to provide a scientific basis for improving fruit quality. 【Methods】The investigation was carried out at the white ripening stage

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(NB vs JB), coloring stage (NZ vs JZ), and mature stage (NC vs JC) on the fruits of Lingwuchangzao propagated by root suckers and grafting as experimental materials. The contents of glucose, fructose, sucrose and soluble sugar in the fruits of the three periods were determined respectively. Combined with transcriptome data analysis, significant differential genes were screened from four key sugar metabolism pathways, glycolysis/gluconeogenesis (ko00010), starch and sucrose metabolism (ko00500), fructose and mannose metabolism (ko00051), and amino sugar and nucleotide sugar metabolism (ko000520) with $FDR < 0.05$ and $|\log_2FC| \geq 1$ as the standard. By integrating phenotypic data with transcriptome data for WGCNA analysis, key differential genes regulating soluble sugar synthesis and metabolism at different developmental stages of Lingwuchangzao fruits were identified, followed by qRT-PCR verification to ensure the reliability of the results. **【Results】** The soluble sugars in Lingwuchangzao included sucrose, fructose, glucose and others. The fructose was the main sugar accumulated at white ripe stage and coloring stage, while sucrose was the main sugar at mature stage. However, sugar accumulation exhibited significant developmental stage specificity in the fruits of Lingwuchangzao propagated with different methods. At the white ripe stage, the soluble sugar content of the fruits from Lingwuchangzao propagated by grafting was 17.55% higher than that from root tillers. At the coloring stage and maturity stage, the soluble sugar content of fruits from the Lingwuchangzao propagated by root tillers was 24.38% and 27.91% higher than that from grafted trees, respectively. At the coloring and mature stages, the sucrose content in the fruits from Lingwuchangzao propagated by root tiller was 50.63% and 49.32% higher than that from grafted trees, respectively. At the coloring stage, the fructose content of in the fruits from root tiller propagated trees was 20.25% higher than that from grafted trees. At the mature stage, the fructose content in the fruits from grafted trees was 13.32% higher than that from root tiller propagated trees. As the fruit grew and developed, the glucose content in the fruits from grafting propagated trees was 36.08%, 20.67%, and 26.85% higher than from the trees propagated by root tiller, respectively. 24 significantly differentially expressed genes (DEGs) were screened. Among them, the genes *EP3* (ncbi_107406053), *BAMI* (ncbi_107422617), *BGLUII* (ncbi_107426268), *PGMP* (ncbi_107414395) showed higher expression level, and the difference of the gene expressions between the coloring period and the maturity period was significant, indicating the potential for further fluorescence quantitative analysis. Through GO functional enrichment analysis, it was found that there were significant differences in carbohydrate metabolism, hydrolytic enzyme activity and secondary metabolite synthesis between the trees propagated by two different methods. These differences might be closely related to the adaptability of trees and the fruit quality. The analysis of soluble sugar metabolism pathways and differential genes revealed that the gene *PGMP* (ncbi_107414395) appeared multiple times in the metabolic pathways, indicating that this gene might play an important role in regulating soluble sugars in Lingwuchangzao and could serve as a key candidate gene for further validation studies. Additionally, weighted gene co-expression network analysis (WGCNA) showed that the black, brown, and green modules were significantly associated with soluble sugar metabolism. Genes in the black module exhibited a strong positive correlation with fructose, with a correlation coefficient of 0.87; genes in the brown and green modules showed strong positive correlations with soluble sugar and sucrose, with correlation coefficients of 0.71, 0.86, 0.74, and 0.83, respectively. Finally, the genes ncbi_112492650 and *HERC2* (ncbi_107420452), which exhibited the highest connectivity and high expression level in the black module, were selected as key candidate genes for subsequent validation. Through the fluorescence quantitative analysis (qRT-PCR), it was found that the trend of gene expression levels in the fruits from the trees grafted by root-tiller was basically consistent with the transcriptome sequenc-

ing results at the white ripe stage, coloring stage and mature stage, indicating that the transcriptome data had high reliability. 【Conclusion】 This study revealed the difference of soluble sugar metabolism in the fruits of Lingwuchangzao propagated by two different methods, providing an important theoretical basis for optimizing the propagation mode of Lingwuchangzao. The genes *ncbi_112492650*, *HERC2* (*ncbi_107420452*) and *PGMP* (*ncbi_107414395*) would play a key role in regulating soluble sugar metabolism of Lingwuchangzao, and could be used as subsequent key verification genes.

Key words: *Ziziphus jujuba* Mill. ‘Lingwuchangzao’; Root tiller propagation; Grafting propagation; Soluble sugars; Differential genes

灵武长枣 (*Ziziphus jujuba* Mill. ‘Lingwuchangzao’) 是宁夏特色的鲜食枣品种, 其肉质鲜嫩、多汁、酸甜适度, 且商品性状优良^[1]。灵武长枣营养丰富, 品质佳, 鲜枣含糖量 $\geq 23.0\%$ ^[2]。在生产上, 灵武长枣主要采取根蘖和嫁接两种方式进行繁殖^[3]。根蘖繁殖的植株栽植方便, 质量好, 可保持母树的优良特性^[4], 但根蘖数量少, 产量低, 生长缓慢。嫁接繁殖具有生长快、树势强、结果早等特点, 但在生产中发现枣果风味及营养品质不如根蘖苗。两种繁殖方式各有特点, 在生产中被广泛应用^[5]。

在鲜食水果中, 甜味是水果感官质量的重要组成部分, 可溶性糖的积累水平决定了果实风味和商品价值, 与果实品质密切相关^[6]。糖分是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。枣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直接影响消费者对鲜食枣的满意度^[7]。果实发育过程中糖类变化的研究在番茄^[8]、葡萄^[9]、桑葚^[10]、草莓^[11]、西瓜^[12]等果实中均有报道。研究发现, 灵武长枣在不同繁殖方式下果实糖含量存在差异^[13], 并通过果实转录组测序, 筛选与根蘖和嫁接长枣果实品质差异相关的基因^[14-15]。但是关于不同繁殖方式下灵武长枣各发育时期果实的可溶性糖变化规律还不清楚。笔者采集3个发育时期的灵武长枣果实, 提取RNA并进行高通量转录组测序, 筛选与根蘖、嫁接长枣果实可溶性糖代谢相关的差异表达基因(DEGs), 探究根蘖和嫁接果实营养品质差异的原因, 为灵武长枣的高品质栽培提供技术支撑。

1 材料和方法

1.1 植物材料

供试样树为8年生灵武长枣根蘖植株和以酸枣为砧木的灵武长枣嫁接植株(嫁接时间一致), 所处

环境一致, 均为壤砂土, 平均地径86 mm, 树高2.54 m, 冠幅2.52 m \times 2.45 m。分别选取5株生长基本一致、无病虫害的灵武长枣根蘖和嫁接植株, 在盛花期50、75、105 d, 即白熟期(JB vs NB)、着色期(JZ vs NZ)和成熟期(JC vs NC)分别采集嫁接与根蘖植株的果实。每株采集5个果实, 各时期每个处理共采集25个枣果, 混合后作为试验材料。果实样品用液氮冷冻后置于 $-80\text{ }^{\circ}\text{C}$ 超低温冰箱保存。

1.2 指标测定

果实纵径、横径使用游标卡尺(0~150 mm)测定; 单果质量采用电子天平称量。参照张友杰^[16]的方法, 称取10.00 g枣果实样品研磨成浆, 采用蒽酮比色法测定果实蔗糖、葡萄糖、果糖含量。使用WPS Office软件对果实糖相对含量数据进行整理, 使用SPSS 26.0软件进行单因素方差分析和指标间相关性分析, 设置显著性水平 $P < 0.05$, 使用Origin软件绘制图表。

1.3 RNA提取、文库构建

对两种繁殖方式下灵武长枣不同时期的果实提取总RNA。总RNA提取使用天根RNA prep Pure总RNA提取试剂盒(RNA prep Kit), 通过1%琼脂糖凝胶电泳检测RNA质量, 使用Nanodrop 2000分光光度计(Thermo Scientific, Waltham, MA, USA)测定RNA浓度, 合格样品用于构建文库。使用Library Prep试剂盒构建转录文库, 质量检测合格的文库用于转录组测序, 测序仪器为Illumina HiSeq 2500。对测序结果进行质量评估与原始数据过滤, 去除接头序列及低质量reads, 获得高质量的质控数据(clean data)。基于所选参考基因组序列, 对Mapped Reads进行拼接, 将质控数据与冬枣的参考基因组进行比对和定位分析。

1.4 差异表达基因筛选及富集分析

基于前期对根蘖和嫁接繁殖灵武长枣果实糖含

量富集通路的研究^[7],笔者聚焦于糖酵解/糖异生(ko00010)、淀粉与蔗糖代谢(ko00500)、果糖和甘露糖代谢(ko00051)以及氨基糖和核苷酸糖代谢(ko000520)等4个关键代谢通路。利用edgeR^[18]软件,以FDR<0.05且|log₂FC|≥1为标准,筛选显著的差异表达基因。对差异表达基因进行GO功能富集分析。

1.5 网络分析

在R中使用默认参数进行WGCNA分析,并将基因简化为共表达模块^[19-20]。对FPKM值进行归一化并构建邻接矩阵。将实验测得的可溶性糖、果糖、蔗糖、葡萄糖含量以及果实纵径、横径和单果质量作为表型数据,导入WGCNA包中。随后,基于默认参数计算各基因模块与上述表型之间的相关性,以评估其关联程度。在构建网络时,首先依据基因表达数据生成邻接矩阵,并进一步转换为拓扑重叠矩阵(TOM)。之后,将表达模式高度相似的基因聚类为共表达模块,并计算各模块的特征基因用于后续

分析。使用Cytoscape 3.7.1软件绘制目标基因互作网络图(PPI, Protein-Protein Interaction Networks)。

1.6 qRT-PCR分析

使用天根生化科技(北京)有限公司的RNAprep Pure Plant Plus Kit(Polysaccharides & Polyphenolics-rich)试剂盒提取灵武长枣白熟期、着色期和成熟期果实的总RNA,使用康为世纪生物科技股份有限公司的HiFiScript gDNA Removal RT MasterMix试剂盒反转录合成cDNA。以灵武长枣PEX13(ncbi_107406518)作为内参基因。使用在线引物设计软件(<https://store.sangon.com/newPrimerDesign>)对筛选的差异基因设计定量引物(表1),通过溶解曲线分析确认其特异性。qRT-PCR使用康为世纪生物科技股份有限公司的MagicSYBR Mixture试剂,在荧光定量PCR仪qTOWER3G IVD上完成,程序设置为95℃预变性30 s;95℃变性5 s,60℃退火30 s,60℃延伸30 s,共45个循环。所有试验均设置3个生物学重复,基因的相对表达量通过2^{-ΔΔCT}法进行计算。

表1 基因的qRT-PCR引物

Table 1 qRT-PCR primer sequences used for genes

基因名称 Gene name	正向引物(5'-3') Forward primer (5'-3')	反向引物(5'-3') Reverse primer (5'-3')
EP3 (ncbi_107406053)	GTGACACCAACTATCCACAGTATCC	TCCCAGCTAGTGC GTAATTGTAATTC
PGMP (ncbi_107414395)	TCGCCACAAC TCCATTTCAGAAC	GGTAGCAGGAGAAGAAGAAGAAG
BAMI (ncbi_107422617)	GCACGGGCTCAAAGTTCAGG	TCTCGGTCTCTGTCAATCTCTTCC
BGLUII (ncbi_107426268)	ACTGGTTAAGGGTTCGTTTGACTTC	TGCTGCGTCTGCGGTGTAG
ncbi_112492650	CGAACGGCATCTAATGGCAATTCC	CCACAGTTGTTGAGGGGCTGATG
HERC2 (ncbi_107420452)	TGCTTTGTCTCCTCTGCCGATTTC	CCACTCCTTCCCCTACCCCAAG
PEX13 (ncbi_107406518)	GGGTGGTTATGGAATGGGCATGG	AAACCCTGGTGGAGATGGAGGAC

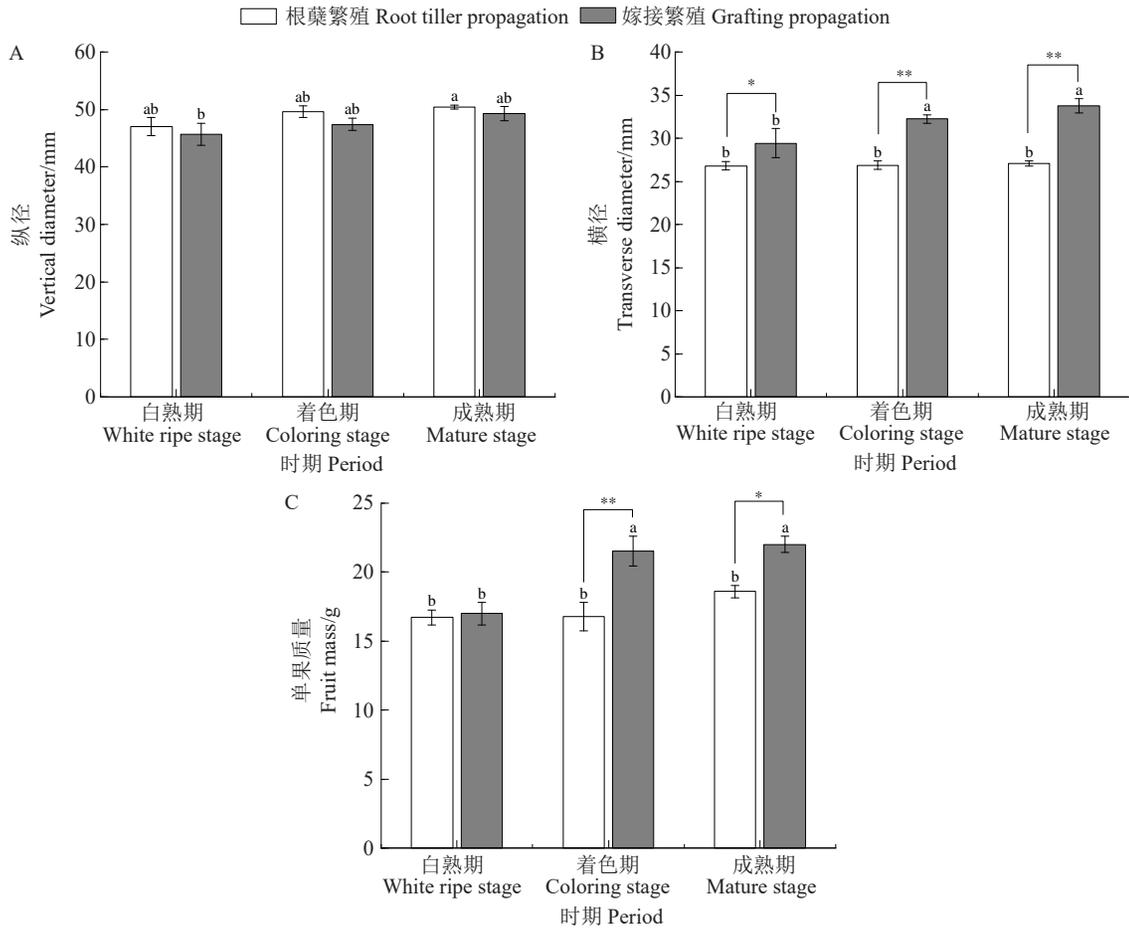
2 结果与分析

2.1 两种繁殖方式下灵武长枣果实不同发育时期可溶性糖含量及相关性分析

根蘖与嫁接灵武长枣果实特征差异见图1。根蘖植株的果实纵径大于嫁接植株,而果实横径和单果质量则呈现相反趋势。灵武长枣果实可溶性糖主要包括蔗糖、果糖、葡萄糖。由图2可知,根蘖和嫁接植株果实可溶性糖含量随果实发育进程显著增加。白熟期,嫁接植株果实的可溶性糖含量显著高于根蘖植株,提高了17.55%;在着色期和成熟期,根蘖植株果实的可溶性糖含量则显著高于嫁接植株,分别提高了24.38%和27.91%。蔗糖含量随发育进

程显著增加;在着色期和成熟期,根蘖植株果实的蔗糖含量显著高于嫁接植株,分别提高50.63%和49.32%。果糖与葡萄糖含量则随发育进程呈现先上升后下降的趋势,在着色期达到最大值。在着色期,根蘖植株果实的果糖含量显著高于嫁接植株,提升幅度为20.25%;而在成熟期,嫁接植株果糖含量高于根蘖植株,提高了13.32%。此外,随着果实的发育,嫁接植株果实的葡萄糖含量显著高于根蘖植株,分别提高了36.08%、20.67%和26.85%。根据根蘖与嫁接植株果实在3个时期的糖含量变化趋势可知,在白熟期与着色期,根蘖和嫁接植株果实糖分的积累形式以果糖为主,而成熟期以蔗糖为主。

为了明确灵武长枣果实品质性状间的内在联



*表示两种繁殖方式在 $P<0.05$ 水平上差异显著,**表示两种繁殖方式在 $P<0.01$ 水平上差异极显著,不同小写字母表示同一处理下不同发育阶段在 $P<0.05$ 水平上差异显著。下同。

* indicates that the difference between the two breeding methods is significant at the $P<0.05$, and** indicates that the difference between the two breeding methods is extremely significant at the $P<0.01$. Different small letters indicate significant differences at the $P<0.05$ at different developmental stages under the same treatment. The same below.

图1 根蘖与嫁接灵武长枣果实不同发育时期形态指标的变化

Fig. 1 Changes of morphological indexes in different development stages of root tillers and grafted Lingwuchangzao fruits

系,相关性分析(图3)表明,单果质量与横径呈极显著正相关($P<0.01$);纵径与可溶性糖含量、蔗糖含量,横径与葡萄糖含量均呈显著正相关($P<0.05$);蔗糖含量与可溶性糖含量呈极显著正相关($P<0.01$),而蔗糖含量与葡萄糖含量呈显著负相关($P<0.05$)。以上表明果实品质和内在营养直接相关。

2.2 根蘖与嫁接灵武长枣果实差异表达基因富集分析

将糖酵解/糖异生途径(Ko00010)、果糖与甘露糖途径(Ko00051)、淀粉与蔗糖途径(Ko00051)、氨基糖和核苷糖途径(Ko00520)4个通路中的基因以 $FDR<0.05$ 且 $|\log_2FC|\geq 1$ 为标准筛选显著差异表达基因,获得24个差异表达基因(表2),这些基因均呈现下调趋势($\log_2FC<0$)。在嫁接植株果实中,基因

BGLU11(ncbi_107426268)在白熟期呈现高表达水平,且随着果实发育,基因表达量显著下降;在根蘖植株果实中,基因 *PGMP*(ncbi_107414395)和 *FBP*(ncbi_107430723)在白熟期表现出较高的表达水平,并随着果实成熟而降低。这表明,一方面 *BGLU11*、*PGMP*和 *FBP*基因可能在灵武长枣白熟期可溶性糖积累过程中发挥关键作用;另一方面基因 *RHMI*(ncbi_107432603)表达量在嫁接植株果实中随着果实发育进程而递增,至成熟期达到峰值。在根蘖植株果实中,基因 *Os06g0675700*(ncbi_107418468)和 *EP3*(ncbi_107406053)表达量同样随着果实成熟而逐渐上调,并在成熟期达到峰值。这表明 *RHMI*、*Os06g0675700*和 *EP3*基因可能在果实成熟期促进了可溶性糖积累,从而影响果实最终糖分含量和风

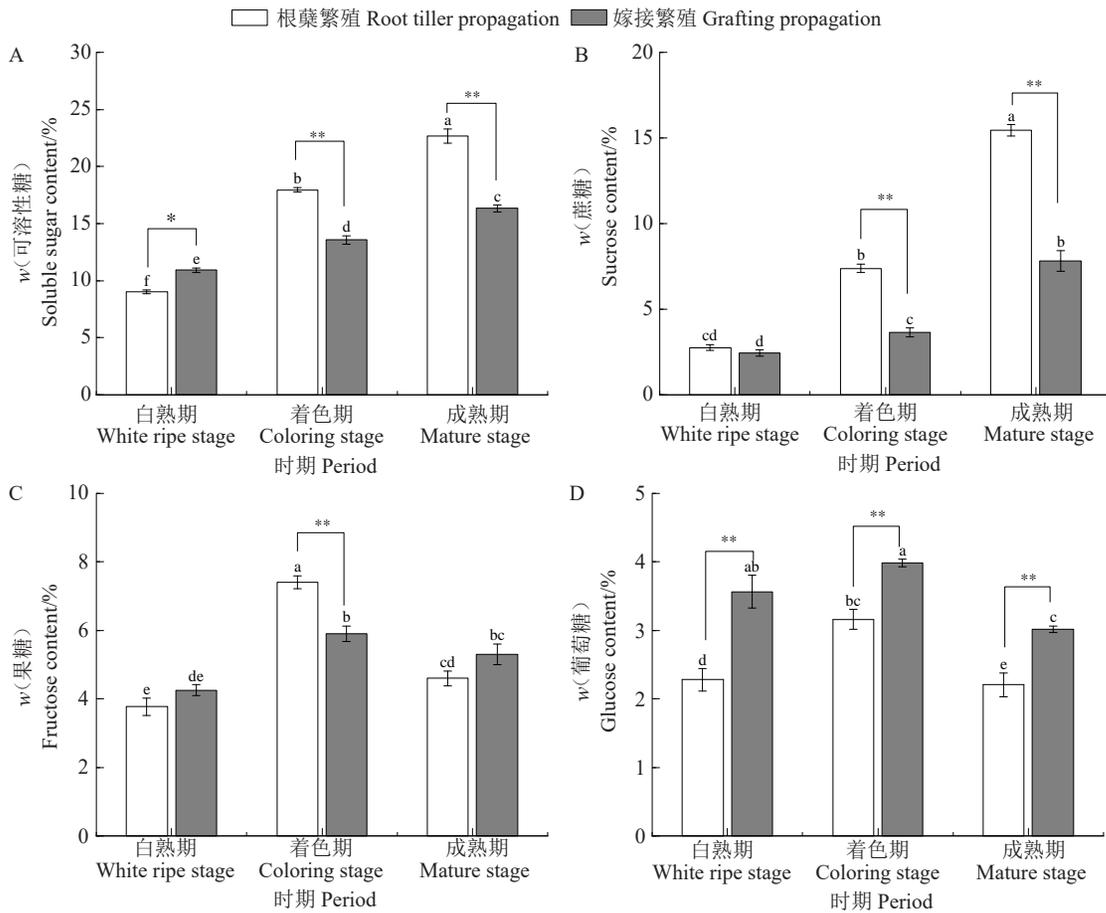


图 2 根蘖与嫁接灵武长枣果实不同发育时期可溶性糖含量的变化

Fig. 2 Changes of soluble sugar content in root tillers and grafted Lingwuchangzao fruits at different developmental stages

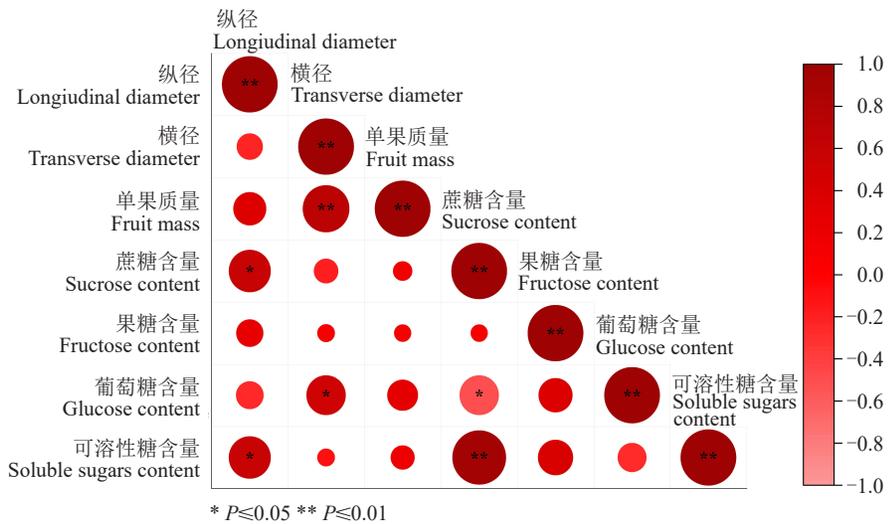


图 3 根蘖与嫁接灵武长枣果实品质性状相关性分析

Fig. 3 Correlation analysis between root tillers and fruit quality traits of grafted Lingwuchangzao

味品质。其中,基因 *EP3*(ncbi_107406053)、*BAMI*(ncbi_107422617)、*BGLU11*(ncbi_107426268)、*PGMP*(ncbi_107414395)表现出较高的表达量,且在着色期与成熟期间差异倍数显著,为下一步荧光定量分

析提供了基础。

根蘖与嫁接繁殖的灵武长枣差异表达基因的GO功能富集分析(图4)揭示,首先DEGs主要富集在碳水化合物代谢过程相关的GO条目,表明碳水化

表2 根蘖与嫁接繁殖灵武长枣差异基因表达量

Table 2 Differential gene expression table of root tillering and grafting propagation of Lingwuchangzao

基因名称(ID) Gene number (ID)	log ₂ FC	符号 Symbol	JB	NB	JZ	NZ	JC	NC
ncbi_107404967	-5.12	CHIT3	0.84±0.32 c	0.02±0.01 c	101.76±32.43 a	14.15±3.56 c	72.18±26.69 ab	31.86±8.04 bc
ncbi_107412669	-2.27	BGLU12	1.22±0.24 a	0.25±0.07 a	0.05±0.02 b	0.06±0.04 b	0.00±0.00 b	0.00±0.00 b
ncbi_107410359	-3.99	BACOVA_02659	0.22±0.05 a	0.18±0.07 a	0.14±0.03 ab	0.01±0.01 b	0.08±0.05 ab	0.11±0.02 ab
ncbi_107406053	-1.79	EP3	27.25±4.92 a	27.89±7.95 a	347.88±58.42 a	100.77±41.96 a	314.64±87.96 a	446.72±44.38 a
ncbi_107430147	-1.10	At1g64390	39.48±4.88 a	31.15±14.93 a	3.72±1.06 a	1.73±0.27 a	0.87±0.18 a	0.19±0.02 a
ncbi_107416873	-1.15	MUR4	17.43±3.73 a	15.58±1.44 b	41.33±16.39 ab	18.68±0.98 ab	34.66±6.59 ab	25.04±0.60 ab
ncbi_107414574	-2.15	TPPD	0.24±0.01 b	0.28±0.06 b	2.17±0.67 a	0.49±0.20 b	1.05±0.19 b	0.98±0.13 b
ncbi_107420179	-1.24	AGPS1	2.94±0.13 bc	2.79±0.25 bc	5.37±0.70 a	2.28±0.52 c	4.10±0.47 ab	1.47±0.46 c
ncbi_107422617	-1.04	BAM1	27.79±3.72 c	32.30±1.58 c	189.71±43.46 a	92.44±8.35 bc	148.84±43.78 ab	100.57±15.05 bc
ncbi_107418468	-1.01	Os06g0675700	2.59±0.30 cd	2.22±0.47 cd	3.31±0.34 c	1.64±0.24 d	4.50±0.42 b	12.83±0.21 a
ncbi_107430723	-1.01	FBP	38.93±6.32 b	53.02±2.73 a	5.01±2.64 d	16.92±3.66 c	1.44±0.49 d	0.41±0.08 d
ncbi_112489059	-1.03	BACOVA_02659	54.71±7.28 a	56.83±11.76 a	22.47±1.26 b	9.65±1.41 bc	8.72±1.47 bc	3.06±1.49 c
ncbi_107426021	-1.03	ISA2	15.08±1.35 a	16.24±0.80 a	1.18±0.29 c	10.49±1.11 b	1.05±0.11 c	0.50±0.05 c
ncbi_107429424	-1.08	LTA2	4.48±0.91 c	3.31±0.23 c	14.98±2.51 a	8.33±0.43 b	4.62±0.61 c	2.21±0.41 c
ncbi_107415022	-1.09	At3g13560	8.20±0.90 a	7.78±1.21 a	1.08±0.53 b	1.86±0.17 b	1.03±0.22 b	0.35±0.01 b
ncbi_107426268	-1.15	BGLU11	87.54±8.15 a	95.08±2.56 a	43.42±3.23 b	100.75±8.71 a	21.92±2.82 c	10.41±2.28 c
ncbi_107405417	-1.20	gmppA	79.43±11.76 b	109.48±9.59 a	2.47±0.27 c	15.86±2.53 c	2.61±0.33 c	1.12±0.08 c
ncbi_107414395	-1.31	PGMP	21.27±1.32 a	23.68±2.22 a	9.86±0.91 b	22.97±2.10 a	10.10±1.93 b	3.83±0.77 c
ncbi_107421001	-1.34	At1g11820	6.83±2.00 a	6.77±0.85 a	0.97±0.26 b	2.44±0.23 b	1.11±0.31 b	0.27±0.04 b
ncbi_107416348	-1.53	RHM1	6.44±1.40 a	6.42±0.83 a	4.23±0.86 bc	3.83±0.11 bc	3.15±0.22 bc	1.47±0.16 c
ncbi_107412550	-1.54	E1-BETA-2	19.49±3.20 bc	17.09±1.73 bc	68.19±6.08 a	75.36±3.96 a	27.48±5.52 b	11.81±2.00 c
ncbi_107432603	-2.19	RHM1	22.91±4.42 b	21.90±2.35 b	44.98±2.09 b	27.59±2.74 b	101.74±30.82 a	35.37±4.63 b
ncbi_107425056	-2.28	glpV	8.47±0.12 b	8.61±0.51 b	3.65±0.21 c	10.15±0.43 a	3.51±0.16 c	1.74±0.14 d
ncbi_107423556	-3.67	PMM	21.17±3.22 b	24.04±1.79 b	24.00±2.56 b	34.53±0.84 a	23.15±1.74 b	11.10±2.46 c

注:不同小写字母表示同一处理下不同发育阶段在 $P<0.05$ 水平上差异显著。

Note: Different small letters indicate significant differences at the $P<0.05$ level at different developmental stages under the same treatment.

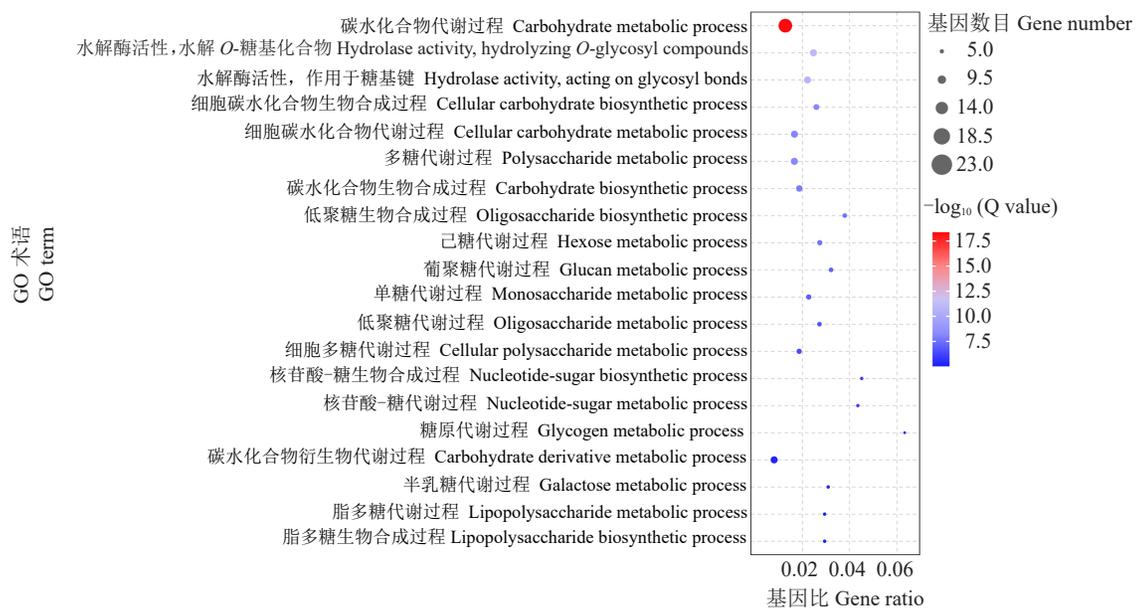


图4 根蘖与嫁接灵武长枣果实差异基因富集分析

Fig. 4 Differential gene enrichment analysis of root tiller and grafted Lingwuchangzao fruits

物代谢在两种繁殖方式之间存在显著差异。其次显著富集于水解酶活性相关的GO条目,尤其是水解O-糖基化合物以及作用于糖基键的水解酶活性。此外,DEGs还富集在碳水化合物衍生物代谢过程相关的GO条目中,暗示不同繁殖方式可能影响细胞内糖类的转化和利用。根蘖与嫁接植株在碳水化合物代谢、水解酶活性以及次生代谢产物合成等方面存在显著差异,这可能与不同繁殖方式的适应性以及枣果品质的形成密切相关。

2.3 灵武长枣果实可溶性糖代谢通路及差异基因分析

如图5所示,根蘖和嫁接植株果实中可溶性糖代谢相关候选基因的表达存在显著差异。果糖与甘露糖途径是灵武长枣可溶性糖代谢的中间途径,在该途径中检测到3个差异表达基因 *PMM*(ncbi_107423556)、*gmppA*(ncbi_107405417)、*FBP*(ncbi_107430723)。其中,*PMM*在根蘖植株白熟期与着色期的表达量均高于嫁接植株;*gmppA*和*FBP*的表达水平则随果实成熟而下降,表明甘露糖代谢在早期阶段更为活跃。在糖酵解/糖异生途径中,检测到1个差异表达基因 *PGMP*(ncbi_107414395)。该基因在根蘖与嫁接植株的白熟期均为高表达,但整体表达水平随果实成熟而下降。白熟期的高表达可能反映了该发育阶段对糖酵解产能的强烈需求,以满足果实早期快速生长和代谢的能量消耗。在淀粉与蔗糖途径中,在蔗糖合酶(*SUS*)催化蔗糖分解为UDP-葡萄糖和果糖过程中检测到1个差异表达基因 *BAMI*(ncbi_107422617)。该基因在根蘖与嫁接植株的白熟期中均为低表达,但在嫁接植株的着色期和成熟期的表达量高于根蘖植株,这可能与淀粉水解有关;在麦芽糖醇酶(*MGAM*)催化糊精生成D-葡萄糖过程中,检测到1个差异表达基因 *Os06g0675700*(ncbi_107418468)。该基因在成熟期高表达,且在根蘖植株中表达量高于嫁接植株,可能促进了淀粉降解为可溶性糖,进而提高灵武长枣成熟期的甜度。在氨基糖和核苷糖途径中,共检测到3个差异表达基因 *MUR4*(ncbi_107416873)与 *RHMI* 基因(ncbi_107416348、ncbi_107432603)。*RHMI*(ncbi_107432603)的表达量随着果实成熟而逐渐上升,且在成熟期,嫁接植株的表达量高于根蘖植株。*PGMP*(ncbi_107414395)在可溶性糖代谢通路中多次出现,表明该基因在调控灵武长枣可溶性糖代谢

过程中可能具有重要功能,可作为后续验证的关键基因。

2.4 加权基因共表达网络分析鉴定根蘖与嫁接灵武长枣可溶性糖关键基因

采用WGCNA分析可溶性糖含量、葡萄糖含量、果糖含量、蔗糖含量、果实纵横径和单果质量在表达模式间的关系。筛选DEGs后,从转录组测序数据中获得5527个基因,将这些基因分为8个共表达模块(图6-A)。结果表明,黑色模块中的基因与果糖含量呈显著正相关($r=0.87$);棕色和绿色模块中的基因与可溶性糖含量($r=0.71$ 、 $r=0.74$)、蔗糖含量($r=0.86$ 、 $r=0.83$)呈显著正相关,其中棕色模块基因与葡萄糖含量呈显著负相关;与横径呈显著负相关的模块有蓝色和黄色;与果实单果质量呈显著负相关的模块有蓝色($r=-0.75$)和绿松石色($r=-0.66$)。值得注意的是,没有检测到与果实纵横径显著相关的模块(图6-B)。选取相关性最强的黑色、绿色和棕色模块绘制基因网络调控图(图6-C~E)。从黑色模块中选取连通性最强且基因表达量高的ncbi_112492650与*HERC2*(ncbi_107420452)基因。

对黑色模块基因进行GO和KEGG富集分析。GO功能富集分析结果(图7-A)显示,该模块的差异表达基因显著富集于海藻糖磷酸合酶活性、葡萄糖甘油磷酸合酶活性及葡萄糖基转移酶活性功能;同时, β -呋喃果糖苷酶活性也呈现显著富集,提示该模块基因可能通过水解蔗糖以释放果糖,为后续代谢提供底物。KEGG富集分析结果(图7-B)显示,该模块的差异表达基因显著富集于脂肪酸生物合成途径;同时,淀粉和蔗糖代谢途径、半乳糖代谢途径也呈现显著富集,这些途径能够将蔗糖水解为果糖,进一步为果糖代谢提供前体底物,暗示该模块基因在糖类代谢中发挥重要作用。

2.5 差异基因qRT-PCR表达分析

基于显著差异表达基因及WGCNA分析结果,从中选取6个高表达且差异倍数较大的基因进行qRT-PCR验证,以嫁接植株白熟期(JB)样品作为对照。结果(图8)显示,在两种繁殖方式下,*EP3*、*BAMI*和ncbi_112492650在着色期与成熟期均呈现显著差异表达;*BGLU11*在白熟期和着色期均显著差异表达;*PGMP*在白熟期显著差异表达;*HERC2*仅在着色期显著差异表达。上述结果与转录组数据基本一致。

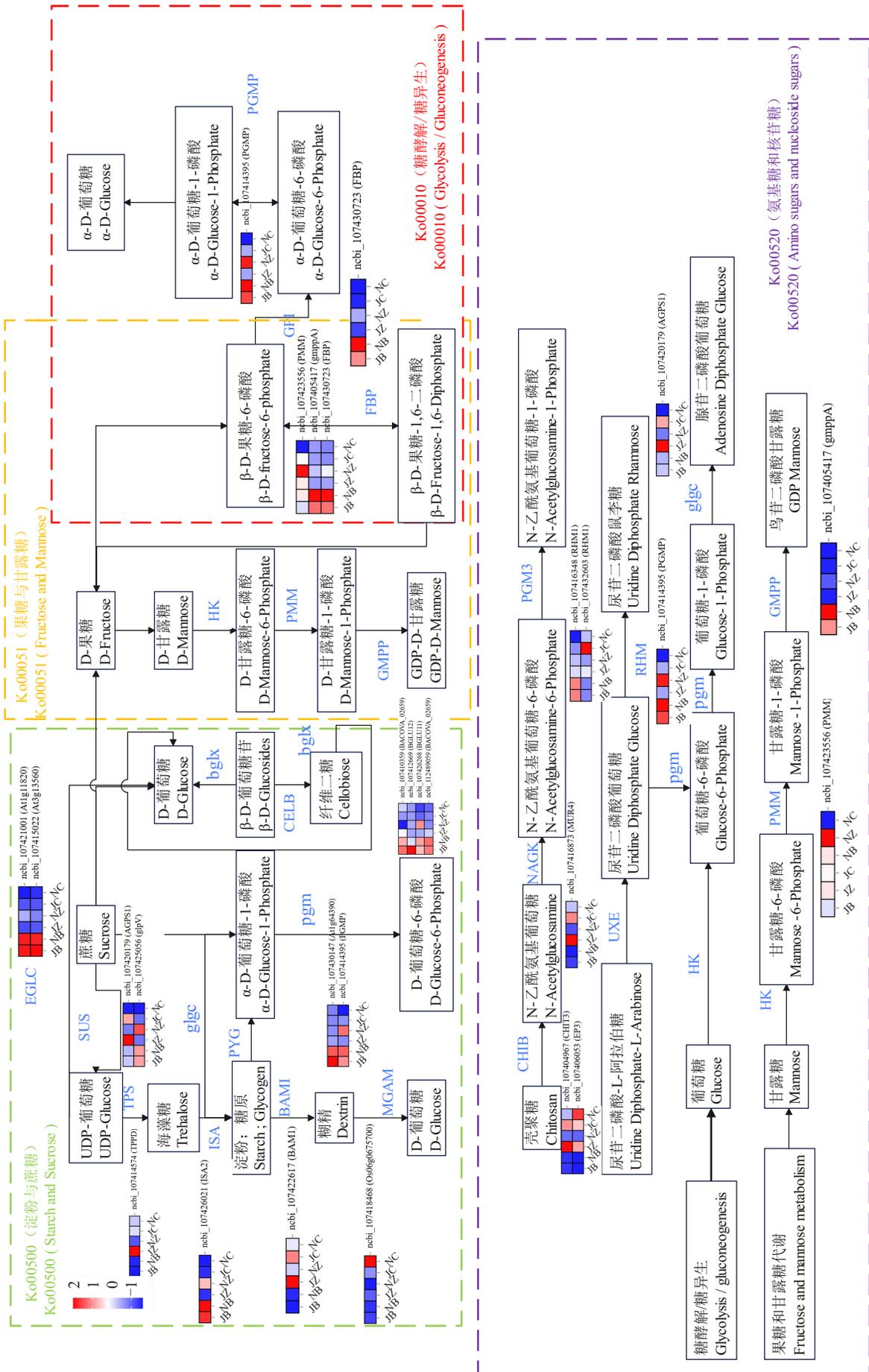


图5 灵武长枣可溶性糖代谢通路及差异基因热图

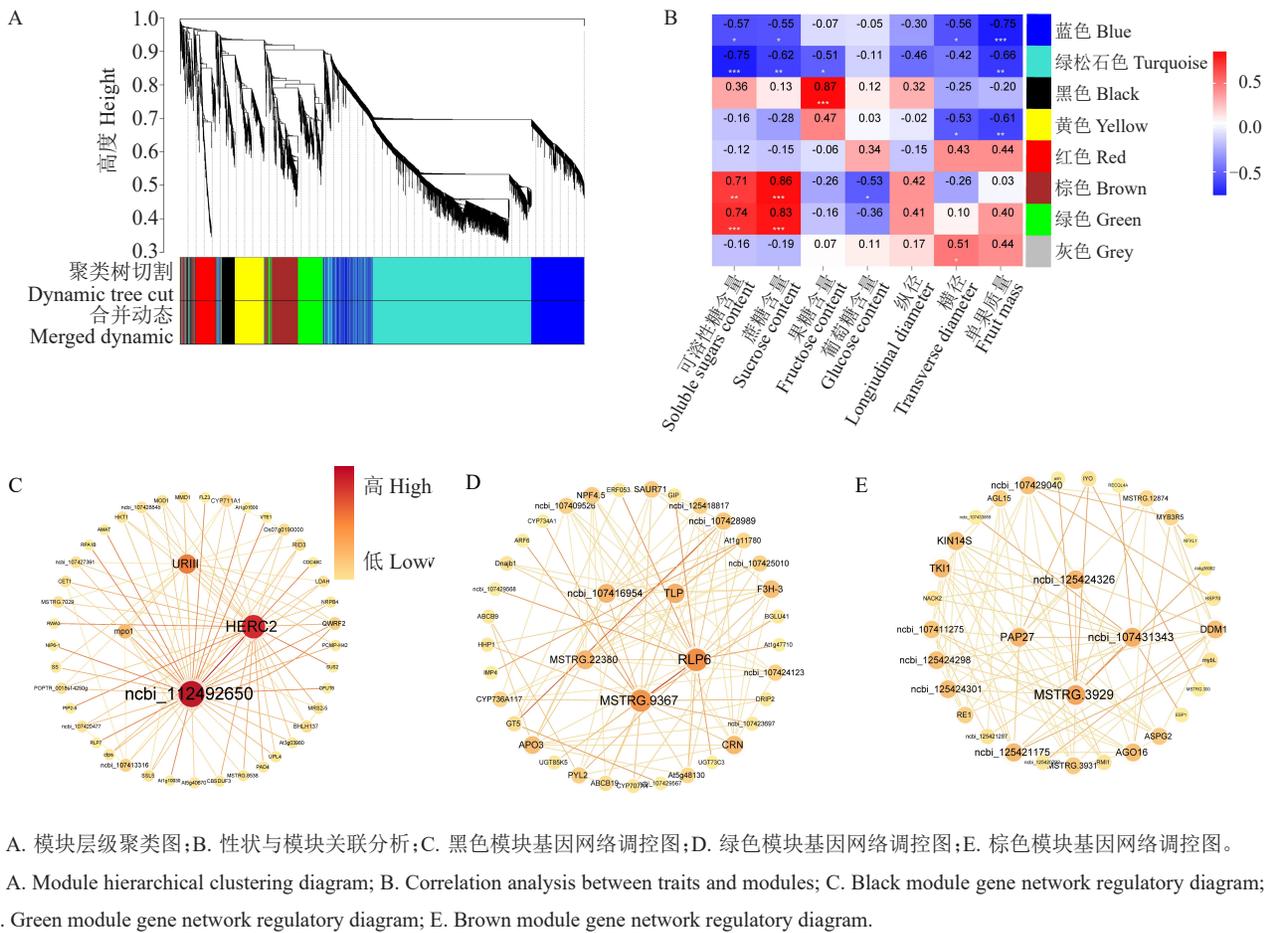
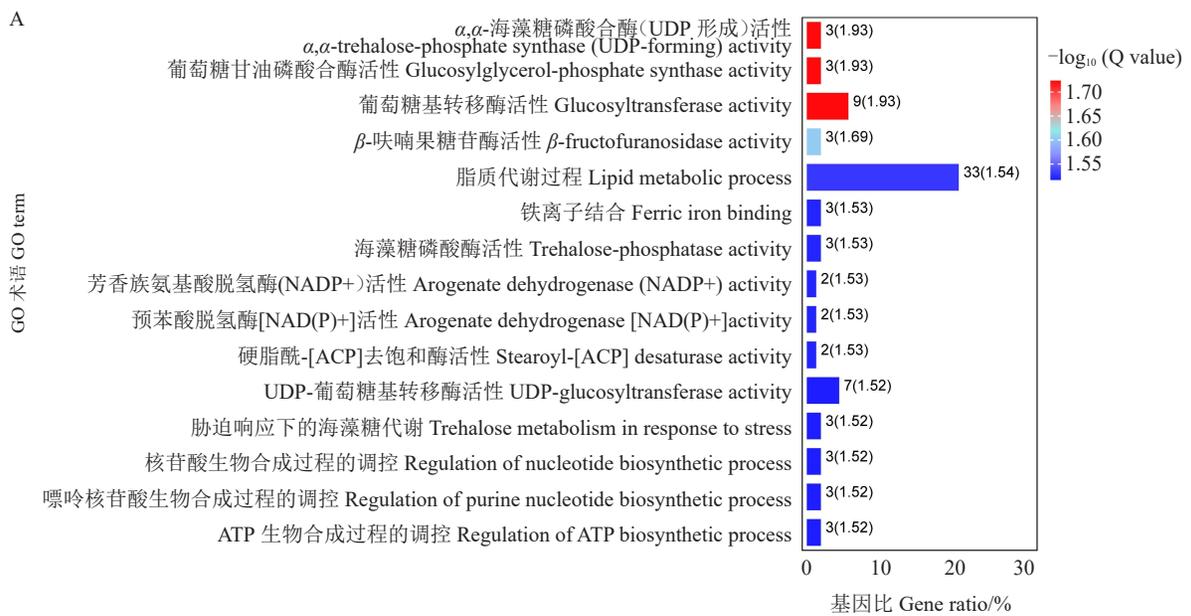


图6 加权基因共表达网络分析

Fig. 6 Weighted gene co-expression network analysis



A. 黑色模块 GO 功能富集分析; B. 黑色模块 KEGG 富集分析。

A. GO functional enrichment analysis of black module; B. KEGG enrichment analysis of black module.

图7 黑色模块富集分析

Fig. 7 Black module enrichment analysis

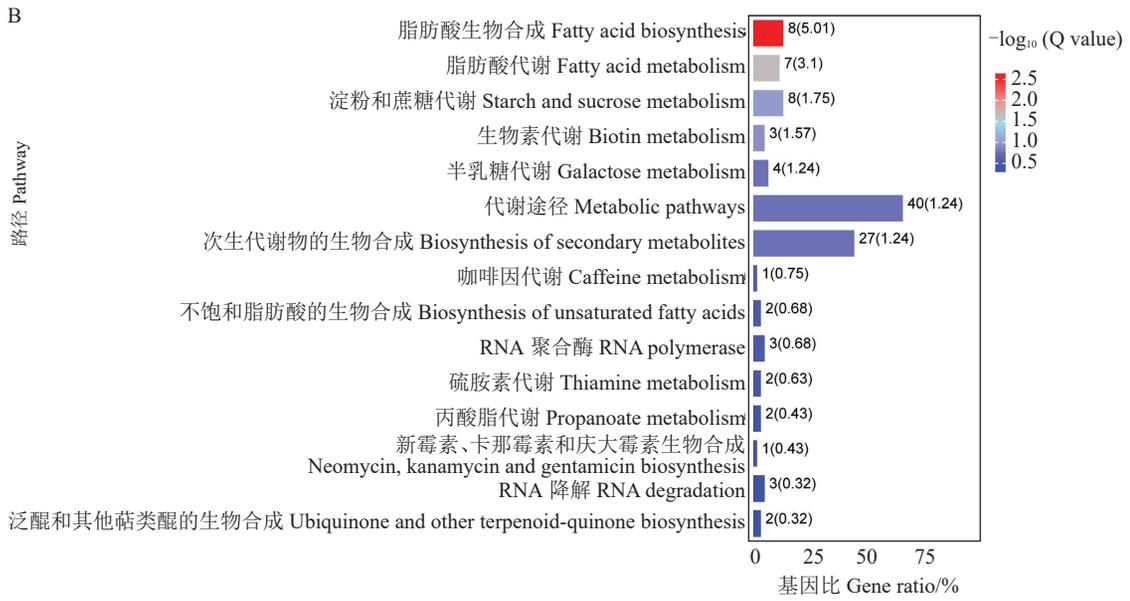


图7 (续) Fig. 7 (Continued)

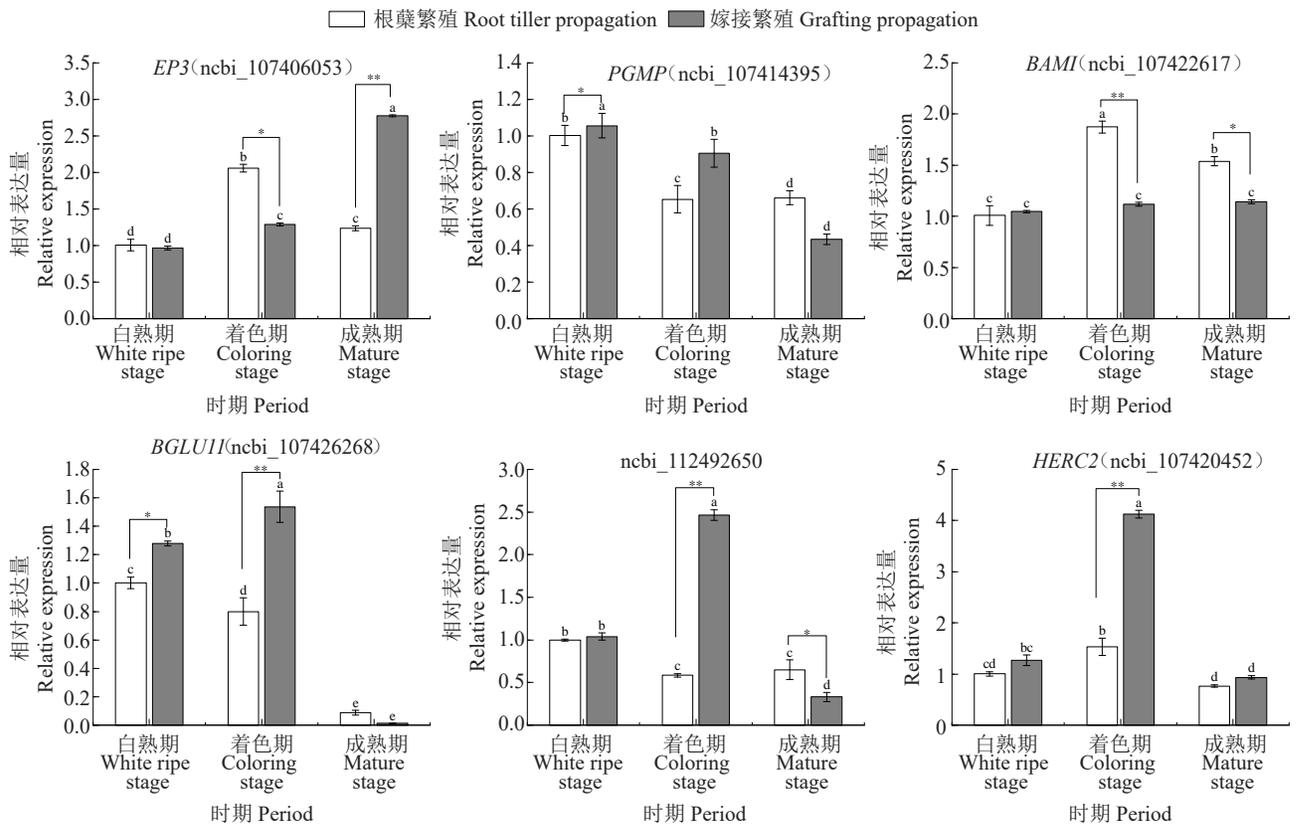


图8 qRT-PCR 验证根蘖与嫁接繁殖灵武长枣果实中与可溶性糖代谢相关的差异表达基因

Fig. 8 Verification of the differentially expressed genes related to soluble sugar metabolism in the fruit of Lingwuchangzao between root tillers and grafting propagation by qRT-PCR

3 讨论

可溶性糖类的积累是决定果实品质的重要因素。不同的可溶性糖成分甜度各异,其含量和比例

对味觉特征和感官品质产生决定性影响^[21-22]。糖在果实品质的形成中起着关键作用,果实中的糖主要通过糖酵解、糖异生及淀粉与蔗糖等的相互转化来进行代谢^[17,23]。在果树生产中,为了保持品种的优

良特性,通常采用嫁接、扦插、根蘖、组织培养等无性繁殖方式^[24]。为了揭示不同繁殖方式下灵武长枣果实品质的差异及其代谢机制,笔者以糖酵解/糖异生、淀粉与蔗糖代谢、果糖和甘露糖代谢以及氨基糖和核苷酸糖代谢这4个关键代谢通路进行差异表达基因分析,深入挖掘参与调控糖代谢的关键基因,以解析不同繁殖方式对糖积累的调控机制。

笔者分别测定了根蘖与嫁接灵武长枣在白熟期、着色期和成熟期果实的可溶性糖含量,结果显示,在白熟期和着色期,根蘖与嫁接植株果实均以果糖和葡萄糖为主要糖类,这与在冬枣、骏枣中的结果一致^[25]。果糖和葡萄糖作为直接能量来源,可能为细胞分裂和膨大提供代谢动力^[7]。然而,在果实成熟期,蔗糖为主要积累糖类,且根蘖植株果实的蔗糖含量显著高于嫁接植株,增加了18%,这与枣果实的糖分动态变化相吻合^[26-28]。研究发现,蔗糖代谢是调控果实品质的重要机制,果实中糖积累、品质维持与蔗糖代谢酶活性密切相关^[29]。本研究结果表明,嫁接植株果实成熟期的果糖和葡萄糖含量高于根蘖植株,分别高出13.32%和26.85%,这可能与两种繁殖方式通过不同代谢策略调控糖分组成有关。嫁接砧木可能通过上调糖代谢关键酶活性,促进蔗糖向果糖和葡萄糖转化,导致成熟期单糖含量升高,这在枸杞研究中得到印证^[30];而根蘖植株可能更依赖淀粉降解途径,其糖分积累以蔗糖为主。研究还发现在白熟期,嫁接植株果实可溶性糖含量显著高于根蘖植株(17.55%)。嫁接可能通过砧木“加速”接穗的生理进程,使糖代谢相关基因如*BGLUI1*在白熟期高表达,激活糖代谢途径,为果实早期发育提供能量。

转录组测序可比较个体在不同发育时期、不同组织或环境下基因的差异表达,以及挖掘与特定生理功能相关的基因^[31-33]。基于转录组数据分析,在桑葚、番茄、黄桃及枸杞等多种水果中均已发现了与糖分差异相关的基因^[8,10,30,34]。研究表明*ZjSPS*(蔗糖磷酸合酶)、*ZjSS*(蔗糖合酶)、*ZjINV*(转化酶)等基因在枣果实糖代谢中起重要作用,其表达水平与糖含量变化密切相关^[35]。笔者还发现*BGLUI1*(ncbi_107426268)在嫁接植株白熟期高表达,表明不同繁殖方式可能通过调控基因的时序表达进而影响果实的糖分积累。研究发现,嫁接在不同砧木上的苹果和两种砧木嫁接的灵武长枣可通过改变接穗基因的

表达,进而影响接穗的生长和果实品质^[33,36]。通过WGCNA共表达网络结合多时期动态表达分析,并基于代谢通路富集分析结果,筛选出ncbi_112492650、*HERC2*(ncbi_107420452)和*PGMP*(ncbi_107414395)等可能在特定发育阶段调控灵武长枣果实可溶性糖代谢的关键基因。而马亚平等^[37]的研究仅基于成熟期转录组数据差异分析(FPKM>1, |log₂FC|≥1),筛选出与糖代谢相关的关键差异基因*BAMI*,可能遗漏了早期的关键调控基因。

4 结 论

以根蘖和嫁接灵武长枣果实为材料,分析了白熟期、着色期和成熟期3个时期的可溶性糖含量变化。从4个主要代谢通路中筛选出24个差异基因。通过加权基因共表达网络分析,黑色、棕色和绿色模块的基因与果糖、可溶性糖、蔗糖、葡萄糖含量显著相关,其中基因ncbi_112492650、*HERC2*(ncbi_107420452)和*PGMP*(ncbi_107414395)表达量高且联系最紧密。

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