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# *PDC*和*ADH*基因家族成员在杨梅果实成熟和包装处理期间的表达及其与乙醛和乙醇积累的关系

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**摘 要:【目的】**探究*PDC*和*ADH*基因家族成员在杨梅果实成熟和包装处理期间的表达模式,分析其与乙醛和乙醇积累的关系。**【方法】**对杨梅*PDC*和*ADH*基因家族进行生物信息学分析;利用RT-qPCR探究*MrPDCs*和*MrADHs*在12个杨梅品种果实成熟期间及主栽品种荸荠和东魁成熟果实包装处理期间的表达情况;应用气相色谱法测定乙醛和乙醇含量;分析*MrPDCs*和*MrADHs*基因表达与乙醛和乙醇积累的关系。**【结果】**从杨梅基因组共鉴定出8个*MrPDC*和22个*MrADH*基因家族成员,其中*MrPDC1*、*MrPDC2*、*MrADH1*、*MrADH2*和*MrADH3*在转录组中的表达量较高。果实成熟期间*MrPDCs*和*MrADHs*的表达模式在品种间差异较大,总体而言,*MrPDC1*、*MrADH1*和*MrADH3*的表达量随果实成熟不断上升,*MrPDC2*和*MrADH2*的表达量在绿果期最高。乙醛含量在果实成熟期间变化幅度以及品种间差异较小;在多数品种上,乙醇在果实成熟期加快积累,其中特早梅成熟果实中乙醇含量比转色期高12.37倍;品种间乙醇含量差异也在成熟期加大,最大差异达15.19倍;乙醛和乙醇含量与*MrPDCs*表达量的相关性不显著,而与*MrADH1*和*MrADH3*表达量呈极显著正相关。就不同包装对果实乙醛和乙醇的积累开展了研究,发现与普通包装和单果包装相比,减压包装导致果实贮运期间异味加重、乙醛和乙醇大量积累,其中荸荠杨梅乙醛含量在10 d内增加3.73倍,乙醇含量在6 d内增加1.86倍,东魁杨梅的乙醛和乙醇含量均在4 d内分别增加2.29倍和1.89倍;与此同时,*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*表达量显著升高,与乙醛和乙醇含量上升呈现显著相关性。**【结论】**杨梅果实成熟期间*MrADH1*和*MrADH3*表达增强,乙醛和乙醇积累,减压包装处理诱导了*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*表达,导致乙醛和乙醇过度积累以及果实异味产生。

**关键词:**杨梅;果实成熟;减压包装;乙醛;乙醇;*PDC*;*ADH*

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# Expression analysis of *PDC* and *ADH* gene family members and their relationship with the accumulation of acetaldehyde and ethanol during fruit ripening and packaging treatments of Chinese bayberry

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**Abstract:**【Objective】Chinese bayberry (*Morella rubra* Sieb. et Zucc.) is a characteristic fruit crop with important medicinal and economic value in China. The fruits develop obvious wine smell during storage and even at harvest. The wine smell is mainly derived from accumulation of acetaldehyde and ethanol. Pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) are the key enzymes in the ethanolic fermentation pathway, where pyruvate is decarboxylated to acetaldehyde through the action of PDC, and thereafter, acetaldehyde is converted to ethanol by ADH. It was shown in other fruits that PDC and ADH played important roles in the formation of acetaldehyde and ethanol during fruit ripen-

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ing and storage. However, identification and expression profiling of the *PDC* and *ADH* gene family members, as well as the correlation analysis between the gene expression and the accumulation of acetaldehyde and ethanol have not been studied in Chinese bayberry.【Methods】Based on the genome database of Chinese bayberry, the *PDC* and *ADH* genes were identified by Hidden Markov Model (HMM) searches using the HMM profiles of PDC and ADH domain (PDC: PF00205, ADH: PF08240) downloaded from Pfam database (http://pfam.xfam.org/). The expression data, by Fragments per Kilobase of exon model per Million mapped fragments (FPKM), were analyzed to identify highly expressed members of the *PDC* and *ADH* based on previously available transcriptome data. In addition, the expression of the *MrPDC1*, *MrPDC2* and *MrADH1*, *MrADH2*, *MrADH3* was determined by RT-qPCR technology. The acetaldehyde and ethanol content were determined by gas chromatography (GC).【Results】In this study, a total of 8 *MrPDCs* and 22 *MrADHs* were identified from genome database of Chinese bayberry. The *MrPDC1* and *MrPDC2*, as well as the *MrADH1*, *MrADH2* and *MrADH3* were identified as highly expressed members and hence used for further analysis. The expression patterns of the *MrPDCs* and *MrADHs* during fruit ripening were differential among 12 cultivars. The expression of the *MrPDC1*, *MrADH1* and *MrADH3* in most cultivars increased as fruit ripened, while the *MrPDC2* and *MrADH2* had higher expression levels at mature green stage (S1). For example, the expression of the *MrPDC1* in many cultivars was the highest at ripe stage (S3), which was 11.30 and 4.70 times higher than those of S1 and breaker stage (S2), respectively, in Longhaishuijing. The *MrPDC2* expression was highest in most cultivars at S1. There were also differences in the expression patterns of the three *MrADHs* during fruit ripening in different cultivars; the expression level of the *MrADH1* in Tezaomei was highest at S3, which was 43.77 and 4.12 times higher than those at S1 and S2. The expression level of the *MrADH2* at S1 of Wumei was 2.59 and 6.30 times higher than those at S2 and S3, respectively. The expression level of the *MrADH3* at S3 of Tezaomei was 9.87 and 50.64 times higher than those at S1 and S2, respectively. The content of acetaldehyde did not vary much throughout fruit ripening and the variation across cultivars was minimal as well. Ethanol significantly accumulated at S3 in most cultivars, the content of ethanol at S3 of Tezaomei was 12.37 times higher than that at S2. The difference of the ethanol content across cultivars was also mainly reflected at S3, with the largest variation reaching 15.19 times. Overall, the acetaldehyde and ethanol contents had no significant correlation with the expression levels of the *MrPDCs*, but had significant and positive correlation with the expression levels of the *MrADH1* and *MrADH3*. In addition, the result of packaging storage experiments showed that compared with ordinary packaging and single fruit packaging, hypobaric packaging resulted in obvious off-flavor and a tremendous accumulation of acetaldehyde and ethanol during storage, among which the acetaldehyde content of Biqi increased by 3.73 times in 10 days and the ethanol content increased by 1.86 times in 6 days. Both the acetaldehyde and ethanol contents of Dongkui increased, by 2.29 and 1.89 times, respectively, in 4 days. RT-qPCR results showed that the expression of the *MrPDC1*, *MrPDC2*, *MrADH1* and *MrADH3* in the fruits of hypobaric packaging were significantly higher than those of ordinary packaging and single fruit packaging in both Biqi and Dongkui. The expression level of the *MrADH3* in Biqi was highest on 2nd day in hypobaric packaging, while there was little difference in the expression levels of each gene between the fruit of ordinary packaging and the single fruit packaging. Meanwhile, the expression levels of the *MrPDC1* and *MrPDC2* as well as *MrADH1* and *MrADH3* were significantly enhanced as storage time prolonged, and being positively correlated with the acetaldehyde and ethanol accumulation.【Conclusion】Among the 8 *MrPDCs* and 22 *MrADHs*, the *MrADH1* and *MrADH3* play an important role in the moderate accumulation of acetaldehyde and ethanol during fruit

ripening in Chinese bayberry. The hypobaric packaging induced the expression of the *MrPDC1, MrPDC2, MrADH1*, *MrADH2* and *MrADH3,* resulting in excessive accumulation of acetaldehyde and ethanol and the production of fruit off-flavor or wine smell.

**Key words:** Chinese bayberry; Fruit ripening; Hypobaric packaging; Acetaldehyde; Ethanol; *PDC*; *ADH*

杨梅(*Morella rubra* Sieb. et Zucc.)是杨梅科杨梅属常绿乔木,是我国特产水果之一,栽培历史悠久,广泛分布于长江以南地区,被吴耕民先生赞为"中国特产的初夏江南珍果"[1]。新鲜的杨梅果实香气宜人,风味浓郁,酸甜多汁,富含多种维生素和有机酸,深受广大消费者青睐。但杨梅成熟与采后贮运期间呼吸剧烈[2],常因"酒味"重而影响消费者品鉴。

"酒味"主要来源于乙醇发酵途径,丙酮酸脱羧酶(pyruvate decarboxylase,PDC;EC 4.1.1.1)和乙醇脱氢酶(alcohol dehydrogenase,ADH;EC 1.1.1.1)是该途径中的两个关键酶,前者催化丙酮酸生成乙醛和$CO_2$,后者则催化乙醛生成乙醇[3]。前人对PDC在酵母和细菌乙醇发酵中的功能研究较为广泛,而在植物中研究较少。PDC通常在低氧或缺氧条件下通过发酵代谢为植物提供能量[4],但涉及PDC参与果实香气物质形成的研究鲜有报道[5]。与PDC相比,前人对植物ADH的研究较为广泛而深入。大量研究表明,ADH参与植物低氧胁迫反应,且在调控果实生长发育和成熟衰老过程中发挥了重要作用。在番茄、苹果、甜瓜、葡萄、杧果、桃、杏等的果实研究中发现,乙醇含量在果实成熟期间不断积累,*ADH*基因的表达量逐渐升高[6-12]。

乙醛和乙醇等风味物质在果实成熟期间和采后贮运过程中的含量和种类发生动态变化,这通常是种类品种(遗传因素)、成熟度与采后贮藏条件等多因素综合作用的结果[13]。随种类品种不同,果实风味物质种类与含量也各不相同;果实风味物质组分及含量在品种间也存在差异,如Wang等[14]研究发现,国内外50个桃品种果实的乙醛、乙醇等挥发性物质组分和含量主要取决于遗传背景。果实发育和成熟阶段对乙醛和乙醇等芳香物质的合成也有影响,如在番茄、草莓等果实上,乙醛和乙醇随着果实成熟而不断积累[7, 15-17]。在采后贮藏中,多数呼吸跃变型和部分非呼吸跃变型果实在不适宜的贮藏环境下积累较大量的乙醛和乙醇,从而造成异味,异味轻重程度受贮藏温度、湿度、气体条件等多因素影响;研究发现,低温贮藏和适宜的透气条件可以显著延缓桃、猕猴桃、柑橘、梨、甜瓜、葡萄等果实乙醛和乙醇积累,防止果实产生"酒味"而影响品鉴[18-25]。

在许多大宗水果中已发现*PDC*和*ADH*基因参与了果实成熟期间香气物质合成和采后贮藏过程异味物质产生,而在杨梅这一特色小众水果上仍缺乏深入研究。Zhu等[26]发现随着杨梅果实成熟,乙醛和乙醇逐渐积累,Chen等[27]发现杨梅PDC和ADH蛋白丰度随着果实成熟而增加,但这些研究均未进一步分析基因表达与乙醛和乙醇含量间的相关性。同时,对于贮运期间杨梅果实乙醇和乙醛积累以及*PDC*和*ADH*基因表达的模式和关系也未见报道。本研究旨在鉴定在杨梅中高表达的*PDC*和*ADH*基因家族成员,探究其在不同杨梅品种果实成熟期间和贮运过程中的表达模式及其与乙醛和乙醇积累的关系,以期为杨梅果实风味形成机制以及果实异味减轻措施研发等相关研究提供参考。

## 1 材料和方法

### 1.1 试验材料与处理

用于果实发育与成熟阶段分析的12个杨梅品种为荸荠、东魁、水晶、粉红、特早梅、浮宫1号、黑晶、落子、八贤道、软丝安海变、乌梅和龙海水晶,其中荸荠和东魁采摘于浙江省金华市兰溪市,水晶采摘于浙江省宁波市余姚市,其余品种采摘于福建省福州市福建省农业科学院。每个品种在绿果期(S1)、转色期(S2)和成熟期(S3)分别采集。采后不同包装处理的研究试材为荸荠和东魁成熟果实,采摘于浙江省台州市仙居县,挑选大小均一、成熟度(果实色泽)一致、无明显外伤和病虫害的果实用于试验。包装处理分为3种:减压包装、普通包装和单果包装。其中减压包装用厚为0.2 mm的聚乙烯(PE)包装袋对装有果实的篮筐封口后进行抽气至真空度为0.07 MPa;在普通包装中,装有果实的篮筐套上包装袋但不封口;在单果包装中,在透气性良好

的颗粒包装盒中放入果实。果实经不同包装后放冷库预冷至10 ℃，然后放入泡沫箱中，在泡沫箱中两个篮筐之间放入经−18 ℃预先冰冻的蓄冷冰袋，封箱，于6 h内运达实验室。抵达实验室后拆开泡沫箱，果实随包装置于冷库贮藏（温度0 ℃，湿度90%），分别于0、2、4、6、8、10 d取样。试验设置3个生物学重复，每个生物学重复包含10个杨梅果实。杨梅果实果肉切碎后用液氮冷冻，存于−80 ℃超低温冰箱中备用。

### 1.2　杨梅*PDC*和*ADH*基因家族成员鉴别

从NCBI数据库（https://www.ncbi.nlm.nih.gov/）下载杨梅基因组注释文件和基因组序列拼接文件。从NCBI数据库查找并获得拟南芥、烟草、番茄等其他植物PDC、ADH蛋白序列，通过BLASTP（*E*-value＜1E-20）在杨梅基因组中搜索同源基因，鉴定同源性。进一步从Pfam数据库（http://pfam.xfam.org/）下载PDC和ADH蛋白保守结构域的隐马尔可夫模型（HMM model）文件（PDC: PF00205，ADH: PF08240），在杨梅基因组中检索杨梅*PDC*和*ADH*基因。将2次鉴定结果并集后，使用NCBI保守结构域数据库（https://www.ncbi.nlm.nih.gov/cdd/）确认所有候选PDC和ADH蛋白的结构域同源性，剔除没有相应PDC和ADH保守结构域的蛋白，仅保留与其他物种中具有相同保守域序列的PDC和ADH蛋白；通过ExPASy在线网站（https://web.expasy.org/compute_pi/）获得杨梅PDC、ADH蛋白分子质量并预测蛋白等电点。

### 1.3　RNA提取与cDNA合成

杨梅果肉总RNA提取采用Shan等[28]描述的十六烷基三甲基溴化铵（CTAB）法。测定总RNA浓度后，参照HiScript® Ⅱ Q RT SuperMix for qPCR（+gDNA wiper）说明书（Vazyme），吸取1 μg总RNA，去除基因组DNA后进行逆转录反应合成cDNA。

### 1.4　实时荧光定量PCR（RT-qPCR）

实时荧光定量PCR（real-time quantitative PCR，RT-qPCR）用于测定*MrPDC1*、*MrPDC2*、*MrADH1*、*MrADH2*和*MrADH3*的表达量。5个基因的引物均由DNAMAN设计（表1），并通过熔解曲线和PCR产物测序对引物的特异性进行验证。以杨梅*MrActin*为内参基因（表1，GenBank GQ340770[29]）；qPCR体系与程序参照ChamQ Universal SYBR® qPCR Master Mix说明书（Vazyme）。每个样品设置2次技术重复。利用$2^{-\Delta CT}$法计算*MrPDCs*和*MrADHs*基因的相对表达量。

**表1　杨梅*PDC*和*ADH*基因RT-qPCR引物**

**Table 1　RT-qPCR primers of *PDC* and *ADH* genes in Chinese bayberry**

| 基因名称 Gene name | 上游引物序列（5’→3’） Forward primer sequence（5’→3’） | 下游引物序列（5’→3’） Reverse primer sequence（5’→3’） |
|---|---|---|
| *MrPDC1* | TACACAATGGGGAGGGAAAG | AGTCTACTGGGGGTTTGGTG |
| *MrPDC2* | TGCTACTCTCGGATATGCTC | CCCAGTTCTTGATGACGTTG |
| *MrADH1* | GGTACCTTCTTTGGCAACTACA | TTCATTCATGCAGCCGGATA |
| *MrADH2* | CAGGAGATATGCACACGG | ACGCACCGGAGACAAGTC |
| *MrADH3* | GTTGGGGTGTTGCAGTGCTT | GAAAGGGACAGAGTGAGTGATG |
| *MrActin* | TGGATTTGCTGGAGACGAT | CTTTCTGTCCCATGCCTACC |

### 1.5　乙醛和乙醇含量测定

乙醛和乙醇含量测定参照Min等[30]的方法。称取3 g经液氮充分研磨的杨梅果肉粉末于10 mL离心管，加入4 mL饱和NaCl溶液，涡旋混匀；从中吸取3 mL匀浆至顶空萃取瓶，加入10 μL 1%（$\varphi$）仲丁醇，混匀。60 ℃水浴加热1 h后在气相色谱仪（Agilent 7890A）上进行静态顶空气相色谱（GC）检测，每个样品进行3次技术重复。配制1%乙醛、乙醇和仲丁醇（内标）溶液制作标准曲线，标准曲线制作以乙醛（或乙醇）浓度为横坐标，乙醛（或乙醇）与仲丁醇的峰面积之比为纵坐标。依据标准曲线计算萃取瓶中的乙醛（或乙醇）质量（μg），样品中的乙醛（或乙醇）含量计算如下：

$$\text{乙醛（或乙醇）含量}(\mu g\cdot g^{-1})=\frac{B\times V_0}{m\times V_1}$$

其中，$B$为萃取瓶中的乙醛（或乙醇）质量（μg），$V_0$为提取液体积（7 mL），$V_1$为萃取瓶中提取液体积（3 mL），$m$为样品质量（3 g）。

### 1.6　果实异味评价

分别在包装处理4 d和8 d时对杨梅异味程度（1无、2轻、3中、4重、5非常重）进行赋分评价，参评人员为10人。

### 1.7 数据分析

试验数据使用Excel 2019进行统计、制图，应用SPSS 23软件进行差异显著性检验（$p<0.05$）和Pearson相关性分析。

## 2 结果与分析

### 2.1 杨梅高表达*PDC*和*ADH*基因家族成员鉴别

通过HMM和BLASTP检索并剔除相似度过高序列，在杨梅基因组中共鉴定出8个*PDC*和22个*ADH*基因。在项目组先前已有的荸荠和东魁杨梅转录组中分析这些基因的表达丰度，发现*MrPDC1*和*MrPDC2*表达量之和占*MrPDCs*的90%以上，*MrADH1*、*MrADH2*和*MrADH3*的表达量之和占*MrADHs*的80%以上。这些基因在基因组中的编号和染色体定位、开放阅读框（open reading frame，ORF）长度、编码蛋白的氨基酸残基数、分子质量以及等电点等信息如表2所示。经过与其他植物*PDC*和*ADH*基因进行比对，发现这5个基因编码完整的蛋白。

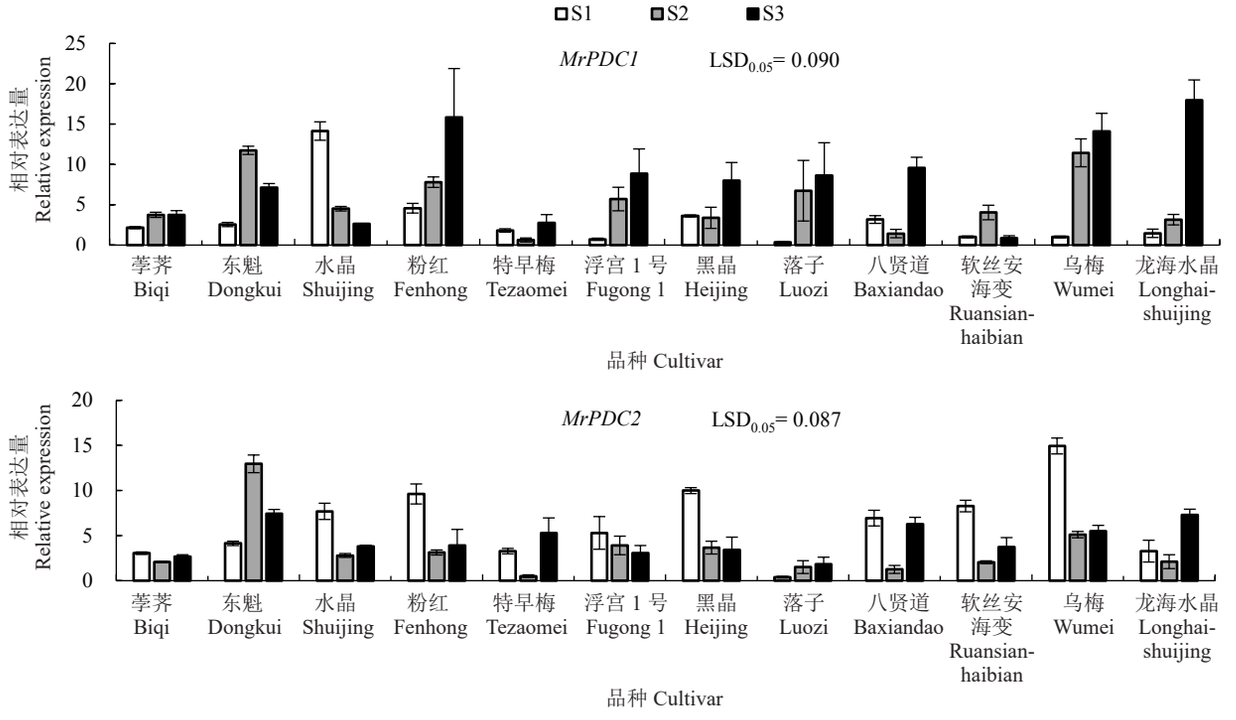
**表2 杨梅2个*PDC*和3个*ADH*基因家族成员信息**

**Table 2 The information of two *MrPDCs* and three *MrADHs* in Chinese bayberry**

| 基因名称 Gene name | 基因ID Gene ID | 染色体 Chromosome | 开放阅读框长度 ORF length/bp | 氨基酸残基数 Amino acid residue number/aa | 分子质量 Molecular weight/ku | 等电点 Isoelectric point |
|---|---|---|---|---|---|---|
| *MrPDC1* | KAB1224381.1 | 2 | 1935 | 644 | 69.70 | 6.19 |
| *MrPDC2* | KAB1223537.1 | 2 | 1713 | 570 | 61.92 | 5.64 |
| *MrADH1* | KAB1220907.1 | 3 | 1143 | 380 | 41.30 | 5.83 |
| *MrADH2* | KAB1208651.1 | 6 | 1140 | 379 | 40.64 | 6.75 |
| *MrADH3* | KAB1220913.1 | 3 | 1383 | 460 | 50.09 | 5.79 |

### 2.2 杨梅果实成熟期间*PDC*和*ADH*基因表达分析

RT-qPCR定量分析结果显示，*MrPDC1*和*MrPDC2*在12个杨梅品种3个果实发育阶段的表达模式存在差异。在9个品种中，*MrPDC1*的表达量在S3最高，其中*MrPDC1*在龙海水晶S3的表达量分别是S1和S2的12.30和5.70倍。而*MrPDC2*在8个品种中在S1表达量最高，其中*MrPDC2*在乌梅S1的表达量分别是S2和S3的2.92和2.73倍（图1）。




误差线代表3个生物学重复的SE值，LSD值代表不同处理间在$p<0.05$水平的显著差异。下同。

Error bars indicate SE from three biological replicates. LSD indicates least-significant difference at $p<0.05$. The same below.

**图1 12个杨梅品种果实成熟期间*MrPDC1*和*MrPDC2*的表达分析**

**Fig. 1 Expression of *MrPDC1* and *MrPDC2* in 12 Chinese bayberry cultivars during fruit ripening**

*MrADHs*的表达量在不同杨梅品种果实成熟过程中差异较大，*MrADH3*的表达量普遍高于*MrADH1*和*MrADH2*。除东魁、落子与水晶S1外，*MrADH1*在其余9个品种上在S3表达量最高，其中在特早梅S3的表达量分别是S1和S2的44.77倍和5.12倍。除落子外，*MrADH2*在其余11个品种上在S1表达量最高，其中在乌梅S1的表达量分别是S2和S3的3.59倍和7.30倍。除水晶和浮宫1号外，*MrADH3*在其余10个品种上在S3表达量最高，*MrADH3*在特早梅S3的表达量分别是S1和S2的10.87倍和51.64倍（图2）。

### 2.3　杨梅果实成熟期间乙醛、乙醇含量与醇醛比值的变化

12个杨梅品种果实在3个发育阶段的乙醛含量（*w*，含量）在10.14~21.76 μg·g$^{-1}$之间，其中以东魁S3果实中的乙醛含量最高。在10个品种中，果实乙醛含量随成熟而不断增加，但粉红果实中乙醛含量在S1最高（19.22 μg·g$^{-1}$），随果实成熟而不断下降；龙海水晶的乙醛含量在S2最高。杨梅果实中的乙醇含量在12.85~307.91 μg·g$^{-1}$之间，其中以特早梅S3

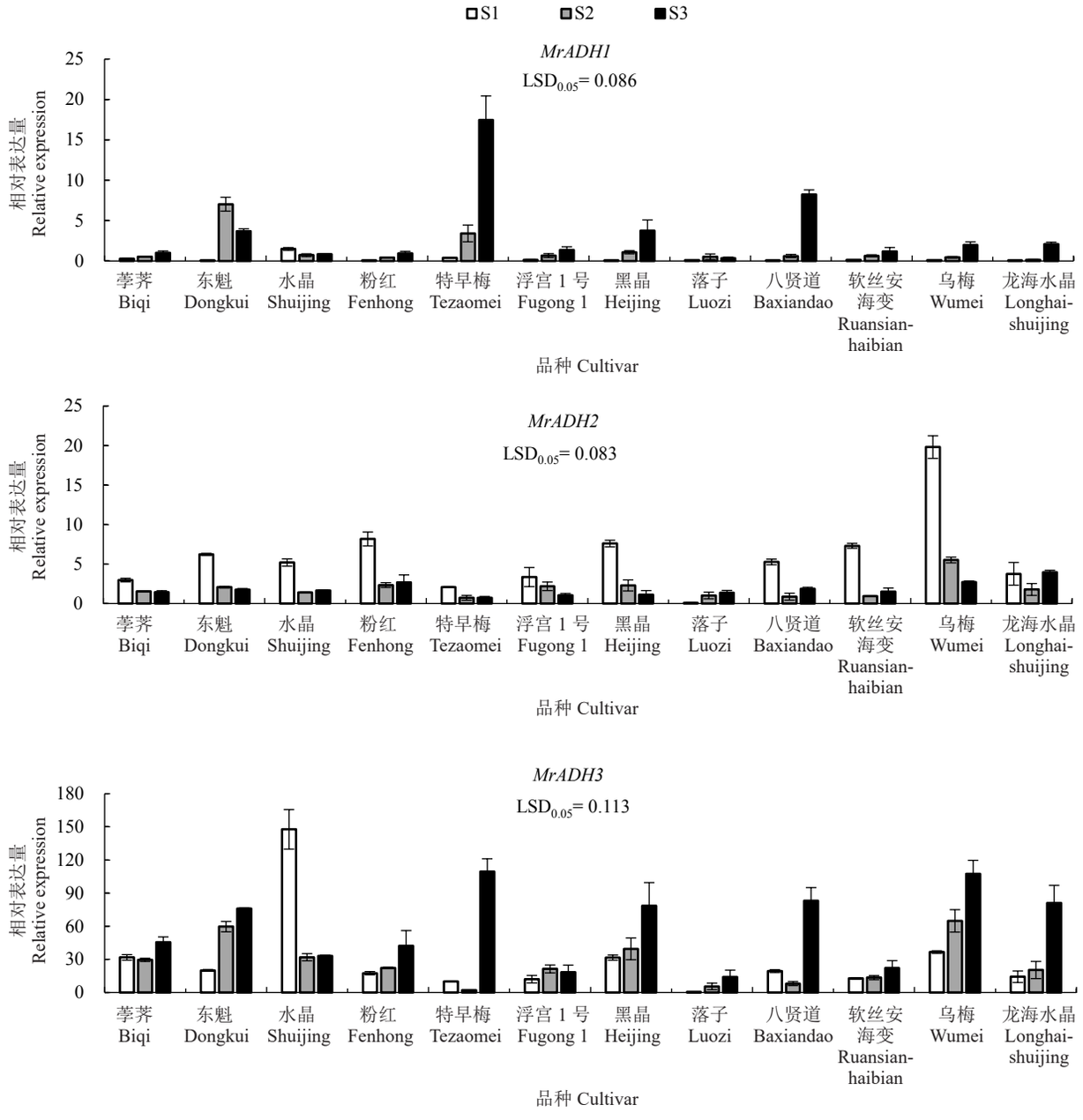



**图2　12个杨梅品种果实成熟期间*MrADH1*、*MrADH2*和*MrADH3*的表达分析**

**Fig. 2　Expression of *MrADH1*, *MrADH2* and *MrADH3* in 12 Chinese bayberry cultivars during fruit ripening**

果实中的乙醇含量最高；除落子外，其余品种的乙醇含量在果实成熟期显著升高。果实醇醛比值变化趋势与乙醇含量变化基本一致，除落子外的其余品种果实醇醛比值在S3明显升高（图3）。

Pearson相关性分析结果表明，乙醛、乙醇含量和醇醛比值均与*MrADH1*和*MrADH3*的表达量呈极显著正相关，且*MrPDC2*与*MrADH2*、*MrADH1*与*MrADH3*的表达量也呈极显著正相关（表3）。此结果与RT-qPCR定量分析中多数品种*MrADH1*和*MrADH3*在果实成熟期表达量最高、*MrPDC2*和*MrADH2*在幼果期表达量最高一致；此外，*MrADH2*的表达量与乙醛、乙醇含量无显著相关性。

### 2.4 杨梅不同包装处理期间果实异味、乙醛含量、乙醇含量和醇醛比值的变化

为防止果实运输期间振动，生产上常采用减压包装处理。对减压包装内气体成分进行了分析，发现在0 d（减压包装后6 h）时荸荠（图4-A）和东魁（图4-B）杨梅减压包装内$O_2$含量（$\varphi$，后同）分别为1.83%和3.20%，在0 ℃贮藏期间$O_2$含量不断下降，到贮藏期结束时包装内$O_2$含量几乎为0。荸荠和东魁在0 d时包装内$CO_2$含量分别为18.07%和24.00%，而后随着贮藏期延长$CO_2$含量不断上升，10 d时分别为

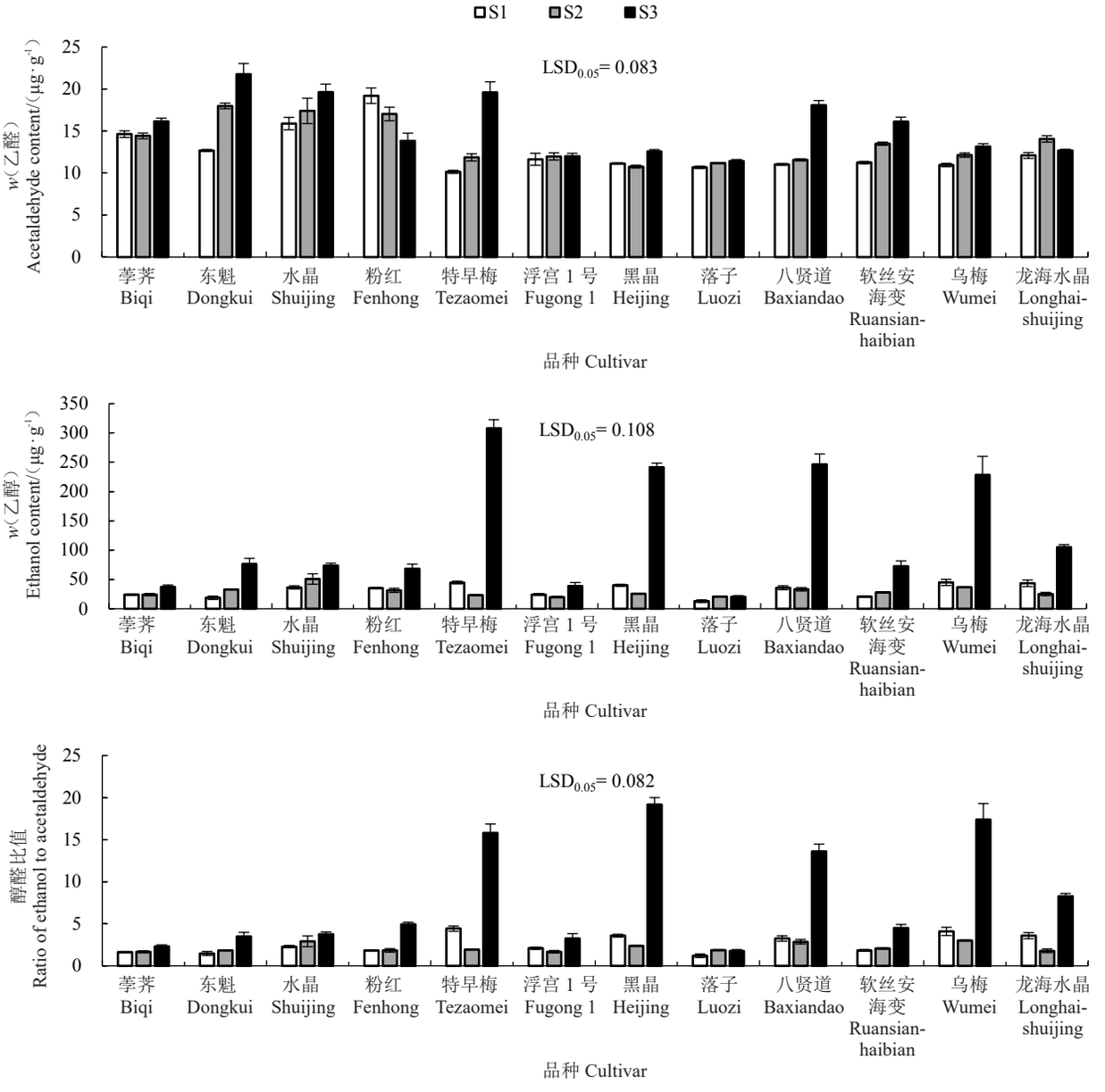



**图3 12个杨梅品种果实成熟期间乙醛、乙醇含量和醇醛比值**

**Fig. 3 Contents of acetaldehyde and ethanol and the content ratio of ethanol to acetaldehyde in 12 Chinese bayberry cultivars during fruit ripening**

**表3　12个品种3个发育阶段杨梅果实乙醛、乙醇含量和醇醛比值与*MrPDCs*和*MrADHs*表达量的相关性**

**Table 3　Correlation between acetaldehyde, ethanol contents as well as the ratio of ethanol to acetaldehyde and the expression of *MrPDCs* and *MrADHs* in Chinese bayberry fruit of 12 cultivars and 3 developmental stages**

| 指标 Index | 乙醛含量 Acetaldehyde content | 乙醇含量 Ethanol content | 醇醛比值 Ratio of ethanol to acetaldehyde | *MrPDC1*表达量 Expression of *MrPDC1* | *MrPDC2*表达量 Expression of *MrPDC2* | *MrPDCs*表达总量 Total expression of *MrPDCs* | *MrADH1*表达量 Expression of *MrADH1* | *MrADH2*表达量 Expression of MrADH2 | *MrADH3*表达量 Expression of *MrADH3* | *MrADHs*表达总量 Total expression of *MrADHs* |
|---|---|---|---|---|---|---|---|---|---|---|
| 乙醛含量 Acetaldehyde content | 1 | | | | | | | | | |
| 乙醇含量 Ethanol content | 0.347* | 1 | | | | | | | | |
| 醇醛比值 Ratio of ethanol to acetaldehyde | 0.162 | 0.964** | 1 | | | | | | | |
| *MrPDC1*表达量 Expression of *MrPDC1* | 0.161 | 0.287 | 0.334* | 1 | | | | | | |
| *MrPDC2*表达量 Expression of *MrPDC2* | 0.193 | 0.102 | 0.092 | 0.208 | 1 | | | | | |
| *MrPDCs*表达总量 Total expression of *MrPDCs* | 0.222 | 0.269 | 0.299 | 0.859** | 0.680** | 1 | | | | |
| *MrADH1*表达量 Expression of *MrADH1* | 0.490** | 0.754** | 0.599** | 0.141 | 0.161 | 0.190 | 1 | | | |
| *MrADH2*表达量 Expression of *MrADH2* | −0.187 | −0.153 | −0.107 | −0.090 | 0.749** | 0.325 | −0.237 | 1 | | |
| *MrADH3*表达量 Expression of *MrADH3* | 0.430** | 0.658** | 0.623** | 0.631** | 0.363* | 0.663** | 0.549** | 0.030 | 1 | |
| *MrADHs*表达总量 Total expression of *MrADHs* | 0.431** | 0.673** | 0.630** | 0.599** | 0.429** | 0. 674** | 0.584** | 0.104 | 0.995** | 1 |

注：**表示在$p<0.01$水平极显著相关，*表示在$p<0.05$水平显著相关。$n$=10。下同。

Note：** Significant difference at $p<0.01$ level, * Significant difference at $p<0.05$ level. $n$=10. The same below.

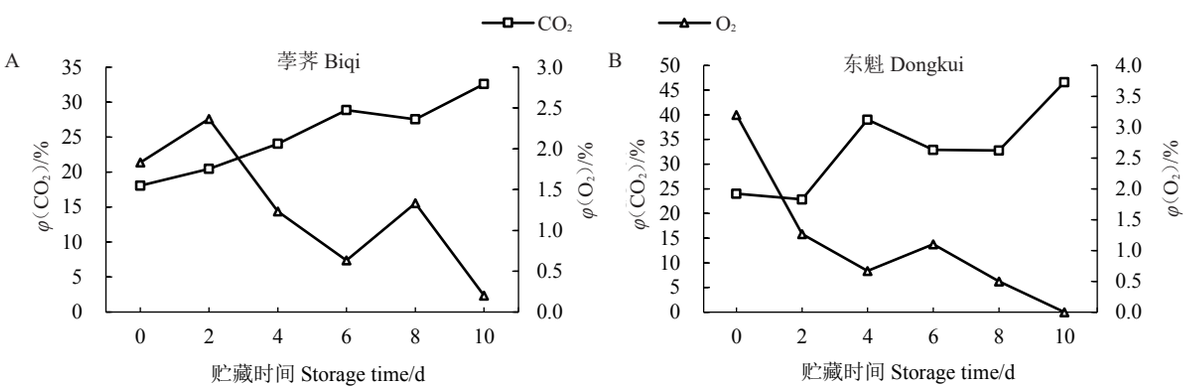



**图4　荸荠和东魁杨梅减压包装处理期间$CO_2$和$O_2$含量**

**Fig. 4　Contents of $CO_2$ and $O_2$ in Biqi and Dongkui fruit during storage following hypobaric packaging**

32.60%和46.63%。

经过果实异味评价，发现荸荠和东魁杨梅在处理4 d和8 d时均表现为经减压包装的果实异味最重，其次是普通包装，单果包装的果实异味最轻。就相同包装和相同贮藏时间进行对比，总体而言东魁比荸荠果实异味重（表4）。

**表4 荸荠和东魁杨梅不同包装处理4 d和8 d的果实异味评价**

**Table 4 Evaluation of off-flavor in Biqi and Dongkui fruits at 4 days and 8 days from different packaging treatments**

| 品种 Cultivar | 处理时间 Time after packaging/d | 减压包装 Hypobaric packaging | 普通包装 Ordinary packaging | 单果包装 Single fruit packaging |
|---|---|---|---|---|
| 荸荠 Biqi | 4 | 2.10±0.46 a | 1.90±0.31 ab | 1.10±0.10 b |
| | 8 | 1.90±0.41 a | 1.50±0.27 a | 1.30±0.15 a |
| 东魁 Dongkui | 4 | 2.70±0.42 a | 1.50±0.22 b | 1.20±0.13 b |
| | 8 | 2.40±0.43 a | 2.00±0.42 a | 1.70±0.26 a |

注：同列不同小字字母表示在0.05水平存在显著差异。

Note: The different small letters in the same column indicate significant differente at 0.05 level.

经过减压包装的荸荠和东魁果实中积累了大量的乙醛和乙醇。减压包装的荸荠果实的乙醛含量（*w*，后同）在0~10 d不断上升，在10 d时高达82.30 μg·g$^{-1}$，是0 d的4.73倍；乙醇含量随着贮藏期延长逐渐上升，在6 d时达到1 091.10 μg·g$^{-1}$，到10 d时仍维持在1 044.10 μg·g$^{-1}$（图5-A，C）。减压包装的东魁果实的乙醛和乙醇含量均在4 d达到最高，分别为71.80 μg·g$^{-1}$和1 683.60 μg·g$^{-1}$（图5-B，D）。对于普通篮筐和单果包装的杨梅果实来说，两品种果实乙醛、乙醇含量和醇醛比值在贮藏期间均维持在较低水平。在10 d时，减压包装果实中乙醛、乙醇含量和醇醛比值分别为其他两种包装的2.31~10.29倍、13.68~27.79倍以及1.53~9.63倍（图5）。

### 2.5 杨梅果实不同包装处理期间*PDC*和*ADH*基因表达分析

由图6可见，*PDC*和*ADH*基因在3种包装的荸

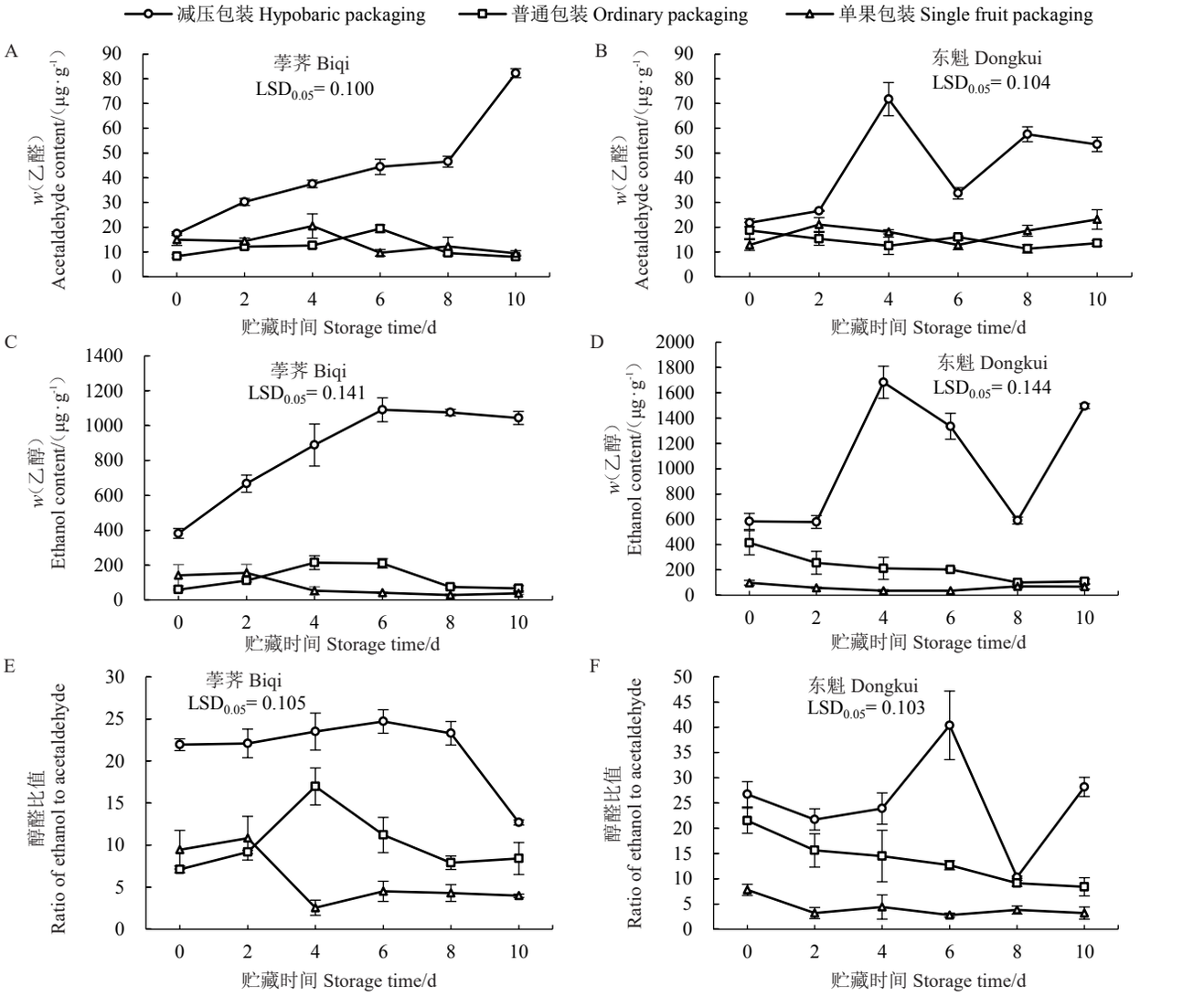



**图5 荸荠（A、C、E）和东魁（B、D、F）杨梅果实包装处理期间乙醛、乙醇含量与醇醛比值**

**Fig. 5 Contents of acetaldehyde and ethanol and the ratio of ethanol to acetaldehyde in Biqi (A, C, E) and Dongkui (B, D, F) fruit during packaging treatments**

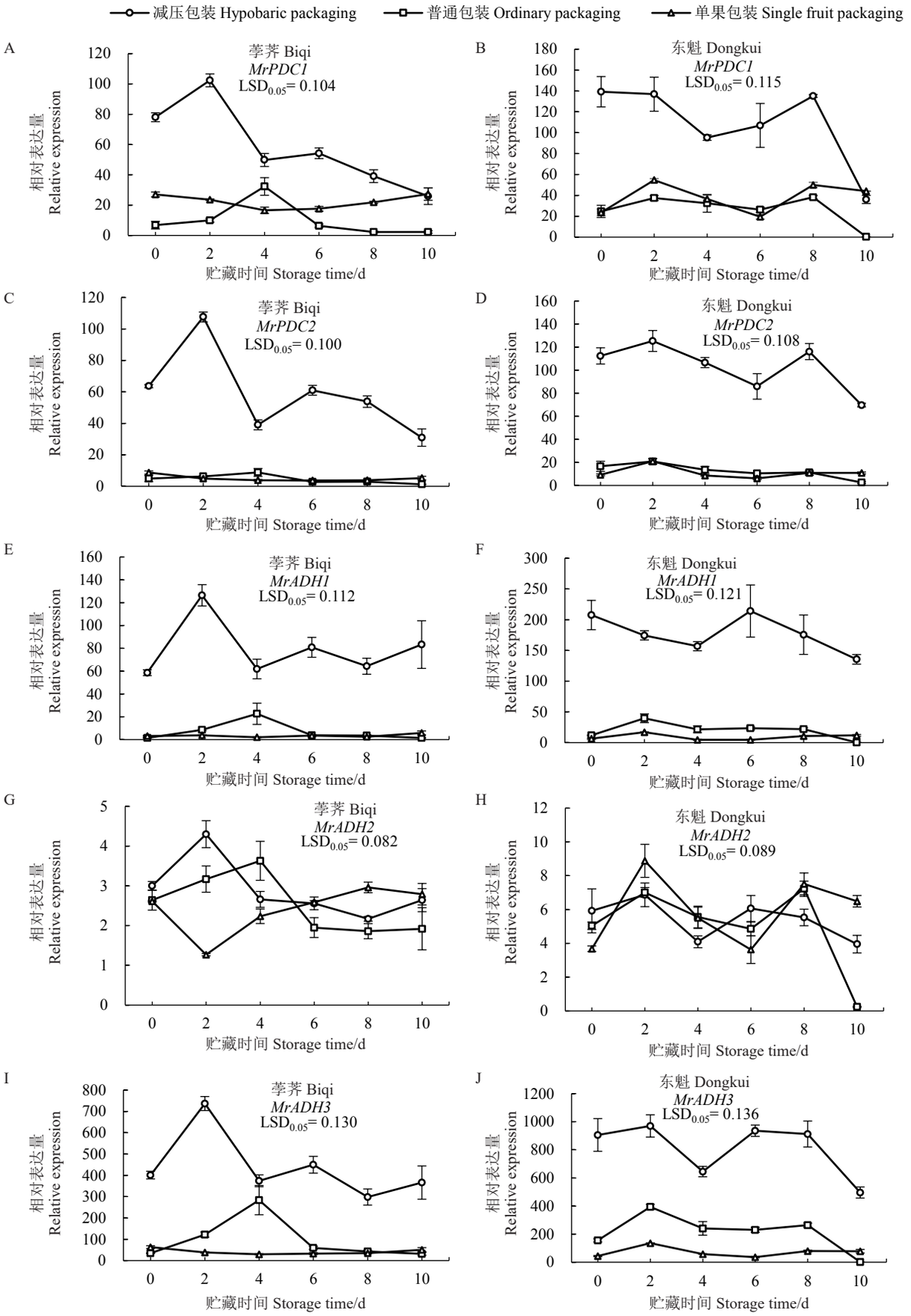



**图 6　荸荠（A、C、E、G、I）和东魁（B、D、F、H、J）杨梅果实包装处理期间 *MrPDCs* 和 *MrADHs* 的表达**

**Fig. 6　Expression of *MrPDCs* and *MrADHs* in Biqi (A, C, E, G, I) and Dongkui (B, D, F, H, J) fruit during packaging treatments**

荠和东魁杨梅果实中表达各异，*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*在减压包装杨梅果实中的表达量明显高于普通篮筐和单果包装。在荸荠杨梅中，*MrPDCs*和*MrADHs*在减压包装果实贮藏2 d时表达量最高，随后保持稳定或下降；各基因表达水平在普通篮筐和单果包装果实中差异较小（图6-A）。对于东魁杨梅，各基因在减压包装果实中的表达量总体呈现下降趋势，其中*MrPDCs*在0~8 d表达量较高，*MrADH1*表达量在6 d达到峰值；*MrADH3*在2~6 d先降后升，呈现“V”形变化，而后不断下降；在贮藏期间，各基因在普通篮筐和单果包装果实中的表达量无明显差异（图6-B）。在2 d时，减压包装果实中*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*分别为其他两种包装的2.50~10.32倍、5.97~21.74倍、4.40~33.19倍和2.46~19.26倍。

结合Pearson相关性分析，发现杨梅不同包装处理过程中乙醛、乙醇含量和醇醛比值与*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*表达量之间均呈极显著正相关，而与*MrADH2*的表达量无显著相关性。其中乙醛含量与乙醇含量相关系数达0.847（$p<0.01$），乙醇含量与醇醛比值相关系数达0.808（$p<0.01$），*PDC*和*ADH*表达总量相关系数高达0.953（$p<0.01$），*MrADH1*与*MrADH3*相关系数高达0.969（$p<0.01$）（表5），表明*MrPDC1*、*MrPDC2*、

**表5 荸荠和东魁果实包装处理期间乙醛、乙醇含量和醇醛比值与*MrPDCs*和*MrADHs*表达量的相关性**

**Table 5 Correlation between acetaldehyde, ethanol contents as well as the ratio of ethanol to acetaldehyde and the expression of *MrPDCs* and *MrADHs* in Biqi and Dongkui fruit from different packaging treatments**

| 指标 Index | 乙醛含量 Acetaldehyde content | 乙醇含量 Ethanol content | 醇醛比值 Ratio of ethanol to acetaldehyde | *MrPDC1*表达量 Expression of MrPDC1 | *MrPDC2*表达量 Expression of *MrPDC2* | *MrPDCs*表达总量 Total expression of *MrPDCs* | *MrADH1*表达量 Expression of *MrADH1* | *MrADH2*表达量 Expression of *MrADH2* | *MrADH3*表达量 Expression of *MrADH3* | *MrADHs*表达总量 Total expression of *MrADHs* |
|---|---|---|---|---|---|---|---|---|---|---|
| 乙醛含量 Acetaldehyde content | 1 | | | | | | | | | |
| 乙醇含量 Ethanol content | 0.847** | 1 | | | | | | | | |
| 醇醛比值 Ratio of ethanol to acetaldehyde | 0.457** | 0.808** | 1 | | | | | | | |
| *MrPDC1*表达量 Expression of *MrPDC1* | 0.427** | 0.496** | 0.556** | 1 | | | | | | |
| *MrPDC2*表达量 Expression of *MrPDC2* | 0.604** | 0.713** | 0.696** | 0.926** | 1 | | | | | |
| *MrPDCs*表达总量 Total expression of *MrPDCs* | 0.527** | 0.617** | 0.639** | 0.981** | 0.982** | 1 | | | | |
| *MrADH1*表达量 Expression of *MrADH1* | 0.629** | 0.766** | 0.756** | 0.885** | 0.949** | 0.935** | 1 | | | |
| *MrADH2*表达量 Expression of *MrADH2* | 0.021 | 0.008 | 0.088 | 0.515** | 0.295 | 0.411* | 0.312 | 1 | | |
| *MrADH3*表达量 Expression of *MrADH3* | 0.552** | 0.685** | 0.756** | 0.918** | 0.950** | 0.952** | 0.969** | 0.390* | 1 | |
| *MrADHs*表达总量 Total expression of *MrADHs* | 0.568** | 0.702** | 0.758** | 0.917** | 0.954** | 0.953** | 0.979** | 0.382* | 0.999** | 1 |

*MrADH1*和*MrADH3*在乙醛和乙醇积累中发挥重要作用。

## 3 讨 论

随着果实成熟，醛醇类物质在果实中积累使得果实呈现浓郁风味，其中乙醇和乙醛起着重要作用。乙醛和乙醇积累期间*PDC*和*ADH*基因的表达情况因种类、品种和成熟度而异[15]。前人研究发现，*FaPDC1*在草莓果实成熟和香气形成中发挥着重要作用[17]；*CmPDC1*、*CmADH1*和*CmADH2*的表达量随着甜瓜果实成熟不断上升[5-6]；*VvADH2*表达量在葡萄果实成熟后期明显增加[31]；然而在部分物种中，

*ADH*基因表达量和醛醇类物质含量随果实成熟而下降；白梨中有2个*ADH*基因表达量随着果实成熟度升高而下降[32]；陈美霞[33]对杏的研究发现，不同发育期的杏果实香气物质积累不一，果实绿果期的醛类和醇类含量最高，成熟果实在最佳采收期前后乙醛和乙醇含量降低。本研究发现，2个*PDC*基因在不同杨梅品种果实成熟期间呈现出不同的表达模式，*MrPDC1*在多数品种成熟期的表达量最高，而*MrPDC2*在绿果期的表达量最高。不同杨梅品种中*MrADH1*和*MrADH3*的表达量呈现与成熟度一致的趋势，*MrADH2*的表达量呈现与成熟度相反的趋势，且果实中*MrADH3*的表达量明显高于*MrADH1*和*MrADH2*，*MrADH3*在10个杨梅品种中的表达量在成熟期达到最高，表明*MrADH3*在调节杨梅果实成熟期间乙醛和乙醇积累中发挥着重要作用。

多数杨梅品种果实乙醛和乙醇含量总体随着果实成熟度增加而不断升高，结合基因表达分析发现，*MrADH1*和*MrADH3*高表达的杨梅品种所积累的乙醛和乙醇较多。Zhu等[26]研究发现，荸荠杨梅中乙醛和乙醇含量随着果实成熟呈现上升趋势，在成熟期的含量显著高于绿果期、转色期和红熟期，且在红熟期和完熟期中*ADH*的增强表达与乙醛和乙醇含量的上升存在密切关系；另一研究结果显示，随着杨梅转色成熟，PDC和ADH蛋白丰度增加[27]。本研究发现*MrPDCs*和*MrADHs*基因在果实成熟期表达增强，与笔者先前研究结果[26-27]相印证，表明PDC和ADH在醛醇转化中发挥重要作用，参与杨梅成熟过程中乙醛和乙醇的合成。

普通篮筐包装是杨梅生产上常用的传统包装形式，后来发展出减压包装，其目的主要是为了防止果实运输期间振动，单果包装是近年来为实现杨梅精品化贮运而不断改良出的新型包装。由于果实呼吸消耗氧气，减压包装造成了低$O_2$和高$CO_2$环境。减压或低氧通过PDC和ADH介导对果实风味产生影响，这在其他果实上已有报道。草莓、番荔枝、葡萄等果实在高$CO_2$条件下乙醛和乙醇含量显著提高，ADH、PDC酶活性明显增强，*PDC*和*ADH*基因表达不断上调[25, 34-35]；但在冬枣上，研究表明减压处理反而对抑制乙醛、乙醇积累有显著效果，研究者认为减压处理可以降低枣果的呼吸强度和乙烯释放量，调节枣果的生理代谢，从而抑制酒化现象的发生[36-37]。本研究表明杨梅减压包装急剧诱导乙醛和乙醇积累，在两个品种上表现一致。乙醛和乙醇是果实采后重要挥发性芳香物质，较低浓度的乙醛和乙醇可以促进果实风味形成并维持果实品质，而高浓度则使果实进行有害代谢而产生异味[38]。李红卫[39]对冬枣乙醇积累机制的研究表明，乙醇含量超过一定阈值则使冬枣果实品质劣化。在本研究中，减压包装明显促进杨梅果实乙醛和乙醇积累的同时也使果实呈现严重酒味和异味，而乙醛和乙醇的积累是由于多个*MrADHs*和*MrPDCs*表达受到强烈诱导。相比之下，普通包装和单果包装的杨梅果实中这些基因表达量以及乙醛和乙醇含量远低于减压包装，果实异味不明显。因此，杨梅生产上如采用减压包装，宜在低温下进行贮运并尽可能缩短处于包装中的时间，果实运达目的地后需及时拆开减压包装袋以避免果实长时间处于密闭环境。本研究表明*MrADHs*和*MrPDCs*表达可受低$O_2$和/或高$CO_2$诱导，但是所涉及的具体机制等有待进一步研究。

## 4　结　论

研究结果表明，*MrADH1*和*MrADH3*在果实成熟期间乙醛和乙醇积累中起着重要作用；减压包装处理诱导了*MrPDC1*、*MrPDC2*、*MrADH1*和*MrADH3*表达，导致乙醛和乙醇过度积累以及果实异味产生。研究结果对指导杨梅果实采后保鲜及异味控制具有重要意义，杨梅果实采后贮运需避免长时间密闭环境，以防止果实产生异味。

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