

着色香葡萄大果型芽变的转录组及赤霉素相关基因表达分析

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摘要:【目的】探究着色香葡萄大果型芽变果粒大的机制。【方法】以着色香葡萄及其大果型芽变果实为材料, 通过转录组测定及qRT-PCR表达分析, 结合果粒大小、果皮厚度、赤霉素酶活性检测和相关性分析, 明确影响果实膨大的关键基因。【结果】着色香大果型芽变的果粒和果穗显著大于着色香。花后15 d, 芽变表皮细胞为三层, 着色香为一层; 芽变果肉细胞为不规则椭圆形, 着色香为不规则卵圆形。果实成熟期, 芽变的果皮较厚且木栓化程度高; 芽变表皮细胞多呈不规则囊泡状, 着色香多呈锥形或长梭形; 芽变果肉细胞呈不规则囊泡形, 着色香呈不规则卵圆形。花后15 d, 幼果转录组测序结果表明, 两者差异基因数2242个, 上调1167个、下调1075个; GO富集分析中, 差异基因主要涉及膜相关基因、转录因子及相关酶活基因, 其中膜相关差异基因最多; KEGG富集分析中, 差异基因主要富集于次级代谢产物的生物合成、氨基酸生物合成以及卡尔文循环固碳等途径。着色香 *VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 基因的表达量显著高于芽变, 且 *VvGA2ox2*、*VvGA2ox4* 表达量为芽变的751.00倍和30.67倍; 着色香GA2ox酶活性为芽变的1.3倍, 芽变幼果中GA₃、GA₄和GA₇含量均显著高于着色香。【结论】赤霉素通过影响次级代谢产物的生物合成、氨基酸生物合成以及卡尔文循环固碳等途径, 调控膜相关基因、转录因子及相关酶活性等基因表达, 促使着色香及其大果型芽变的果实大小及细胞形态产生明显差异。赤霉素相关基因 *VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 为影响着色香葡萄大果芽变果实发育的重要因子。

关键词: 葡萄; 大果芽变; 转录组; 赤霉素; 基因表达

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Transcriptome and expression analysis of gibberellin-related genes in large-fruit type bud mutant of Zhuosexiang grape

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Abstract: 【Objective】The study aimed to explore the difference of morphological structure affecting large-fruit type grape bud mutant, and the relationship between gibberellins (GAs) and large-fruit type grape bud mutant. Mutants of fruit trees can produce new traits so they can be used for variety selection. GAs play key role in regulating cell elongation and promoting fruit enlargement. The increase of endogenous GAs content is positively correlated with the size of fruit and the number of peel cells. 【Methods】Zhuosexiang grape and its large-fruit type bud mutant were used as experimental materials. Through the determination of fruit transcriptome at 15 days after flowering and the qRT-PCR expres-

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sion analysis of gibberellin-related genes *VvKO*, *VvGA2ox2*, *VvGA2ox4* and *VvGA3ox4*, combined with the measurement of fruit size and morphology at 15 days after flowering and at fruit maturity stage, the paraffin section was made to compare the peel thickness, and the enzyme activity of the screened GAs enzyme was detected. The correlation analysis of the vertical and horizontal diameters of the fruits, the key genes *VvKO*, *VvGA2ox2*, *VvGA2ox4* and *VvGA3ox4*, and the screened GAs enzyme activity was investigated. **【Results】** The results showed that the fruit grains and ears of the large-fruit type bud mutant of Zhuosexiang were significantly higher than those of at 15 days after flowering and fruit maturity. There were some differences in peel morphological structure between the two test materials at 15 days after flowering and fruit maturity. At 15 days after flowering, the epidermal cells of the large-fruit type bud mutant were three layers, and the epidermal cells of the Zhuosexiang were only one layer. There was no significant difference in the morphology of subepidermal cells between the two, both were irregularly oval, and there was no significant difference in peel thickness between the two. At fruit maturity stage, the peel thickness of large-fruit type bud mutant grapes was significantly larger than that of Zhuosexiang, and the corky epidermal cells were thicker (black area). The subepidermal cells of the large-fruit type bud mutant were larger and mostly irregularly vesicular, while the subepidermal cells of the Zhuosexiang were smaller and mostly conical or long spindle-shaped. At 15 days after flowering, the flesh cells of Zhuosexiang were irregular oval, and the flesh cells of the large-fruit type bud mutant were irregular oval. The subepidermal cells of the large-fruit type bud mutant were larger and mostly irregularly vesicular, while the subepidermal cells of the Zhuosexiang were relatively smaller and mostly conical or long spindle-shaped. At the mature stage, the flesh cells of Zhuosexiang were irregularly oval, and the flesh cells of large-fruit type bud mutant were irregularly vesicle-shaped. The transcriptome sequencing results of the young fruits at 15 days after flowering showed that the number of differentially expressed genes was 2242, with 1167 up-regulated genes and 1075 down-regulated genes. In order to explore the biological functions and properties of differentially expressed genes between Zhuosexiang and its large-fruit type bud mutant, GO enrichment analysis was performed on differentially expressed genes between Zhuosexiang and large-fruit type bud mutant. The results showed that differentially expressed genes (DEGs) were mainly annotated into three functional groups: the first was biological process, which was enriched in phosphorylation, regulation of DNA-templated transcription and protein phosphorylation; the second was biological process, which was enriched in phosphorylation and regulation of DNA-templated transcription and protein phosphorylation. The second is the cell component, and the more enriched is the membrane-related gene; the third is molecular function, which is enriched in enzyme activity and binding-related genes. The results of KEGG enrichment showed that there were more differential genes in the following pathways: 59 genes were up-regulated and 33 genes were down-regulated in the biosynthesis of secondary metabolites pathway; there were 16 up-regulated genes and 3 down-regulated genes in the biosynthesis of amino acids pathway. There were 9 up-regulated genes and 0 down-regulated genes in the carbon fixation by Calvin cycle pathway. Phagosome pathway up-regulated 11 genes and down-regulated 0; Glycolysis/Gluconeogenesis pathway up-regulated 12 genes, down-regulated 0; Phenylpropanoid biosynthesis pathway up-regulated 10 genes and down-regulated 4 genes. GAs is an important factor for grape fruit enlargement. In order to study the relationship between GAs and the mutant of Zhuosexiang, the expression of four gibberellin-related genes was analyzed by qRT-PCR. The results showed that the expression levels of *VvKO*, *VvGA3ox4*, *VvGA2ox4* and *VvGA2ox2* genes in Zhuosexiang were significantly higher than those in large-fruit type bud mutant ($P < 0.05$), which were 2.33 times, 5.13 times, 30.67 times and 751 times higher than those in large-fruit

type bud mutant. GA2ox enzyme is an important enzyme for the degradation of GAs in plants. In order to further clarify the role of GA2ox gene in the large-fruit type bud mutant, the GA2ox enzyme activity in young fruit at 15 days after flowering was determined. The results showed that the GA2ox enzyme activity in the young fruit of Zhuosexiang and large-fruit type bud mutant were $17.58 \text{ U} \cdot \text{g}^{-1}$ and $13.54 \text{ U} \cdot \text{g}^{-1}$. The GA2ox enzyme activity in the fruit of Zhuosexiang was 1.3 times as high as that of large-fruit type bud mutant, which was significantly higher than that of large-fruit type bud mutant ($P < 0.05$). The correlation analysis between four key differential genes, one enzyme activity and fruit longitudinal and transverse diameter was carried out. The *VvGA2ox2*, *VvGA3ox4* and GA2ox enzyme, *VvGA2ox4* and *VvGA3ox4*, fruit transverse diameter and longitudinal diameter were significantly and positively correlated, and the *VvGA2ox2*, *VvGA2ox4*, *VvGA3ox4* and GA2ox enzyme were significantly and negatively correlated with fruit longitudinal and transverse diameter. The *VvGA2ox4*, *VvGA3ox4* and *VvGA2ox2*, *VvGA2ox4* and GA2ox were significantly positively correlated. The results showed that the GA2ox enzyme activity of *VvGA2ox2*, *VvGA2ox4* and *VvGA3ox4* increased when the expression of the three genes was up-regulated, thereby inhibiting the increase of the vertical and horizontal diameters of the fruit. The contents of common GA₃, GA₄ and GA₇ in the young fruit of large-fruit type bud mutant were significantly higher than those of Zhuosexiang. 【Conclusion】 There were significant differences in pericarp morphological structure between the two test materials. The number of epidermal cell layers of large-fruit type bud mutant was more at 15 days after flowering. During the ripening period, the peel of large-fruit type bud mutant grape was thicker, and the cork-like epidermal cells were thicker, and the subepidermal cells were larger and mostly irregularly vesicle-like, while the subepidermal cells of Zhuosexiang were smaller and mostly conical or long spindle-shaped. The number of significantly different genes between the two was 2242, involving multiple membrane-related genes, transcription factors and enzyme activity genes, of which the number of membrane-related differential genes was the largest. In terms of metabolic pathways, there were many differentially expressed genes involved in amino acid biosynthesis, amphetamine biosynthesis, biosynthesis of secondary metabolites, Calvin cycle carbon fixation, phagosome and glycolysis/glucose production. The expression levels of the *VvKO*, *VvGA2ox2*, *VvGA2ox4* and *VvGA3ox4* genes in Zhuosexiang grape were significantly higher than those in large-fruit type bud mutant, especially the *VvGA2ox2* and *VvGA2ox4*, and their corresponding GA2ox enzyme activities were also significantly higher than those in large-fruit type bud mutant. The correlation analysis results were also consistent with the research results, indicating that gibberellin-related genes were important factors affecting the development of Zhuosexiang grape large-fruit type bud mutant.

Key words: Grape; Large-fruit type bud mutant; Transcriptome; Gibberellin; Gene expression

果实大小作为园艺作物的重要经济性状之一,直接影响商品价值及农业生产效益,相关调控机制为当前园艺领域的研究热点^[1]。随着分子生物学的发展,果实大小形成的遗传基础及其受环境因素和激素调控的复杂网络逐渐被揭示^[2]。王乐乐等^[3]通过对葡萄户太八号和赤霞珠果实的细胞数目和体积进行观测,发现品种间果型大小差异的主要诱因是细胞数目的不同。翠冠梨大果芽变的研究也表明果肉细胞的增大是果实变大的重要原因^[4]。已有研究表明细胞通过改变细胞壁的结构和组成,使体积增

大,从而促进果实的整体膨大,在此过程中赤霉素通过调控细胞壁松弛基因的表达,促进细胞壁的伸展性增加,实现细胞伸长^[5]。例如,在金手指葡萄果实的研究中发现,外源赤霉素处理能够显著促进果实的纵向伸长,导致果形指数升高、果实变得更加细长^[6]。分子方面研究表明,不同基因通过直接或间接调控植物激素从而影响果实大小,如bHLH转录因子通过调控生长素和赤霉素代谢及信号转导,促进葡萄果实的膨大^[5]。在翠冠梨^[4]和锦红冰糖橙^[7]的研究中发现,在果实发育早期赤霉素正调控基因

GRP6 显著上调表达而负调控基因 *GA2ox1* 和 *GA3ox1* 则呈现下调趋势,这表明赤霉素通过调节这些基因的表达来影响果实细胞的分裂和伸长。在葡萄中,已经进行了一些研究来调查浆果大小表型变异或其相关性状的遗传决定因素,并确定了不同染色体上的数量性状位点(quantitative trait locus, QTL)。大多数控制果实发育的QTL对应浆果质量定位于18号染色体上,在控制果实大小的QTL区间内,发现了编码细胞分裂素合成酶(CKS)、生长素响应因子(ARF)和细胞壁代谢相关酶(如 *expansin*)的基因,这些基因通过调控细胞分裂、激素信号转导和细胞膨大过程影响果实发育^[8]。

芽变是植物芽分生组织中遗传物质的自然变异,是一种体细胞突变。发生在果树上的芽变可以给传统品种带来多种新性状,如果实大小^[9]、颜色^[10]、风味^[11]以及成熟期的变化^[12]。芽变育种周期短、见效快、目标明确,是果树品种改良的高效途径。受栽培品种的遗传基础、栽培区域和时期等因素影响,不同葡萄品种的芽变数量和芽变性状存在差异^[13]。1974—2022年,通过芽变选种培育出的葡萄新品种共65个,为除杂交育种外选育葡萄品种数量最多的一个途径^[14-15]。大果型芽变特指在果实大小方面发生显著增大的芽变类型。通过大果型芽变选育,中国已成功培育出多个葡萄优良品种,例如大粒玫瑰香、大粒无核白、红地球的大果芽变品种紫提988和红太阳。

着色香葡萄香味浓郁、含糖量高、口感好,适合设施和露地栽培,为中国东北地区的主栽品种之一,其大果型芽变(俗称巨茉莉)于多年前在吉林省内首次被发现。本研究通过石蜡切片技术分析果皮细胞的形态差异,利用高通量测序技术筛选与芽变相关的信号通路和关键基因,对赤霉素相关基因进行qRT-PCR表达分析及检测关键酶的活性,旨在探索赤霉素与葡萄大果型芽变之间的关系,为葡萄品种改良提供理论依据。

1 材料和方法

1.1 试验地点

本试验于吉林省农业科学院果树研究所葡萄试验园进行。试验园位于吉林省中部地区公主岭市(43°29'32.7" N、124°51'53.3" E,海拔220 m),地势平坦,土壤为壤质黏土。该地属中温带大陆性季风气候,四季分明,冬冷夏热,年平均气温5.9℃,年平均

日照时数2743 h,年平均降雨量594.8 mm,无霜期约140 d。

1.2 试验材料

本研究以着色香及其大果型芽变(巨茉莉)(图1)为试验材料,砧木为贝达。树龄8 a(年)生,厂字形、直立叶幕。每份供试材料选取长势一致、生长健壮的植株各5株,常规田间管理。



着色香
Zhuosexiang

大果型芽变
Large-fruit type bud mutant

图1 着色香及其大果型芽变的果实

Fig. 1 The fruit of Zhuosexiang and its large-fruit type bud mutant

1.3 果粒大小测定

于果实成熟期,每份供试材料选取果穗中部10粒果实,使用游标卡尺测量果粒的横径和纵径,分别取平均值。

1.4 石蜡切片制作

于盛花后15 d及果实成熟期,分别选取着色香及其大果型芽变果穗中部发育良好的葡萄果实10粒,投入70% FAA固定液,室温固定24 h以上。石蜡切片制作方法:将果粒从固定液中取出,剥离果皮并置于脱水盒内,采用不同梯度酒精脱水,二甲苯透明后浸蜡置于组织包埋机中包埋,将修整后的蜡块置于石蜡切片器切片,盛花期后15 d果皮切片厚度为5 μm,成熟期果皮切片厚度为15 μm,放入60℃烘箱内烤片。切片用番红-固绿染色,中性树脂封片,置于Nikon Eclipse E100显微镜下拍照采集图片。

1.5 酶活性及常见赤霉素含量检测

以着色香葡萄及其大果型芽变花后15 d的幼果为试验材料,利用植物赤霉素2氧化酶(GA2ox)

ELISA 检测试剂盒,GA₃、GA₄、GA₇ ELISA 检测试剂盒(上海酶标生物科技有限公司)进行植物赤霉素2氧化酶活性和赤霉素GA₃、GA₄、GA₇含量检测。酶标仪为SpectraMax i3x,测定波长为450 nm,3次重复。

1.6 转录组测序与分析

花后15 d,采集着色香葡萄及其大果型芽变果穗中部发育良好、无病虫害的幼果20粒,3次生物学重复。果粒样品采集后装入锡纸包,立即液氮速冻,-80℃冰箱保存备用。果粒样品RNA提取以及转录组测序委托上海百趣生物医学科技有限公司完成,依据齐茹雪等^[16]的方法进行转录组测序和差异表

达基因(differentially expressed genes,DEGs)分析。

1.7 qRT-PCR 检测

在本课题组前期研究基础上,选择赤霉素相关基因 *VvKO*、*VvGA3ox4*、*VvGA2ox4* 和 *VvGA2ox2* 进行检测。*VvKO* 和 *VvGA3ox4* 基因正向调控赤霉素合成,*VvGA2ox4* 和 *VvGA2ox2* 基因负向调控赤霉素合成。在NCBI(National Center for Biotechnology Information)数据库中查找 *VvKO* (JQ086553)、*VvGA2ox2* (JQ086554)、*VvGA2ox4* (JQ086555)、*VvGA3ox4* (JQ086556)的DNA序列,并采用Primer 5.0设计引物,引物序列及目的片段大小详见表1。

表1 引物序列及目的基因片段大小

Table 1 Primer sequence and target gene fragment size

基因名称 Genes name	登录号 Accession No.	引物序列(5'→3') Primer sequence(5'→3')	目的片段大小 Target fragment size/bp
<i>KO</i>	JQ086553	F:TGGAGGAGGAAAGAGGGTGT R:ATGGGATGGAGTTTCTGACTGGTG	159
<i>GA2ox2</i>	JQ086554	F:GTGTTATCGCAGAATGGTCG R:TTGGCGTGAGGGCTTGTC	107
<i>GA2ox4</i>	JQ086555	F:CCAATGACCCAACAAAGT R:TGGACCCACAATCCCTCT	106
<i>GA3ox4</i>	JQ086556	F:TGCCACTGGAATAGCAACTT R:AGGAGGAGGACTGTGGGTGT	105
<i>UBI</i>		F:AGTAGATGACTGGATTGGAGGT R:GAGTATCAAAAACAAAAGCATCG	150

用多糖多酚植物RNA提取试剂盒(DP441)(天根生化科技(北京)有限公司),提取着色香及其大果型芽变葡萄花后15 d果实的总RNA,用PowerScript II TM反转录试剂盒反转录成总cDNA,利用SYBR Green-based One-Step qRT-PCR kit试剂盒(北京全式金公司)进行qRT-PCR检测,以葡萄中的*UBI*基因为管家基因。经筛选优化后的qRT-PCR反应体系(20 μL)如下:10 μL SYBR Green PCR Master Mix,2 μL 400 ng cDNA,正向与反向引物各0.4 μL和7.2 μL ddH₂O。qRT-PCR反应参数为,第一阶段:95℃预变性30 s;第二阶段:95℃变性5 s,60℃退火34 s,循环扩增56次;第三阶段:95℃延伸15 s,60℃延伸60 s,95℃延伸1 s,进行1次循环。使用2^{-ΔΔCt}方法^[17]计算相对表达量。试验设置3个生物学重复,每个生物学重复包含3个技术重复。

1.8 数据统计与处理

试验数据采用Excel 2023和R语言软件进行统计处理、差异显著性及相关性分析。

2 结果与分析

2.1 果实成熟期果粒大小比较

由表2可知,花后15 d,着色香和大果型芽变的果粒纵径分别为1.19和1.43 cm,横径分别为0.83和1.07 cm;果实成熟期,两者果粒纵径分别为1.77和2.04 cm,横径分别为1.35和1.72 cm,果穗长度分别为10.83和14.25 cm,果穗宽度分别为5.51和8.32 cm。花后15 d和果实成熟期时,大果型芽变的果粒纵径、横径和果穗长度与宽度均显著大于着色香,即芽变的果粒更大。

2.2 果皮果肉形态结构分析

花后15 d和果实成熟期两份供试材料间的果皮

表 2 着色香及其大果型芽变果实形态测定

Table 2 Determination of fruit morphology of Zhuosexiang and its large-fruit type bud mutant

试验材料 Test material	花后 15 d 15 days after flowering		成熟期 Mature stage			
	果粒纵径 Vertical diameter/ cm	果粒横径 Transverse diameter/ cm	果粒纵径 Vertical diameter/ cm	果粒横径 Transverse diameter/cm	果穗长度 Length/cm	果穗宽度 Width/cm
着色香 Zhuosexiang	1.19±0.12 b	0.83±0.08 b	1.77±0.15 b	1.35±0.16 b	10.83±1.03 b	5.51±1.01 b
大果型芽变 Large-fruit type bud mutant	1.43±0.10 a	1.07±0.06 a	2.04±0.14 a	1.72±0.12 a	14.25±1.43 a	8.32±0.82 a

注:不同小写字母表示差异显著($P<0.05$)。

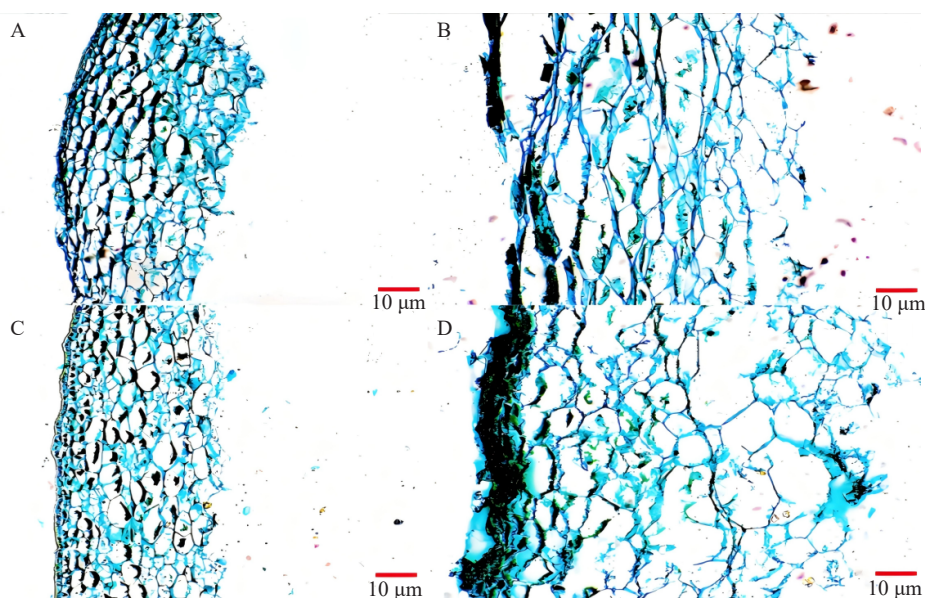
Note: Different small letters indicate significant difference at $P<0.05$.

形态结构存在一定差异(图2)。花后 15 d,大果型芽变表皮细胞为三层,着色香表皮细胞只有一层;两者亚表皮细胞形态无明显差异,均呈不规则卵圆形,两者果皮厚度无明显差异。果实成熟期,大果型芽变葡萄果皮厚度明显大于着色香,且木栓化的表皮细胞较厚(黑色区域);大果型芽变的亚表皮细胞较大、多呈不规则囊泡状,而着色香亚表皮细胞较小、多呈锥形或长梭形。花后 15 d着色香果肉细胞为不规则卵圆形,大果型芽变果肉细胞则为不规则椭圆形,二者大小无太大差异;成熟期着色香果肉细胞呈不规则卵圆形,大果型芽变果肉细胞呈现不规则囊泡形,且大果型芽变果肉细胞明显大于着色香。

2.3 转录组测序及分析

Illumina 测序的 raw reads 经质控后,所检测基因共有 25 260 个,在基因组上的覆盖度为 87.1%,其中差异表达基因有 2242 个,包括显著上调基因 1167 个,显著下调基因有 1075 个。获得着色香和大果型芽变的 Q30 均大于 97.69%,Q20 均大于 99.60%;有效 reads 所占比例分别为 97.41%、96.67%、97.32%和 97.48%、97.33%、97.00%,GC 含量分别为 45.50%、46.50%、45.50%和 45.50%、45.50%、46.50%。以上结果表明测序数据较好,质量较高,可用于后续分析。

为探究着色香及其大果型芽变差异表达基因的生物功能和属性,将差异表达基因进行 GO 和 KEGG 富集分析。GO 富集结果见图 3,两个品种果



A. 着色香花后 15 d 果皮切片;B. 着色香成熟期果皮切片;C. 大果型芽变花后 15 d 果皮切片;D. 大果型芽变成熟期果皮切片。显微镜放大倍数为 100 倍(10×10)。

A. Peel slices of 15 days after colored scented flowers; B. Peel slices of mature period of coloring aroma; C. Peel section of large-fruit type bud mutant 15 days after flowering; D. Large-fruit type bud mutant mature peel section. The magnification of the microscope is 100 times (10×10).

图 2 着色香及其大果型芽变不同时期果皮厚度对比

Fig. 2 Comparison of pericarp thickness of Zhuosexiang grape and its large-fruit type mutant

粒中多个膜相关基因、转录因子活性基因、相关酶活性基因均呈上调趋势,其中,膜相关基因通路差异基因最显著。结果显示,差异表达基因主要被注释到了3个功能组:第一个是生物学过程,富集较多的是磷酸化(phosphorylation),其中上调57个、下调117个,DNA模板转录调节(regulation of DNA-templated transcription)和蛋白质磷酸化(protein phosphorylation),其中上调62个、下调105个;第二个是细胞

组分,富集较多的是两类膜相关(membrane)基因,其中外膜类基因上调430个、下调404个,内膜类基因上调402个、下调380个;第三个是分子功能,富集较多的是酶活性和结合相关基因,共上调883个、下调1088个。

KEGG 富集结果(图4)表明:次级代谢产物的生物合成(biosynthesis of secondary metabolites)途径上调基因59个、下调33个;氨基酸生物合成(biosyn-

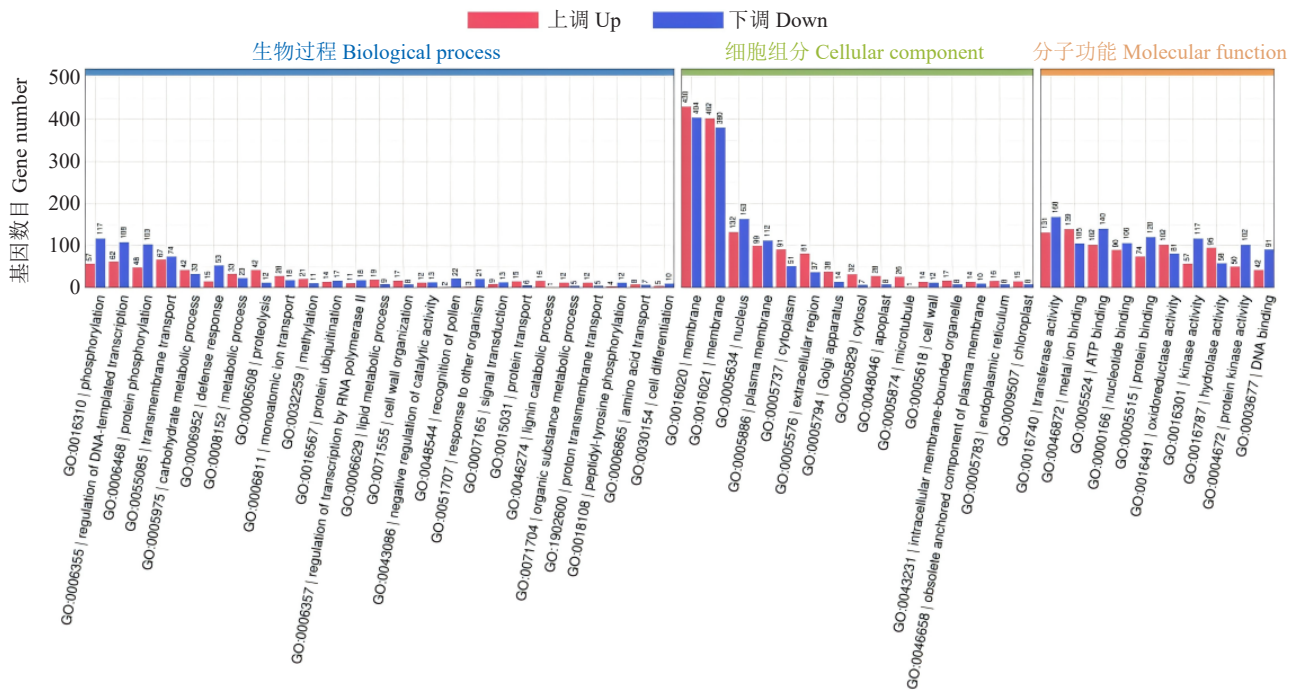


图3 样本 GO 富集分类

Fig. 3 Sample GO enrichment classification

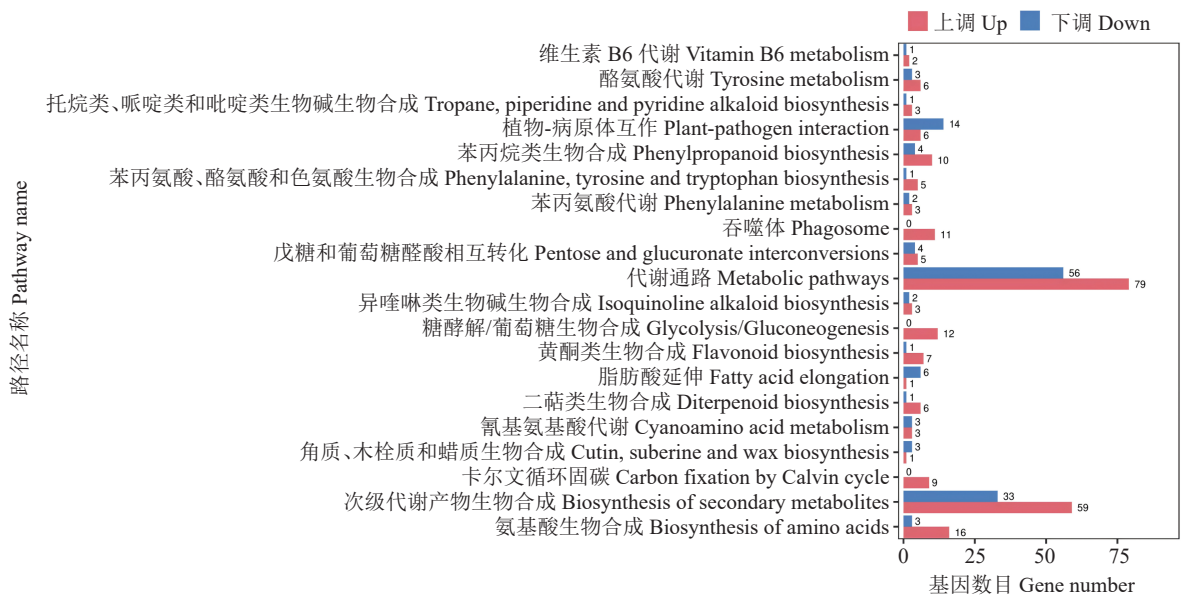


图4 样本 KEGG 富集 Top20

Fig. 4 Sample KEGG enrichment Top20

thesis of amino acids)途径上调基因 16 个、下调 3 个；卡尔文循环固碳(carbon fixation by Calvin cycle)途径上调基因 9 个、下调 0 个；吞噬体(phagosome)途径上调基因 11 个、下调 0 个；糖酵解/葡萄糖生成(glycolysis/gluconeogenesis)途径上调基因 12 个、下调 0 个；苯丙胺生物合成(phenylpropanoid biosynthe-

sis)途径上调基因 10 个、下调 4 个。

2.4 qRT-PCR 定量检测分析

赤霉素为葡萄果实膨大的重要作用因子。为研究赤霉素与着色香大果芽变之间的关系,对 4 个赤霉素相关基因进行 qRT-PCR 验证。结果(图 5)表明,着色香 *VvKO*、*VvGA3ox4*、*VvGA2ox4* 和 *VvGA2ox2* 基

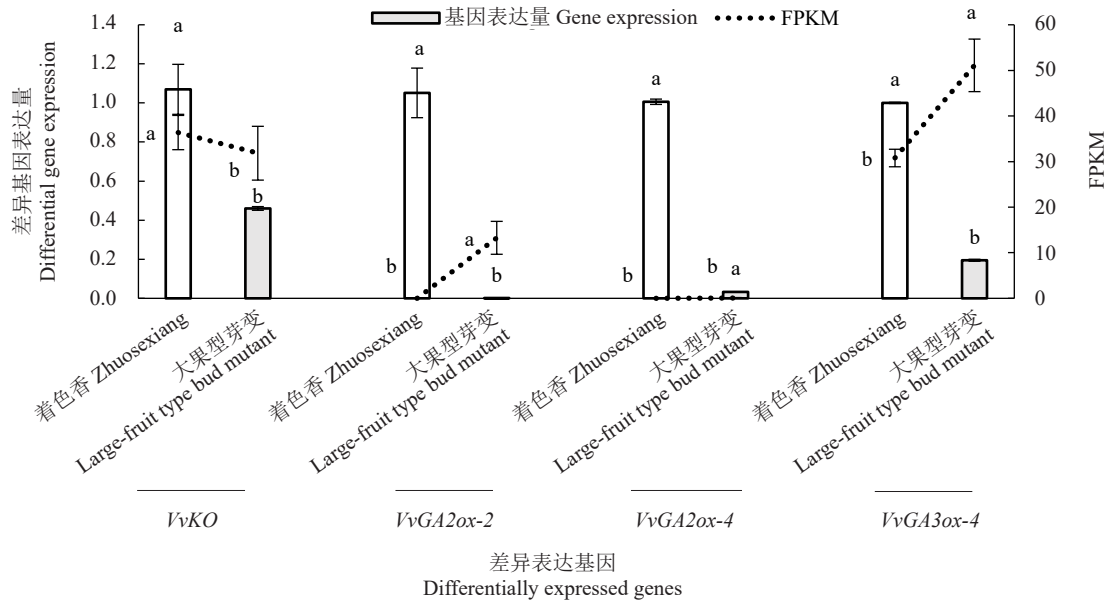


图 5 qRT-PCR 试验着色香及其大果型芽变 4 个赤霉素相关基因表达量
Fig. 5 The expression levels of four gibberellin-related genes in the Zhuosexiang grape and its large-fruit type bud mutant by qRT-PCR

因的表达量均显著大于大果型芽变($P < 0.05$),分别为大果型芽变的 2.33、5.13、30.67 和 751.00 倍。

转录组测序结果(图 6)显示,着色香及大果型芽变的 *VvKO* 基因表达量分别为 3690 和 3347, *VvGA2ox2* 基因表达量分别为 1419 和 0, *VvGA2ox4* 基因表达量分别为 9461 和 5354, *VvGA3ox4* 基因表达量分别为 11 个和 0 个,着色香 *VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 基因的表达量均显著大于大果型芽变($P < 0.05$),转录组测序的基因表达趋势与荧光定量一致,说明 *VvGA2ox* 基因可能为着色香葡萄发生大果芽变的关键基因。

2.5 GA2ox 酶活性检测

GA2ox 酶为植物体内降解赤霉素的重要酶类。为进一步明确 *GA2ox* 基因在大果芽变中的作用,对花后 15 d 幼果内的 GA2ox 酶活性进行测定。结果(图 7)表明,着色香和大果型芽变幼果内的 GA2ox 酶活性分别为 17.58 和 13.54 $U \cdot g^{-1}$,着色香果实中 GA2ox 酶活性显著高于大果型芽变($P < 0.05$)。

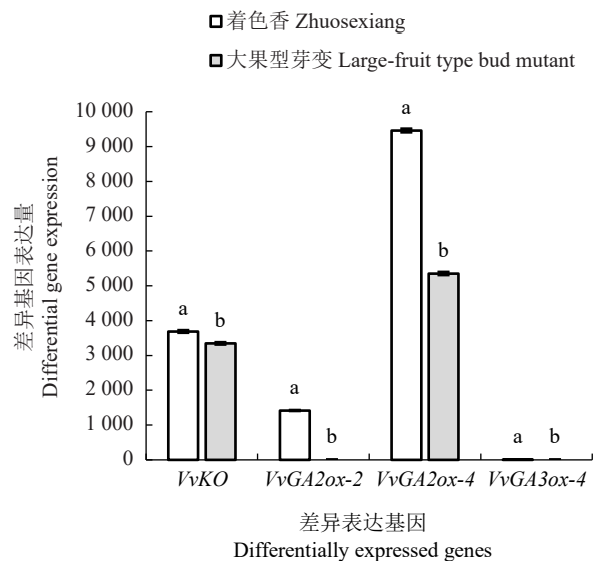


图 6 转录组测序着色香及其大果型芽变 4 个赤霉素相关基因表达量
Fig. 6 The expression levels of four gibberellin-related genes in the Zhuosexiang grape and its large-fruit type bud mutant in transcriptome sequencing

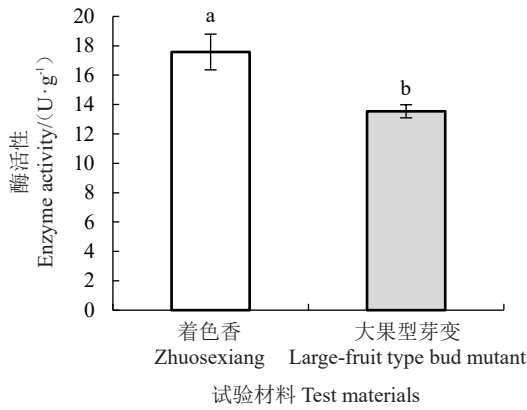


图7 着色香及其大果型芽变的GA2ox酶活性

Fig. 7 GA2ox enzyme activity of Zhuosexiang grape and its large-fruit type bud mutant

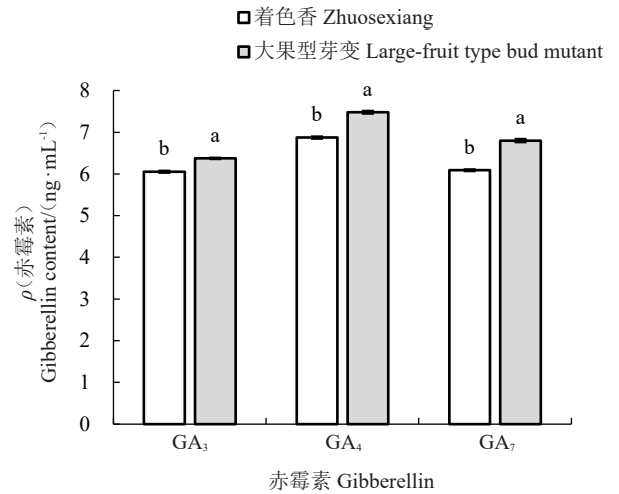


图8 着色香及其大果型芽变的常见赤霉素含量

Fig. 8 Common gibberellin content of Zhuosexiang grape and its large-fruit type bud mutant

2.6 常见赤霉素含量的测定

果实内的赤霉素含量影响果实膨大。为验证GA2ox酶在两个品种内的作用情况,对着色香葡萄及其大果型芽变花后15 d幼果内的常见赤霉素GA₃、GA₄和GA₇含量进行了测定。结果(图8)表明着色香和大果型芽变幼果内的GA₃含量(ρ,后同)分别为6.053和6.373 ng·mL⁻¹,GA₄含量分别为6.871和7.479 ng·mL⁻¹,GA₇含量分别为6.088和6.800 ng·mL⁻¹,大果型芽变幼果中常见赤霉素GA₃、GA₄和GA₇含量

均显著高于着色香(P<0.05)。

2.7 相关性分析

如表3所示,4个关键差异基因表达量、1种酶活性、花后15 d果粒纵横径、果穗长宽及3种常见赤霉素含量之间大多具有相关性。VvGA2ox-2、VvGA3ox-4表达量与GA2ox酶活性,VvGA2ox-4与VvGA3ox-4表达量,果粒纵径、果穗宽度与果穗长

表3 果粒纵横径相关性分析

Table 3 Correlation analysis of vertical and horizontal diameter of fruit grain

	VvKO	VvGA2ox-2	VvGA2ox-4	VvGA3ox-4	GA2ox酶活性 GA2ox enzyme activity	果粒纵径 Vertical diameter	果粒横径 Transverse diameter	果穗长度 Length	果穗宽度 Width	GA ₃ 含量 GA ₃ content	GA ₄ 含量 GA ₄ content	GA ₇ 含量 GA ₇ content
VvKO	1.000											
VvGA2ox-2	0.431	1.000										
VvGA2ox-4	0.782	0.879*	1.000									
VvGA3ox-4	0.800	0.883*	0.984**	1.000								
GA2ox酶活性 GA2ox enzyme activity	0.549	0.971**	0.890*	0.930**	1.000							
果粒纵径 Vertical diameter	-0.713	-0.859*	-0.883*	-0.926**	-0.924**	1.000						
果粒横径 Transverse diameter	-0.257	-0.656	-0.453	-0.558	-0.742	0.799	1.000					
果穗长度 Length	-0.741	-0.920**	-0.987**	-0.994**	-0.947**	0.922**	0.567	1.000				
果穗宽度 Width	-0.786	-0.886*	-0.981**	-0.994**	-0.927**	0.902*	0.521	0.987**	1.000			
GA ₃ 含量 GA ₃ content	-0.718	-0.269	-0.639	-0.539	-0.243	0.397	-0.155	0.531	0.509	1.000		
GA ₄ 含量 GA ₄ content	-0.794	-0.834*	-0.917*	-0.967**	-0.922**	0.963**	0.701	0.955**	0.941**	0.457	1.000	
GA ₇ 含量 GA ₇ content	-0.777	-0.898*	-0.985**	-0.998**	-0.937**	0.912*	0.541	0.995**	0.998**	0.518	0.953**	1.000

注:**. 在0.01水平(双侧)上显著相关;*. 在0.05水平(双侧)上显著相关。

Note: **. Significant correlation at the 0.01 level (bilateral); *. Significant correlation at the 0.05 level (bilateral).

度,果穗长度、果穗宽度、果粒纵径与GA₄含量,果穗长度与宽度、GA₄与GA₇含量均呈极显著正相关,VvGA3ox-4表达量、GA2ox酶活性与果粒纵径,VvGA2ox-2、VvGA2ox-4、VvGA3ox-4表达量、GA2ox酶活性与果穗长度,VvGA2ox-4、VvGA3ox-4表达量、GA2ox酶活性与果穗宽度,VvGA3ox-4表达量、GA2ox酶活性与GA₄含量,VvGA2ox-2、VvGA3ox-4表达量、GA2ox酶活性与GA₇含量呈极显著负相关;VvGA2ox-4、VvGA3ox-4与VvGA2ox-2表达量,VvGA2ox-4表达量与GA2ox酶活性,果穗宽度、GA₇含量与果粒纵径呈显著正相关;果粒纵径、果穗宽度、GA₄、GA₇含量与VvGA2ox-2表达量,果粒纵径、果穗宽度与VvGA2ox-4表达量,果粒纵径、GA₄与GA₇含量呈显著负相关。根据以上结果推测,VvGA2ox-2、VvGA2ox-4、VvGA3ox-4三种基因上调表达时GA2ox酶活性增高,降低GA₃、GA₄、GA₇含量,进而抑制果粒纵径和果穗长宽增大。

3 讨 论

果实体积大小与细胞数量和大小密切相关^[18]。蒋爽等^[4]通过比较翠冠梨和大翠冠梨果实发育期的石蜡切片,结果表明大翠冠梨果肉细胞横切面积明显大于翠冠梨。卢登洋等^[19]研究发现,果实发育中后期,库尔勒香梨大果型芽变的果肉细胞长度明显大于库尔勒香梨,在果实成熟期,大果型芽变的果肉细胞长度比库尔勒香梨增大1.03倍。许园园等^[7]对锦红冰糖橙及其大果芽变果实进行比较发现,大果芽变的汁胞细胞数量多于锦红。Harada等^[20]研究发现,苹果果实细胞的增殖能力和细胞扩张的程度可以共同影响果实最终的大小。然而,也有研究表明,果实的细胞数量与果实大小关系不大。如卢登洋等^[19]在研究库尔勒香梨芽变过程中发现,在果实成熟期库尔勒香梨果肉的细胞数量是芽变果实的1.08倍。本试验中大果型芽变在花后15 d外果皮细胞层数多于着色香,成熟期亚果皮细胞和果肉细胞体积大于着色香。

果实生长发育主要是由生长前期的细胞分裂和后期的细胞伸长引起的^[21]。植物激素是影响细胞分裂和膨大的主要因素之一^[22],在果树光合作用、碳素同化、产物的运输和分配等过程中至关重要,与果实发育关系密切^[23]。早花荔枝形成大果,与果皮中ZR含量和ZR/ABA比值较高有关^[24]。果实中ABA含量的升高,抑制了果实细胞的分裂,并最终影响果实

的大小^[22,25-26]。在梨、葡萄、苹果和柑橘等园艺作物中,已对*POSI*、*YABBY*、*SUN*、*OVATE*、*FAS*、*LC*、*WOX*、*CRC*、*WUSCHEL* (*WUS*)、*CLAVATA* (*CLV*)、*SIAS2*、*SITKN3*等基因进行了相关研究^[27-31],证实了这些基因对果实的大小和形状都有调控作用。以番茄为模式体系的研究,已经鉴定出*FAs*、*fw2.2*、*fw3.2*和*WUS*等基因,通过对细胞分裂次数和子房室数目改变等方面来调控果实的大小。卜海东^[32]以龙丰苹果及其大果变异为试材,利用农杆菌介导的遗传转化,发现生长素响应基因*MdAux/IAA2*负调控苹果果实大小。

在对果实大小和形状具有调控作用的基因中,*FAS*和*LC*为参与脂质代谢和次生代谢物生物合成的基因;*POSI*、*WUS*、*CLV*为负责植物激素信号转导的相关基因;*YABBY*、*WOX*、*CRC*、*SIAS2*、*SITKN3*、*Mdux/IAA2*为负责遗传信息处理的转录因子;*SUN*、*OVATE*为调控蛋白相关基因。本试验中,着色香葡萄及其大果型芽变花后15 d果粒的差异表达基因涉及多个膜相关基因、转录因子和酶活性基因,其中膜相关差异基因数量最多。植物激素和膜相关基因的表达具有重要的作用^[33],这与该时期细胞的旺盛分裂需求密不可分;氨基酸生物合成、苯丙胺生物合成、次级代谢产物的生物合成、卡尔文循环固碳、吞噬体和糖酵解/葡萄糖生成等几个途径差异基因富集较多,其中苯丙胺生物合成通路参与信号转导过程,其他代谢通路参与细胞分裂过程。在细胞组成类注释中,主要涉及细胞部分和膜结合细胞器两方面。张树军^[34]以南果梨及其大果型芽变为材料进行转录组分析,表明生物学过程中的代谢过程占55% (主要包括大分子代谢过程、初级代谢过程、细胞代谢过程和氮化合物的代谢过程)、生物合成过程占11.9%、信号转导占3.57%;Huang等^[35]以希姆劳德葡萄及其大果芽变为材料进行转录组分析,表明主要差异基因表达产物包括生长素反应因子(*ARF*)、*NAC*转录因子(*TF*)和蛋白激酶等。与上述研究结果相类似,本研究中代谢过程占36.07%,合成过程占33.79%,主要包括氨基酸生物合成、苯丙胺生物合成、次级代谢产物的生物合成和糖酵解/葡萄糖生成等;主要差异表达基因包括多个膜相关基因、转录因子以及相关酶活性基因等。

赤霉素能够控制细胞伸长^[36],内源GA含量与成熟期果实的大小、果皮细胞数量呈正相关^[37]。赤霉素各相关基因表达具有组织特异性。赤霉素早期合

成步骤(萜烯合成途径): CPS(ent-copalyl diphosphate synthase); 中期合成步骤(内根-贝壳杉烯 → GA12): KO(ent-kaurene oxidase); 后期合成步骤(GA12 → 活性GA4/GA1)。赤霉素代谢通路的核心是活性GA的水平,它由三类关键酶(GA2ox酶、GA3ox酶、GA20ox酶)动态调控,其中GA3ox酶、GA20ox酶分别通过产生最终有活性的GA、催化合成GA前体提高活性GA的水平,GA2ox酶通过使活性GA或前体失活降低活性GA的水平^[38]。王西成等^[39]研究表明,葡萄 *Vv GA2ox2* 主要在果实中表达, *Vv GA2ox4* 主要在果实和叶片中表达, *Vv GA3ox4* 主要在花、幼叶和幼果中表达; *VvKO* 在各个组织中均有表达。翠冠梨 *GA2ox1* 和 *GA3ox1* 表达量下降而果实增大^[4], 无核白葡萄败育初期 *VvGA2ox2* 表达上调抑制胚珠发育^[40], 番茄 *GA2ox1* 过表达果皮细胞数量减少、果实变小^[41]。植物体内赤霉素作用的发挥受 *GA2ox1*、*VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 等的多重调控。本试验中,着色香 *VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 的表达量显著高于大果型芽变, *VvGA2ox2* 和 *VvGA2ox4* 的表达量分别为大果型芽变的751.00倍和30.67倍,所对应的GA2ox氧化酶活性也显著高于大果型芽变,酶活结果与基因表达结果相对应。

赤霉素2-氧化酶(GA2oxs)是一种2-氧代戊二酸依赖性双加氧酶,可通过2 β -羟基化反应促使具有活性的赤霉素或其前体失活, *VvGA2ox* 家族基因在调控植物体内活性赤霉素含量方面发挥着重要作用^[42]。着色香及其大果型芽变各数据的相关性分析也表现出 *VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 表达量与GA2ox氧化酶活性呈显著正相关,3个基因表达量、酶活性又与果粒纵横径呈极显著负相关。大果型芽变幼果中常见赤霉素GA₃、GA₄和GA₇含量均显著大于着色香。相较于大果型芽变,着色香 *VvGA2ox2* 和 *VvGA2ox4* 的高表达增强了GA2ox氧化酶活性,降低了赤霉素含量,使果实相较于大果型芽变更小,这与草原早熟禾 *PpGA2oxs* 过表达^[43]、中矮1号^[16]和杧果^[44] *GA2ox2* 增量表达降低GA含量导致矮生的研究结果相似。也有研究表明,过表达 *GA2ox2* 可促进植株生长或果实发育。Jia等^[45]研究表明,过表达 *DcGA2ox2* 显著促进了Kurodagosun、本红金石和七头黄胡萝卜中活性GAs的积累,促进植株生长。何红红^[46]在黑比诺葡萄上的研究表明,

VvGA2ox-2 在整个果实发育时期表达量均较高。上述研究表明, *GA2ox2* 基因功能对赤霉素的活性调控具有多重功能,其具体作用可能与物种以及环境调控等因素有关。

4 结 论

赤霉素通过影响次级代谢产物、氨基酸生物合成及卡尔文循环等途径,调控膜相关等基因表达,促使着色香及大果型芽变的果实大小及细胞形态产生差异。赤霉素相关基因 *VvKO*、*VvGA2ox2*、*VvGA2ox4* 和 *VvGA3ox4* 为影响着色香葡萄果实发育的重要因子。

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