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水分胁迫对马瑟兰葡萄果实挥发性物质合成的影响

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摘　要：【目的】探明水分胁迫对马瑟兰葡萄果实挥发性风味物质的影响。【方法】以5年生马瑟兰葡萄为试材，根据黎明前叶片水势设置三个水分处理：对照为无胁迫、轻度胁迫（T1）和中度胁迫（T2），通过控制灌水量使植株维持在目标范围内。分别测定各处理葡萄果实挥发性有机化合物及其相关基因表达等指标。【结果】在马瑟兰葡萄成熟期，对照、轻度和中度水分胁迫分别检测出挥发性有机化合物41、45和36种；轻度胁迫（T1）可显著提高果实挥发性物质种类，分别较对照和中度胁迫（T2）提高了9.7%和25.0%。与对照相比水分胁迫下更有利于葡萄果实中 *VvCCD1* 的表达，但不利于 *VvGPPS* 和 *VvHPLA* 的表达。【结论】适度的水分胁迫可以促进果实中挥发性有机化合物种类和含量的增加。

关键词：葡萄；水分胁迫；挥发性化合物；基因表达

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Effects of water stress on the synthesis of volatile compounds in Marselan grape berries

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Abstract:【Objective】Water is one of the important factors that restrict agricultural production. The grape producing area in the eastern foot of Helan Mountain in Ningxia is located in the inland of northwest China, which belongs to temperate continental climate. The annual rainfall is small and the climate is dry. Relying on the Yellow River water for irrigation, however, there is excessive irrigation and unreasonable utilization, resulting in serious waste of water resources, which restricts the healthy and sustainable development of grape industry. Therefore, advocating scientific and efficient use of water resources is an important measure for agricultural sustainable development. In order to explore the effects of different water stress on the metabolism of aroma compounds synthesis during the berry development of Marselan grape, the present experiment was undertaken to obtain the technical measures of water management for improvement of the fruit quality of Marselan grape, and optimize the irrigation conditions suitable for arid and semi-arid areas as well as lay a theoretical foundation for the optimization of the cultivation and management of Marselan grape.【Methods】Taking 5-year-old Marselan grapevines as the test materials, three water treatments were set according to the water potential of leaves before dawn: no stress (control), light water stress (T1) and moderate stress (T2), and the vines were kept within the target range by controlling the irrigation amount. Extraction of free aroma: 15 g of crushed fruit samples was added into a centrifuge tube, and 1 g of cross-linked polyvinylpyrrolidone (PVPP) and 0.5 g of *D*-gluconolactone were added. The centrifuge tube was placed in a 4 °C refrigerator for 120 min. Then it was centrifuged at 10 000 $r \cdot min^{-1}$ for 15 min at 4 °C to obtain clear grape juice. Headspace solid-phase microextraction (HS-SPME): Take 5 mL of grape juice into a 15 mL headspace bottle, add 1 g of sodium chloride, 5 μL of internal standard 2-octanol and a magnetic rotor, then quickly tighten the bottle

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cap, the extraction head was inserted into the sample headspace vial and placed on a magnetic stirrer for adsorption at 60 °C for 40 min. After adsorption, the extraction head was taken out and inserted into the gas chromatography injection port, and decomposed at 250 °C for 5 min. Gas chromatography separation conditions: Column: HP-INNO-Wax capillary column (length 30 m, inner diameter 0.25 mm, liquid film thickness 0.25 μm), carrier gas He (99.99%), flow rate 1.0 $mL \cdot min^{-1}$; Inlet temperature: 250 °C, desorption for 5 min; programmed temperature was 50 °C for 1 min, and then increased to 220 °C at a rate of 3 $°C \cdot min^{-1}$ and held for 5 min; mass spectrometry interface temperature was 280 °C, ion source temperature was 230 °C, ionization method was EI, the ionization energy was 70 eV, and the scanning range was 30−350 amu. Qualitative analysis and quantitative analysis: using the total ion current spectrum in the full ion scanning mode of mass spectrometry, the collected total ion map current was searched and data were analyzed with NIST08 and RTLPEST3 spectral libraries, combined with the retention index (Retention Index, RI) and references of identify volatile aroma components. The internal standard method was used for relative quantification, and 2-octanol was used as the internal standard to determine the relative content. The calculation formula was: relative content of aroma components ($\mu g \cdot L^{-1}$) = [peak area of each component/internal standard peak area × internal standard mass (μg)]/sample mass (kg). Grape fruit (without seeds) RNA was extracted with RNA Extraction Kit (spin column type). cDNA was synthesized by reverse transcription using TranScript kit. Fluorescence quantitative PCR was performed with Actin as the internal reference gene, and the specific sequences of *VvGPPS*, *VvHPLA* and *VvCCD1* were searched in GeneBank, and primers were designed and synthesized by Shanghai Sheng Gong. Relative quantification was performed using the $2^{-\Delta\Delta Ct}$ method.【Results】41, 45 and 36 volatile organic compounds were detected in the control, light stress and moderate stress, respectively, during the ripening stage of Marselan grape. The number of compound species was significantly less than that of light stress treatment. It can be seen that light water stress can significantly increase the types of volatile compounds in berries, which increased by 9.7% and 25.0% compared with the control and moderate stress, respectively. Under moderate stress, the types of volatile compounds in the berry decreased by 13.8% compared with the control. A total of 12 aldehydes and 12 alcohols were detected, and their contents increased with the development of Marselan grape berry. 120 days after flowering, the content of n-hexanol in berries treated with T1 was 54.7% and 60.9% higher than that with control and T2, respectively. Nine esters were detected, among which ethyl caprate, dibutyl phthalate, diethyl phthalate and propyl heptyl lactone were the main ester volatile substances in Marselan grape berry. Twelve kinds of volatile acids were detected, among which nonanoic acid had unpleasant pungent odor, and its content increased with berry development, indicating that water stress would aggravate the inferior aroma brought by nonanoic acid. At maturity, the expression of *VvGPPS* with control was higher than that of T1 and T2, which indicated that water stress would reduce the expression of this gene. The expression of *VvHPLA* decreased with the development of Marselan grape berry. The expression of *VvCCD1* showed a downward trend, but the expression of *VvCCD1* in T2-treated grape fruit was always higher than control. It was observed that the expression of *VvCCD1* in T1-treated grape berry was significantly higher than control and T2 at 87th day after anthesis, which indicated that water stress treatment could effectively improve the expression of *VvCCD1* in Marselan grape berry.【Conclusion】In conclusion, compared with the control, moderate water stress can significantly increase the variety and relative content of volatile organic compounds in Marcelan grape berry. Compared with the control, water stress is not conducive to the expression of *VvGPPS* and *VvHPLA*, but beneficial to the expression of *VvCCD1*.

Key words: Grape; Water stress; Volatile compounds; Gene expression

水分是限制农业生产的重要因素之一[1]，我国酿酒葡萄栽培区主要集中在西北干旱半干旱地区，大量研究表明水分胁迫会导致植物在形态和生理生化方面发生差异性变化[2-4]。如在一定水分胁迫下可以有效地限制葡萄枝叶徒长[5]、提高果实品质[6-8]等。果实品质不仅包括果实在生长和成熟过程中颜色、风味和质地的变化[9-10]，也包括果实释放出来的挥发性有机物质[11-12]；香气是葡萄果实品质之一，其种类、含量和感官阈值决定了葡萄品种香气的典型性[13-14]。适度的水分胁迫对葡萄的挥发性物质有影响，且对不同种类的香气产生不同的影响。Brillnate等[15]的研究显示‘西拉’葡萄进行70%水分灌溉降低了浆果的质量，从而导致果树两年的产量和作物负载量降低，但是70%水分灌溉使果实的花青素、丹宁和总酚含量增加，果实香气（萜烯类化合物、*β*-大马酮和降碳倍半萜及其衍生物）的含量提高。70%水分胁迫处理可能有助于改善浆果果皮和葡萄酒酚类物质，并在实现高产的同时减少葡萄酒中的甲氧基吡嗪（IBMP）。Ju等[16]对葡萄进行代谢分析的结果表明，浆果在水分胁迫后(E)-2-己醛和3-己醛含量显著升高。通过多元统计分析，结果表明葡萄果实中脯氨酸、过氧化氢酶、丙二醛和超氧化物歧化酶与青叶醛和3-己烯醛的含量相关性较强。因此，水分胁迫可以与活性氧自由基清除系统协同作用，调节浆果挥发物的积累，尤其是(E)-2-己醛和3-己醛。这些化合物将用作信号化合物，以对抗水分胁迫对葡萄藤的影响。葡萄潜在香气在轻度水分胁迫和中度氮供应状态下含量最高，重度水分胁迫和缺氮会减弱葡萄香气[17]。

葡萄香气合成具有多种途径，萜烯类合成途径是合成葡萄果实中挥发性有机化合物的主要途径，萜类化合物以游离态化合物和糖苷结合态化合物的形式存在，是葡萄浆果和葡萄酒香气中最重要的芳香化合物的来源[18]。研究表明，异戊二烯类化合物及其衍生物是果实中重要的一类挥发性化合物，这类化合物是类胡萝卜素在类胡萝卜裂解双加氧酶（CCDs）作用下氧化分解而成[19]，Zhang等[20]研究发现，在果实成熟过程中，类胡萝卜素类香气挥发性化合物含量增加，尤其是*β*-紫罗兰酮含量显著增加，并鉴定出可能参与这些化合物生物合成的CCD1基因。单萜合成代谢途径中期的关键基因是香叶基二磷酸合成酶基因（*VvGPPS*），GPPS基因表达量上调，对响应合成单萜物质有促进作用[21]。植物脂氢过氧化物裂解酶（hydropenoxide lyase，HPL）作为植物不饱和脂肪酸氧化途径中的关键酶，与植物的特有香气、抗逆反应及信号传导和老化等生理过程有关，醛类进而氧化生成酸或经醇脱氢酶（ADH）作用生成醇，最后在醇酰基转移酶（AAT）催化下生成酯类[22-23]。

马瑟兰（Marselan）是赤霞珠（Cabernet Sauvignon）和黑歌海娜（Grenache Noir）的杂交品种。经过杂交选出的马瑟兰既具有歌海娜的耐热性又兼备赤霞珠的细致感[24-25]，用马瑟兰酿制的干红葡萄酒品质优良，酒色紫黑不透光，香气浓郁，单宁含量高，适合长期陈酿[26]。目前，国内外对赤霞珠葡萄果实的香气组分研究的报道较多，而对马瑟兰葡萄的香气组分研究较少。本试验中以马瑟兰葡萄为试材，探究不同水分胁迫程度对马瑟兰葡萄果实中挥发性有机化合物及其相关基因的变化，以期为马瑟兰葡萄栽培中的水分利用提供理论依据。

1 材料和方法

1.1 试验设计

试验在宁夏农垦集团玉泉营农场国家葡萄产业技术体系水分生理与节水栽培岗位试验基地（38.28°N，106.24°E）进行，供试材料为5年生马瑟兰葡萄，东西行向，株行距0.6 m ×3 m，采用倾斜独龙蔓整形。水分胁迫从花后50 d至采收期进行，采用滴灌方式灌溉，每个处理均装有控水阀门，通过不同灌水量使各处理黎明前叶片基础水势值达到各胁迫参考范围，实现轻度、中度水分胁迫，以无水分胁迫作为对照，设置3个处理。对照浇灌时长12 h，轻度胁迫浇灌时长4 h，中度胁迫浇灌时长2 h。每3 d测量1次水势，通过控制灌水量使植株维持在目标范围内。试验从水分胁迫开始每10 d采样一次，每次取样部位为阴、阳两面及上中下，每个处理随机采取100粒果实，立刻用液氮速冻，用塑封袋装好放在−80 ℃的冰箱中保存待测（表1）。

表1 不同处理叶片水势参考标准

Table 1 Reference standard of leaf water potential of different treatments

处理 Treatment	黎明前叶片水势 Ψb/MPa Predawn leaf water potential
对照 Control	−0.40~−0.20
轻度胁迫 Light water stress	−0.60~−0.40
中度胁迫 Moderate stress	≤−0.60

1.2　黎明前叶片水势测定

于黎明前分别摘取各处理葡萄植株新梢中部健康的功能叶，每个处理随机选取3株葡萄，每株葡萄随机采3枚叶片。立即利用水势压力室（美国Soil Moisture Equipment公司）测定叶片的水势值，并读数记录。

1.3　葡萄果实挥发性有机化合物的测定

采用顶空固相微萃取（HS-SPME）结合气质联用（GC-MS）方法。

游离态香气的提取。在离心管加入破碎成粉末的果实样品15 g，加入1 g交联聚乙烯基吡咯烷酮（PVPP）和0.5 g *D*-葡萄糖酸内酯。将离心管置于4 ℃冰箱浸提120 min。然后4 ℃、10 000 r·min^{-1}离心15 min，得到澄清葡萄汁。

顶空固相微萃取（HS-SPME）。取葡萄汁5 mL于15 mL顶空瓶中，加入1 g氯化钠、5 μL内标物2-辛醇和磁力转子后迅速拧紧瓶盖，将萃取头插入样品顶空瓶，置于磁力搅拌器于60 ℃吸附40 min。吸附后将萃取头取出插入气相色谱进样口，于250 ℃解析5 min。

气相色谱分离条件。色谱柱：HP-INNO-Wax毛细管柱（长30 m，内径0.25 mm，液膜厚度0.25 μm），载气He（99.99%），流速1.0 mL·min^{-1}；进样口温度：250 ℃，解析5 min；程序升温为50 ℃下1 min后，以3 ℃·min^{-1}的速度升温到220 ℃并保持5 min；质谱接口温度为280 ℃，离子源温度为230 ℃，电离的方式为EI，电离能是70 eV，扫描范围为30~350 amu。

定性分析与定量分析。利用质谱全离子扫描模式下的总离子流图谱，对采集的总离子图流用NIST08和RTLPEST3两个谱库检索及资料分析，结合保留指数（Retention Index，RI）和参考文献确定挥发性香气组分。采用内标法相对定量，以2-辛醇作为内标来确定相对含量，计算公式为香气组分的相对含量（*w*）（μg·kg^{-1}）=[各组分的峰面积/内标峰面积×内标质量（μg）]/样品质量（kg）。

1.4　总RNA提取及荧光定量PCR

用RNA提取试剂盒（离心柱型）提取葡萄果实（不含种子）RNA。利用TranScript试剂盒反转录合成cDNA。以Actin为内参基因进行荧光定量PCR，在GeneBank中，查找*VvGPPS*、*VvHPLA*和*VvCCD1*的特异性序列，由上海生工进行引物设计和合成。引物序列如表2所示。采用$2^{-\Delta\Delta Ct}$法进行相对定量分析。

表2　实时荧光定量PCR引物序列

Table 2　Primer sequences for real-time quantitative PCR

基因名称 Gene name	引物序列（5’－3’） Sequence of primer (5’－3’)	
Actin	F：CTTGCATCCCTCAGCACCTT	R：TCCTGTGGACAATGGATGGA
CCD1	F：TGGCACTTTCGGAGGCTGATAAAC	R：GGGTCAACCTTTGGATGAGCAGTG
GPPS	F：AACTGCGGAAGTTCAATGTTGGC	R：ATGGCGGATGTCAGACAATGAACC
HPLA	F：CGGTGGCTTTACCATCTTCT	R：TCTTAGCGGCAAACCGGAGTTACA

1.5　数据分析

试验数据采用Microsoft office excel 2010、Origin 2018和SPSS Statistics 23.0进行绘图分析。

2　结果与分析

2.1　水分胁迫对马瑟兰葡萄果实挥发性化合物的影响

2.1.1　水分胁迫对马瑟兰葡萄果实挥发性化合物种类数量的影响　马瑟兰葡萄成熟期时对照、轻度胁迫和中度胁迫分别检测出挥发性有机化合物41、45和36种，如表3所示，轻度胁迫可显著增加果实挥发性物质种类，分别较对照和中度胁迫增加了9.7%和25.0%，中度胁迫和对照相比较，中度胁迫处理使果实内挥发性化合物种类和数量均减少，较对照减少了13.8%。表4所示证明轻度水分胁迫下马瑟兰葡萄果实内醇类和醛类挥发性物质的含量均较对照有所提高，而中度胁迫下各类挥发性物质含量较对照均降低。

2.1.2　水分胁迫对马瑟兰葡萄发育过程中主要的醇类和酯类化合物含量的影响　醇类为马瑟兰葡萄果实香气贡献很大，本次试验检测出12种醇类。如表5所示，主要的醇类含量随着葡萄果实的发育而上升。例如正己醇是一种具有水果香气的醇类化合物，在三种胁迫处理下正己醇均能被检测出来，与对照和中度胁迫处理相比轻度胁迫处理所检测出来的正己醇含量最高，花后120 d，轻度水分胁迫果实

表3　水分胁迫下成熟期马瑟兰葡萄果实挥发性物质的种类

Table 3　Number of species of water stress on volatile compounds of Marselan grape at mature stage

处理 Treatment	醇类 Alcohol	酯类 Ester	醛类 Aldehyde	酮类 Ketone	酸类 Acid	酚类 Phenolic	烃类 Hydrocarbons	其他 Others	总计 Total
对照 Control	6	4	9	5	8	3	3	3	41
轻度胁迫 Light	8	4	9	6	10	3	2	3	45
中度胁迫 Moderate	6	3	8	6	6	3	2	2	36

表4　水分胁迫下成熟期马瑟兰葡萄果实挥发性物质含量

Table 4　Effect of water stress on volatile compounds content of Marselan grape at mature stage　（μg·L-1）

处理 Treatment	醇类 Alcohol	酯类 Ester	醛类 Aldeyde	酮类 Ketone	酸类 Acid	烃类 Hydrocarbons	其他类 Others	总计 Total
对照 Control	655.365±106.07 b	645.595±87.194 a	3 336.452±242.653 b	1 051.845±71.698 b	644.817±93.768 b	122.501±6.621 a	1 488.402±11.698 b	7 944.976±143.146 b
轻度胁迫 Light	1 008.842±93.797 a	344.743±41.082 b	5 309.754±164.181 a	1 250.616±55.489 a	1 877.787±101.646 a	45.003±7.084 b	8 198.378±75.972 a	18 035.123±83.172 a
中度胁迫 Moderate	509.022±35.014 b	73.554±9.28 c	1 918.041±115.144 c	922.962±11.496 c	694.149±27.598 b	41.706±8.381 b	58.498±8.734 c	4 217.933±10.872 c

注：数据由平均值±标准差（$n=3$）表示，不同小写字母表示差异达到0.05显著水平。下同。

Note：The data are represented by the mean±standard deviation（$n=3$）. Different letters mean significant different at 0.05 level. The same below.

中正己醇的含量较对照和中度水分胁迫分别高出54.7%和60.9%。图1显示正己醇、芳樟醇、α-松油醇、苯甲醇及正壬醇随着果实发育其相对含量增加；且轻度胁迫处理下含量最高。而十二醇、2-乙基己醇和1-辛烯-3-醇其相对含量随果实发育而降低。由此可得出适度的水分胁迫（T1）可以提高香气物质的相对含量。

酯类挥发性化合物在葡萄的品种香气中不是很突出，一般在经酵母发酵后的葡萄酒中表现出种类和含量很高。酯类的相对含量较低，本次试验中共检测出9种酯类。其中癸酸乙酯、邻苯二甲酸二丁酯、邻苯二甲酸二乙酯和丙位庚内酯是马瑟兰葡萄果实中主要的酯类挥发性物质。在表5中可以发现，花后77 d具有椰子香气和麦芽气味的丙位庚内酯不能被检测出来，而具有芳香气味的邻苯二甲酸二乙酯在花后110 d才能被检测出。

2.1.3　水分胁迫对马瑟兰葡萄发育过程中主要的醛类和酮类化合物含量的影响　本次试验共检测出醛类12种，如表6所示，主要醛类挥发性物质随着马瑟兰葡萄果实的发育其相对含量升高。正己醛具有青草和苹果的香气，在整个发育过程中均能被检出，且其相对含量是醛类挥发物中最高的。2-己烯醛具有浓郁新鲜水果的香气，在7个时期中均能被检测出，且与对照相比轻度水分胁迫下2-己烯醛的相对含量最高，而中度水分胁迫2-己烯醛的相对含量降低。花后120 d，2-己烯醛的相对含量在轻度水分胁迫下较对照提高了40.3%；在中度水分胁迫下较对照降低了43.4%。由此得出，轻度水分胁迫促进2-己烯醛含量的升高，但中度水分胁迫降低其含量。部分醛类物质在果实发育前期未能被检出，但在果实发育后期能被检出，如山梨醛在花后87 d后才能被检测出。

如图2所示，2-甲基苯甲醛、反式-2,4-庚二烯醛和2,5-二甲基苯甲醛在果实发育前期各水分胁迫下均可被检出，但在果实成熟期其相对含量极低。但正己醛、苯甲醛、5-羟甲基糠醛、山梨醛及正壬醛的相对含量随果实发育而增加，呈上升趋势。

酮类挥发性物质共检测出10种，大马士酮有强烈的玫瑰花香气，在7个时期中均存在，随果实的发育其相对含量也随之增加。花后120 d，轻度和中度水分胁迫下大马士酮的含量均低于对照。说明水分胁迫不利于大马士酮物质的积累。

2.1.4　水分胁迫对马瑟兰葡萄发育过程中主要的酸类、酚类及其他类化合物含量的影响　共检测出12种酸类挥发性物质，正壬酸具有令人不愉快的刺激气味，随着果实发育其含量呈上升趋势，花后110 d，轻度和中度水分胁迫下正壬酸的含量均比对照高40.0%和51.4%，表明水分胁迫会加剧正壬酸带来的劣质香气；表中还显示，在马瑟兰果实发育前期能被检测出来的酸类挥发性物质很少，到果实发育后期

表5　水分胁迫对马瑟兰葡萄果实发育过程中主要醇类和酯类物质含量的影响

Table 5　Effects of water stress on the content of main alcohols and esters during fruit development of Marselan grape

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量 Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
醇类 Alcohol	正己醇 1-Hexanol	对照 Control	0.599±0.026 a	0.314±0.013 a	0.447±0.178 a	1.336±0.625 a	1.560±0.346 b	170.130±2.398 b	246.471±40.404 b
		轻度胁迫 Light	0.613±0.027 a	0.280±0.024 a	0.537±0.272 a	1.136±0.826 a	3.040±2.265 b	253.823±36.669 a	381.393±22.978 a
		中度胁迫 Moderate	0.709±0.168 a	0.369±0.186 a	0.771±0.343 a	0.244±0.021 a	70.509±21.132 a	215.573±16.898 b	237.021±2.984 b
	芳樟醇 Linalool	对照 Control	0.757±0.025 a	0.502±0.004 a	–	0.336±0.036 b	–	16.154±2.129 a	55.319±5.575 a
		轻度胁迫 Light	0.587±0.014 b	0.522±0.101 a	0.354±0.062 a	0.651±0.010 a	2.506±0.697 a	18.513±0.630 a	14.533±1.663 b
		中度胁迫 Moderate	0.379±0.005 c	0.446±0.333 a	0.316±0.027 a	–	2.010±0.255 a	18.704±1.275 a	9.140±0.176 b
	苯甲醇 Benzyl alcohol	对照 Control	–	–	0.556±0.030 a	0.584±0.068 a	–	138.618±8.185 c	145.964±18.217 b
		轻度胁迫 Light	–	–	0.451±0.041 a	3.022±3.963 a	31.899±1.963 b	244.071±6.619 b	365.526±27.037 a
		中度胁迫 Moderate	–	–	0.475±0.151 a	–	211.633±1.228 a	203.997±2.979 a	153.265±25.070 b
	4-萜烯醇 Terpinen-4-ol	对照 Control	0.407±0.248 a	1.033±0.030 a	–	–	–	20.654±0.339 b	–
		轻度胁迫 Light	0.402±0.025 a	0.436±0.021 b	–	–	–	–	–
		中度胁迫 Moderate	0.224±0.020 a	–	–	–	9.587±0.361 a	20.777±0.942 b	14.622±0.487 a
	α-松油醇 *α*-Terpineol	对照 Control	0.821±0.124 b	0.470±0.001 a	0.742±0.240 a	–	–	39.332±0.426 b	62.092±10.125 b
		轻度胁迫 Light	1.089±0.022 a	0.540±0.240 a	0.400±0.212 b	1.766±0.023 a	–	53.945±7.078 b	82.728±0.186 a
		中度胁迫 Moderate	0.525±0.047 c	0.322±0.015 a	–	–	131.026±52.777 a	66.421±3.774 a	57.334±4.513 b
酯类 Ester	癸酸乙酯 Ethyl caprate	对照 Control	0.680±0.041 b	–	–	–	–	–	–
		轻度胁迫 Light	0.732±0.086 a	–	–	–	–	7.385±0.511 a	–
		中度胁迫 Moderate	0.515±0.009 b	–	–	–	–	–	–
	邻苯二甲酸二丁酯 Dibutyl phthalate	对照 Control	0.806±0.130 a	0.694±0.575 a	0.564±0.017 a	–	1.470±0.613 a	10.223±0.966 a	28.411±3.650 a
		轻度胁迫 Light	0.631±0.017 b	0.348±0.062 a	–	0.454±0.162 a	2.845±2.015 a	13.128±0.842 a	26.597±29.657 a
		中度胁迫 Moderate	0.534±0.028 b	0.318±0.019 a	–	–	45.070±37.467 a	33.849±25.080 a	12.150±0.605 a
	丙位庚内酯 4-Heptanolide	对照 Control	1.168±0.093 a	1.215±0.278 a	–	1.724±0.467 a	–	–	–
		轻度胁迫 Light	–	1.405±0.732 a	1.537±0.779 a	–	–	–	–
		中度胁迫 Moderate	0.273±0.025 b	0.797±0.252 a	1.396±0.795 a	0.345±0.010 b	–	–	–
	邻苯二甲酸二甲酯 Dimethyl phthalate	对照 Control	–	86.340±58.925 a	15.103±0.127 a	7.914±0.249 a	–	–	36.661±9.964 b
		轻度胁迫 Light	0.768±0.036 a	43.443±14.659 a	16.595±1.447 a	–	3.307±0.592 b	46.258±3.257 a	87.610±2.129 a
		中度胁迫 Moderate	0.415±0.019 b	17.647±5.599 a	14.091±1.449 a	1.627±1.962 b	17.577±2.688 a	53.385±9.207 a	34.111±7.170 b
	邻苯二甲酸二乙酯 Diethyl phthalate	对照 Control	–	–	–	–	–	18.036±2.344 b	55.564±4.542 b
		轻度胁迫 Light	–	–	–	–	–	–	75.549±5.262 a
		中度胁迫 Moderate	–	–	–	–	–	31.506±6.560 a	27.293±1.505 c

注：–未检测到。下同。

Note：– undetected. The same below.

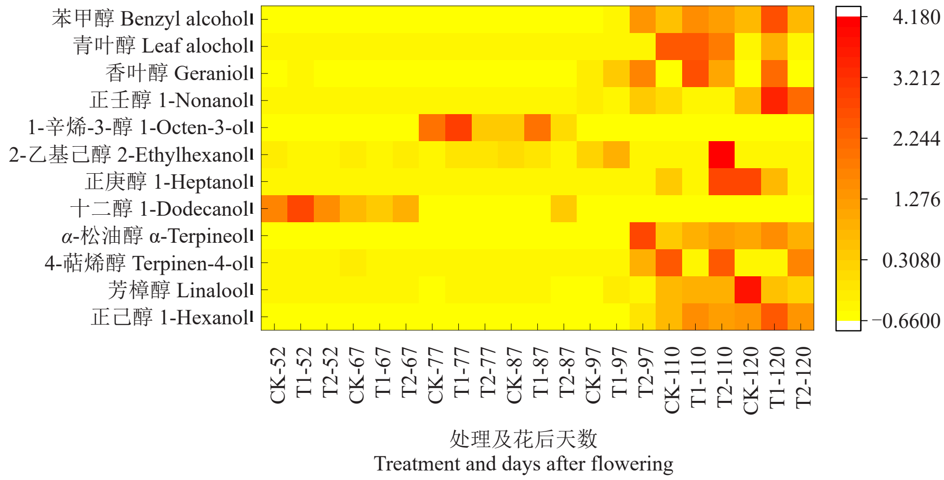

图 1 马瑟兰葡萄果实中不同醇类化合物含量在不同时期与各胁迫处理间的关系

Fig. 1 The relationship between the content of different alcohol compounds in Marselan grape fruit at different times and different stress treatments

表 6 水分胁迫对马瑟兰葡萄果实发育过程中主要醛类和酮类物质含量的影响

Table 6 Effects of water stress on the content of main aldehydes and ketones during fruit development of Marselan grape

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量 Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
醛类 Alde-hyde	正己醛 Hexanal	对照 Control	52.663±7.005 a	65.171±8.394 a	90.928±0.422 a	107.064±15.735 a	201.840±53.465 b	1 191.837±135.748 b	1 525.539±14.285 b
		轻度胁迫 Light	56.043±7.931 a	33.414±33.677 a	66.294±69.655 a	96.419±1.614 a	481.708±53.912 a	3 428.472±99.550 a	3 485.572±57.307 a
		中度胁迫 Moderate	20.889±0.174 b	37.953±15.249 a	47.385±32.460 a	27.233±5.028 b	149.442±6.897 b	1 150.446±86.034 b	748.843±25.051 c
	2-己烯醛 E-2-Hexenal	对照 Control	2.329±0.028 a	3.919±0.990 a	6.298±0.056 a	4.521±1.004 b	16.989±5.972 a	113.599±10.785 b	253.085±54.423 b
		轻度胁迫 Light	2.439±0.407 a	4.731±1.383 a	6.318±1.432 a	5.555±0.176 a	16.458±14.303 a	259.864±32.375 a	355.092±39.305 a
		中度胁迫 Moderate	2.237±0.058 a	4.213±0.190 a	5.708±0.716 a	2.075±1.161 b	14.421±3.541 a	322.581±23.553 a	176.479±19.019 b
	苯甲醛 Benzaldehyde	对照 Control	1.559±0.182 a	2.378±0.110 a	4.555±0.491 a	1.512±0.038 b	1.585±0.252 a	87.390±11.211 a	161.755±17.970 a
		轻度胁迫 Light	1.498±0.004 a	2.556±0.440 a	1.986±0.056 b	3.166±0.203 a	5.155±4.384 a	71.674±1.868 a	93.430±0.579 b
		中度胁迫 Moderate	1.314±0.049 a	1.783±0.275 a	2.042±0.444 b	1.143±0.774 b	1.446±0.542 a	139.912±40.940 a	94.262±3.554 b
	5-羟甲基糠醛 5-Hydroxymethyl-furfural	对照 Control	–	–	2.104±0.020 a	–	2.823±2.023 b	77.484±63.956 b	289.257±104.572 b
		轻度胁迫 Light	–	–	–	–	3.876±0.245 b	80.990±54.153 b	604.161±4.541 a
		中度胁迫 Moderate	–	–	–	0.784±0.017 a	25.954±2.978 a	541.604±39.524 a	262.304±14.689 b
	山梨醛 (E,E)-2,4-Hexadienal	对照 Control	–	–	–	–	0.807±0.130 a	64.709±10.405 b	250.464±15.094 b
		轻度胁迫 Light	–	–	–	0.449±0.008 a	2.877±1.197 a	219.042±22.463 a	338.528±15.371 a
		中度胁迫 Moderate	–	–	–	–	0.763±0.068 a	96.759±37.807 b	35.156±6.410 c
	2-羟基乙醛 2-Oxoethanol	对照 Control	–	–	0.393±0.041 a	–	–	8.052±4.556 a	28.109±9.623 a
		轻度胁迫 Light	–	–	–	–	5.897±1.167 b	40.094±7.333 a	23.773±6.132 a

表 6 （续） Table 6 (Continued)

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量 Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
		中度胁迫 Moderate	–	–	–	–	43.789± 0.317 a	39.442± 23.858 a	59.082± 17.835 a
	正壬醛 1-Nonanal	对照 Control	–	–	–	–	3.006± 0.070 a	20.019± 10.128 a	42.047± 8.035 a
		轻度胁迫 Light	–	–	–	1.169± 0.010 a	3.224± 0.711 a	–	24.318± 0.626 b
		中度胁迫 Moderate	–	–	–	0.445± 0.222 b	2.954± 0.327 a	–	45.724± 2.853 a
酮类 Ketone	大马士酮 Damascenone	对照 Control	0.831± 0.181 a	7.441± 1.364 a	4.552± 0.170 a	5.255± 1.888 a	22.909± 7.503 b	160.598± 20.902 b	256.409± 44.891 a
		轻度胁迫 Light	0.959± 0.072 a	8.967± 1.053 a	6.115± 0.222 a	1.082± 0.428 a	4.797± 3.131 b	452.893± 5.829 a	78.348± 0.173 b
		中度胁迫 Moderate	0.930± 0.013 a	3.187± 4.008 a	5.149± 1.202 a	2.079± 2.502 a	293.746± 59.681 a	127.536± 24.121 b	51.866± 1.208 b
	2-吡咯烷酮 pyrrolidin-2-one	对照 Control	11.717± 4.021 a	11.303± 4.004 a	1.025± 0.301 a	13.908± 4.290 a	3.971± 4.135 b	13.087± 0.391 c	34.415± 8.338 b
		轻度胁迫 Light	8.683± 0.408 b	10.004± 3.207 a	21.723± 12.330 a	–	6.021± 6.389 b	45.071± 1.906 a	117.153± 6.893 a
		中度胁迫 Moderate	3.402± 0.396 b	8.991± 5.574 a	11.335± 5.560 a	0.445± 0.429 b	54.830± 22.232 a	26.513± 2.308 b	28.546± 0.395 b
	羟基丙酮 Hydroxyacetone	对照 Control	–	–	–	–	–	40.110± 12.471 a	38.448± 0.749 c
		轻度胁迫 Light	–	–	–	0.214± 0.140 a	7.448± 7.944 b	56.147± 4.758 a	66.802± 1.579 b
		中度胁迫 Moderate	–	–	–	–	110.536± 88.190 a	45.739± 3.134 a	82.936± 2.370 a
	1,3-二羟基丙酮 1,3-Dihydroxyacetone	对照 Control	–	–	–	–	–	–	–
		轻度胁迫 Light	–	–	–	–	31.935± 1.368 b	221.441± 4.153 a	221.011± 5.735 a
		中度胁迫 Moderate	–	–	–	–	131.245± 11.066 a	183.860± 6.465 b	207.072± 2.474 b

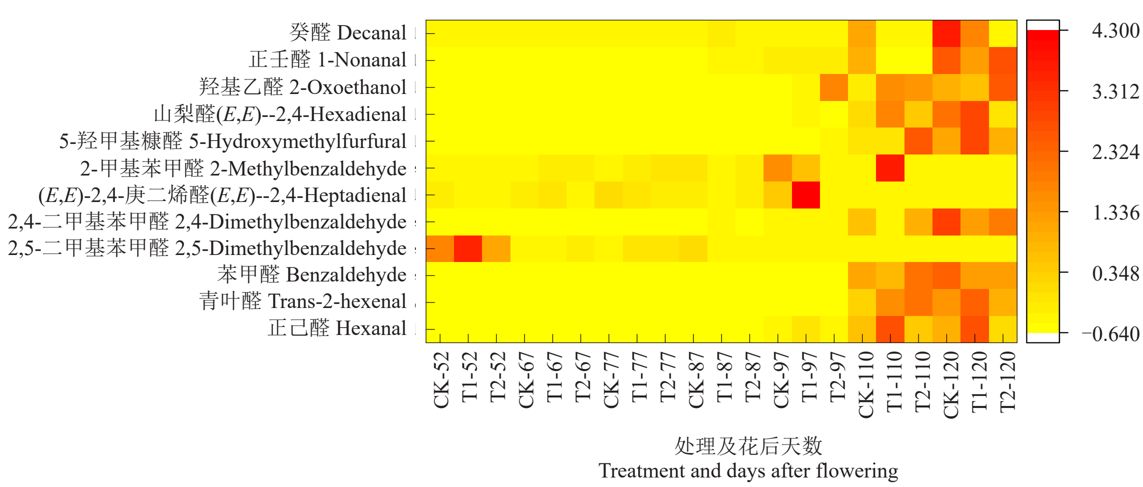

图 2　马瑟兰葡萄果实中不同醛类化合物含量在不同时期与各胁迫处理间的关系

Fig. 2　The relationship between the content of different aldehydes in Marselan grape fruit at different times and different stress treatments

酸类挥发性物质种类增加(表7)。

酚类物质中2,4-二叔丁基酚的相对含量最高,且在葡萄果实的全发育阶段均能被检测出来。其他类化合物中包括含氮化合物和其他烃类化合物,其中四甲基琥珀腈和2,1,3-苯并噻二唑含量最高(表7)。

2.2 水分胁迫对马瑟兰葡萄果实挥发性化合物合成相关基因的影响

香叶基二磷酸合成酶基因(*VvGPPS*)为单萜合成代谢途径中期的关键基因,如图3所示,*VvGPPS*表达量随着马瑟兰葡萄果实的发育呈现先下降随后上升的趋势,花后87 d前,T2处理下*VvGPPS*表达量显著高于对照和T1;成熟期时,对照处理下*VvGPPS*表达量高于T1和T2。表明水分胁迫会降低该基因的表达量。

如图4所示,在马瑟兰葡萄果实整个发育过程中,各处理下*VvHPLA*表达量呈下降趋势,但是花后87 d时T1的*VvHPLA*表达量最高。花后67~120 d对照的相对表达量均处于较低水平,T1和T2的表达量高于对照。说明水分胁迫可以促进*VvHPLA*表达量升高,但是总体来说成熟期的表达量降低。

如图5所示,在马瑟兰葡萄果实发育过程中,*VvCCD*1表达量呈现出下降趋势,但中度水分胁迫处理(T2)的葡萄果实*VvCCD1*表达量始终高于对照组,花后87 d观察到轻度水胁迫处理(T1)的

表7 水分胁迫对马瑟兰葡萄果实发育过程中主要酸类、酚类和其他物质含量的影响

Table 7 Effects of Water Stress on Contents of Main Acids, Phenols and Other Substances During Fruit Development of Marselan Grape

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
酸类 Acid	己酸 Hexanoic acid	对照 Control	0.356±0.018 b	0.406±0.049 a	–	0.707±0.266 a	2.833±0.438 a	–	–
		轻度胁迫 Light	0.434±0.030 a	0.436±0.133 a	1.890±1.890 a	–	3.105±0.244 a	–	56.262±4.079 a
		中度胁迫 Moderate	–	0.434±0.039 a	0.695±0.244 a	0.294±0.015 b	–	204.786±11.431 a	–
	反式-2-己烯酸 trans-2-Hexenoic acid	对照 Control	0.253±0.013 a	–	2.508±0.662 a	–	–	109.127±48.782 b	157.008±37.194 b
		轻度胁迫 Light	–	–	0.984±0.019 b	1.811±0.410 a	–	242.388±15.994 a	276.338±30.322 a
		中度胁迫 Moderate	–	–	–	0.346±0.000 b	–	221.724±30.281 a	–
	正壬酸 Nonanoic acid	对照 Control	–	–	3.268±0.181 a	–	1.066±0.184 c	58.857±18.595 a	131.452±37.877 a
		轻度胁迫 Light	–	–	–	0.919±0.066 a	8.755±0.239 a	90.623±0.129 a	124.442±4.521 a
		中度胁迫 Moderate	–	–	–	–	5.529±0.455 b	89.134±4.962 a	107.611±8.926 a
	月桂酸 Lauric acid	对照 Control	–	–	5.109±0.106 a	–	1.579±0.582 b	2.816±0.049 a	24.424±8.708 a
		轻度胁迫 Light	–	–	–	1.149±0.129 a	1.676±0.906 b	4.378±2.040 a	24.774±0.330 a
		中度胁迫 Moderate	–	–	–	–	47.264±6.634 a	4.221±0.117 a	22.891±1.770 a
	2-乙基戊酸 2-Ethylhexanoic acid	对照 Control	–	–	–	–	1.612±1.156 b	22.147±5.768 c	58.172±0.794 b
		轻度胁迫 Light	–	–	–	–	5.229±0.242 b	84.929±2.068 a	189.770±11.120 a
		中度胁迫 Moderate	–	–	–	–	57.737±27.988 a	48.870±10.325 b	48.455±2.345 b
	苯甲酸 Benzoic acid	对照 Control	–	–	–	–	0.424±0.124 a	–	13.096±0.607 b
		轻度胁迫 Light	–	–	–	–	2.126±0.247 a	1.622±0.561 b	20.888±0.234 a

表7 （续） Table 7 (Continued)

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
		中度胁迫 Moderate	–	–	–	0.221±0.012 a	23.186±18.208 a	12.118±4.006 a	–
	乙酰基丙酸 Levulinic acid	对照 Control	–	–	–	–	–	13.626±1.829 c	22.685±1.480 c
		轻度胁迫 Light	–	–	–	–	6.288±0.374 b	76.988±1.255 a	86.744±0.607 a
		中度胁迫 Moderate	–	–	–	–	30.889±0.292 a	29.251±6.803 b	71.877±3.849 b
酚类 Phenolic	2,4-二叔丁基酚 2,4-Ditert-butylphenol	对照 Control	2.006±0.010 b	0.465±0.130 b	16.929±1.672 a	–	19.770±7.148 b	73.086±3.008 b	213.424±2.262 a
		轻度胁迫 Light	–	16.929±1.672 a	5.454±2.595 b	15.437±0.446 a	32.176±20.047 b	180.466±0.424 a	138.993±11.239 b
		中度胁迫 Moderate	2.412±0.106 a	5.454±2.595 b	–	–	232.831±109.386 a	76.272±0.521 b	152.688±21.445 b
	丙泊酚 Propofol	对照 Control	–	–	0.359±0.031 a	–	–	–	–
		轻度胁迫 Light	–	–	–	0.346±0.066 a	–	1.239±0.057 a	–
		中度胁迫 Moderate	–	–	–	–	–	–	–
	百里酚 Thymol	对照 Control	–	–	1.428±0.184 a	–	–	24.079±2.477 b	–
		轻度胁迫 Light	–	–	–	1.291±0.118 a	–	82.087±2.392 a	–
		中度胁迫 Moderate	–	–	–	–	36.223±2.161 a	32.414±17.534 b	19.103±7.895 a
	甲苯 Toluene	对照 Control	–	–	–	–	–	–	–
		轻度胁迫 Light	–	–	–	–	0.648±0.676 a	–	–
		中度胁迫 Moderate	–	–	–	–	–	–	–
	苯酚 Phenol	对照 Control	–	–	–	–	2.068±0.936 b	17.056±0.872 b	22.318±10.987 b
		轻度胁迫 Light	–	–	–	–	2.909±0.155 b	61.821±0.262 a	74.479±0.672 a
		中度胁迫 Moderate	–	–	–	–	31.955±1.255 a	12.617±0.862 c	61.893±1.588 a
	香芹酚 Carvacrol	对照 Control	–	–	–	–	–	–	81.661±0.614 b
		轻度胁迫 Light	–	–	–	–	–	4.202±0.042 a	86.314±0.315 a
		中度胁迫 Moderate	–	–	–	–	65.325±4.230 a	–	–
其他类 Others	2,3-二甲基氢醌 2,3-Dimethylhydroquinone	对照 Control	2.492±0.056 a	–	–	–	–	–	–
		轻度胁迫 Light	–	–	2.854±0.069 a	–	–	–	–
		中度胁迫 Moderate	0.854±0.206 b	2.471±0.530 a	–	–	–	–	–
	偶氮二异丁腈 2,2'-Azobis（2-methyl-propionitrile）	对照 Control	2.802±0.057 a	–	–	–	2.772±0.139 a	–	–
		轻度胁迫 Light	1.844±0.057 b	6.345±0.492 a	–	–	–	–	–
		中度胁迫 Moderate	1.530±0.067 c	–	–	0.429±0.029 a	–	–	–

表 7 （续） Table 7 (Continued)

种类 Species	化合物名称 Compound name	处理 Treatment	不同时期相对含量 Relative content						
			52 d	67 d	77 d	87 d	97 d	110 d	120 d
	四甲基琥珀腈 Tetramethyl-succinotrile	对照 Control	4.525±0.365 b	6.033±0.785 a	–	8.876±0.332 a	–	–	–
		轻度胁迫 Light	5.336±0.026 a	3.303±0.163 a	5.411±0.418 b	–	6.200±0.081 a	322.424±11.792 b	1 442.574±10.481 b
		中度胁迫 Moderate	–	4.488±2.207 a	6.660±3.250 a	–	2.648±0.752 a	1 732.166±418.460 a	8 105.446±70.906 a
	乙酸铵 Ammonium acetate	对照 Control	–	–	12.010±0.322 a	–	11.293±1.219 b	322.424±11.792 b	–
		轻度胁迫 Light	–	–	–	7.266±0.016 a	–	–	–
		中度胁迫 Moderate	–	–	–	0.280±0.022 b	–	–	–
	环己酮肟 Cyclohexa-none oxime	对照 Control	–	–	2.718±0.159 a	–	–	53.420±0.039 a	10.823±0.686 c
		轻度胁迫 Light	–	–	–	2.402±0.129 a	14.215±0.143 a	130.772±85.671 a	33.694±4.263 a
		中度胁迫 Moderate	–	–	–	–	175.193±110.760 a	53.427±0.039 a	23.075±2.786 b
	2,1,3-苯并噻二唑 2,1,3-Ben-zothiadiazole	对照 Control	–	–	1.090±0.122 a	–	–	13.618±7.945 a	35.004±0.531 b
		轻度胁迫 Light	–	–	–	0.846±0.031 a	2.855±0.072 b	44.146±28.466 a	59.238±0.803 a
		中度胁迫 Moderate	–	–	–	–	49.422±24.802 a	13.618±7.945 a	–
	乙二醇苯醚 2-Phenox-yethanol	对照 Control	3.736±0.536 b	2.142±0.563 a	–	2.86±0.093 a	8.849±3.683 a	–	–
		轻度胁迫 Light	5.467±0.134 a	1.679±0.244 a	2.897±1.407 a	–	7.523±6.002 a	–	–
		中度胁迫 Moderate	1.304±0.019 c	1.442±0.387 a	2.129±0.911 a	0.837±0.123 b	–	–	–
	γ-松油烯 γ-Terpinen	对照 Control	0.535±0.096 a	0.383±0.016 a	–	–	–	–	–
		轻度胁迫 Light	–	–	–	–	–	–	–
		中度胁迫 Moderate	–	–	–	–	–	–	27.061±2.366 a
	1,4-桉叶素 1,4-Cineole	对照 Control	0.238±0.009 a	–	–	–	–	–	–
		轻度胁迫 Light	0.212±0.004 a	–	–	–	–	–	–
		中度胁迫 Moderate	–	–	–	–	–	–	–
	正己醚 dihexyl ether	对照 Control	–	0.207±0.293 a	–	–	–	–	–
		轻度胁迫 Light	–	–	–	–	–	–	–
		中度胁迫 Moderate	–	–	–	–	–	–	–
	三十六烷 hextriacon-tane	对照 Control	–	–	–	0.328±0.007 a	3.894±1.435 a	4.392±0.509 b	5.351±0.633 a
		轻度胁迫 Light	–	–	–	0.376±0.252 a	4.996±0.831 a	5.022±0.447 b	–
		中度胁迫 Moderate	–	–	–	–	4.587±0.721 a	21.539±0.754 a	–

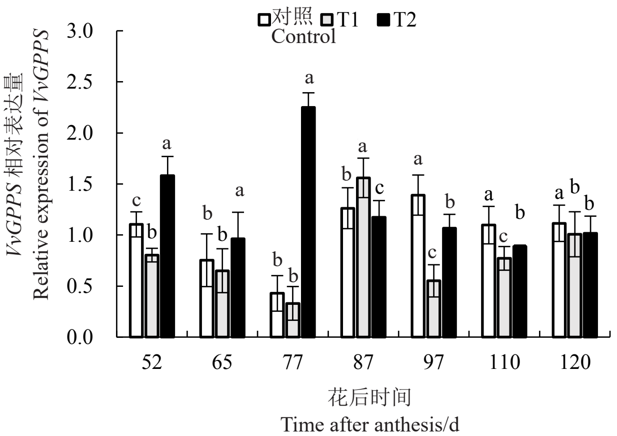

图3　水分胁迫对马瑟兰葡萄果实 *VvGPPS* 表达量的影响

Fig. 3　Effects of water stress on the expression of *VvGPPS* in Marselan grape fruit

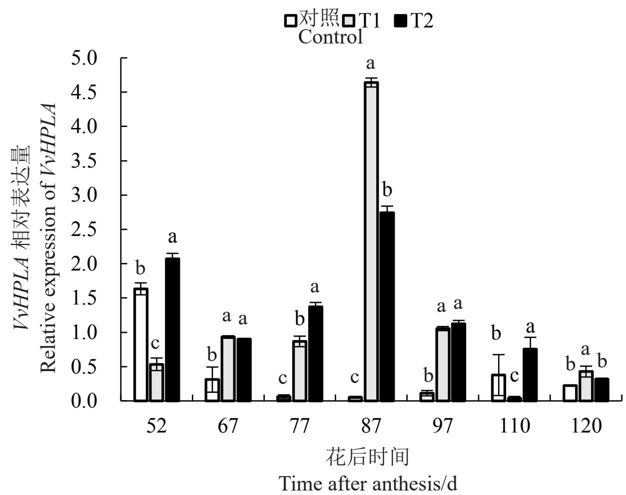

图4　水分胁迫对马瑟兰葡萄果实 *VvHPLA* 表达量的影响

Fig. 4　Effects of water stress on the expression of *VvHPLA* in Marselan grape fruit

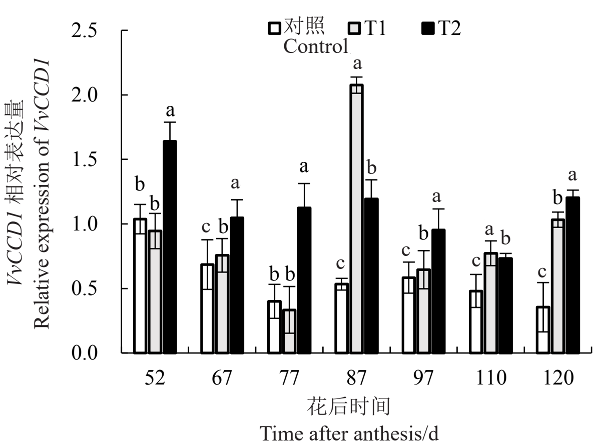

图5　水分胁迫对马瑟兰葡萄果实 *VvCCD1* 表达量的影响

Fig. 5　Effects of water stress on the expression of *VvCCD1* in Marselan grape fruit

*VvCCD1*表达量显著高于对照组和中度水分胁迫。结果表明，水分胁迫处理可以有效提高马瑟兰葡萄果实*VvCCD1*的表达量。

3　讨　论

环境因素通过影响植物基因的表达及植物体内的生理生化反应，进而调控植物的生长和次生代谢产物的变化[26-27]。水分是一切生物维持生命活动不可或缺的因素，水分匮乏已成为影响经济植物生长及产量形成的决定性环境因素[28-29]。水分不足会损害葡萄生长，降低产量，水分严重不足时会影响葡萄和葡萄酒的质量[30]。

据报道，调亏灌溉可以提高葡萄的水分利用率和抑制葡萄的营养生长，这可能会影响果实的生长和品质，特别是多酚和香气[30]。本研究中轻度水分胁迫的香气总量显著高于其他两个处理；成熟期时马瑟兰葡萄果实内醛类挥发性化合物的含量高于其他种类。本研究表明，轻度水分胁迫下马瑟兰葡萄果实内醇类和醛类挥发性物质的含量均较对照有所提高，而中度胁迫下各类挥发性物质含量较对照均降低。果实成熟过程中大多数萜醇类物质含量呈上升趋势[31]。本研究显示正己醇和芳樟醇是马瑟兰葡萄果实发育过程中含量最高的两种萜醇类化合物，二者分别具有水果和玫瑰的香气。其中正己醇的含量随水分胁迫程度的增高而增加，由此表明，水分胁迫可以提高马瑟兰葡萄果实内正己醇的含量。大马士酮是马瑟兰葡萄果实中含量最高的酮类物质，与对照相比，轻度和中度胁迫处理的果实中大马士酮含量分别降低了27.3%和43.7%，说明水分胁迫不利于大马士酮在马瑟兰葡萄果实中的积累。综上，为提高酿酒葡萄果实品质，可在实际生产中应用节水灌溉如滴灌等措施。

香叶基二磷酸合成酶基因（*VvGPPS*）为单萜合成代谢途径中期的关键基因[20]，本研究中马瑟兰葡萄果实中的*VvGPPS*表达量随果实成熟表现出先下降后上升的趋势，且水分胁迫使*VvGPPS*表达量下调。表明水分胁迫不利于*VvGPPS*的表达。研究表明异戊二烯类化合物及其衍生物是果实中一类重要的挥发性化合物，这些挥发性化合物是类胡萝卜素在类胡萝卜裂解双加氧酶（CCDs）作用下氧化分解而成的[18]，这些类胡萝卜素衍生物的C13-降异戊二烯化合物在许多植物的花、果实和叶片中存在且具

有不同的生物学作用[32]。本研究显示，整体 *VvCCD1* 表达量呈现出下降趋势且水分胁迫下 *VvCCD1* 表达量显著高于对照。植物脂氢过氧化物裂解酶（HPL）作为植物不饱和脂肪酸氧化途径中的关键酶，与植物的特有香气、抗逆反应及信号传导和老化等生理过程有关[33-34]；本研究 *HPLA* 基因表达前期，轻度和中度胁迫处理下表达量呈上升趋势，而对照逐渐下降，花后120 d，轻度胁迫表达量最高，水分胁迫可以促进 *HPLA* 基因表达量的升高；与花后52 d相比，其表达量降低。

4 结 论

综上所述，适度的水分胁迫可显著增加马瑟兰葡萄果实中挥发性有机化合物的种类和相对含量。与对照相比水分胁迫不利于 *VvGPPS* 和 *VvHPLA* 的表达，但有利于 *VvCCD1* 的表达。

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