

Article

Effects of Rootstocks on the Physicochemical Properties and Volatile Profiles of ‘Shine Muscat’ Cv Grape Grown in Hot Regions of Southern China

Zhaofei Lan ^{1,2,†}, Rongfu Wei ^{2,†}, Haiyan Chen ¹, Jiemei Liang ¹, Guo Cheng ^{2,3} , Yingfen Yu ¹, Wenrui Zheng ¹, Jing-Ke Lu ¹, Zihang Zhang ¹, Fan Zhang ¹, Fengping Pan ², Xiaoying Liang ¹, Jin-Biao Liu ^{2,*} and Sihong Zhou ^{1,*} 

¹ College of Agriculture, Guangxi University, Nanning 530004, China

² Grape and Wine Research Institute, Guangxi Academy of Agricultural Sciences, Nanning 530007, China

³ Guangxi Fruit and Vegetable Industry Technological Innovation Center, Nanning 530007, China

* Correspondence: liujinbiao9707@163.com (J.-B.L.); zhousihong@gxu.edu.cn (S.Z.)

† These authors contributed equally to this work.

Abstract

The effects of different rootstocks on the grape quality and volatile aromatic compounds of ‘Shine Muscat’ were investigated. The basic physicochemical parameters of berries from five scion–rootstock combinations (SM-Beta, SM-SO4, SM-5C, SM-Fercal, SM-YN2) and own-rooted ‘Shine Muscat’ grape were measured, and their volatile aromatic compounds were determined using headspace solid-phase microextraction (HS-SPME) combined with gas chromatography–mass spectrometry (GC-MS). Our results showed that the SM-YN2 combination exhibited the highest berry weight, and increased by 28.13% compared with SM self-rooted seedling. In addition, the ‘5C’ and ‘YN2’ rootstocks could better maintain total soluble solids (TSS), titratable acidity (TA), TSS/TA and pH in the berries, whereas the ‘Beta’, ‘SO4’ and ‘Fercal’ rootstocks impaired TSS. Volatile profiling identified 841 volatile compounds classified into 15 categories, among which terpenoids constituted the predominant contributors to berry aroma. Furthermore, 22 characteristic aroma compounds were screened, and linalool presented the highest concentration among all terpenoids in ‘Shine Muscat’ fruit. Odor activity values (OAVs) and aroma proportion analyses further revealed that linalool is the key compound for the characteristic ‘muscat’ aroma of ‘Shine Muscat’. In addition, the SM-YN2 combination exhibited 31.96% and 4.61% higher concentration and proportion of linalool compared to own-rooted vines. Notably, with the exception of ‘YN2’, ‘Beta’, ‘SO4’, ‘5C’ and ‘Fercal’ downregulated the expressions of one or more terpenoid synthesis-related genes. In conclusion, grafting onto rootstock could improve berry quality, particularly the ‘YN2’ rootstock, which yielded ‘Shine Muscat’ grapes with the highest overall quality. As a resource of the East Asian grape group, ‘YN2’ can be utilized as a rootstock in future production.



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Keywords: ‘Shine Muscat’; rootstock; volatiles; ‘Yeniang No.2’; hot regions

1. Introduction

Grapes are one of the fruits with the largest planting area and highest production in the world, and China is the world’s largest producer and consumer of table grapes [1]. In 2024, the table grape production of China is 14.2 million tons, accounting for 43% of the world’s total production [2]. ‘Shine Muscat’ grape is a mid-to-late maturing table cultivar bred in Japan from a cross of Akitsu-21 (*Vitis labruscana* × *V. vinifera*) and Hakunan (*V.*

vinifera) [3], characterized by goldish-green berries with a lustrous surface, crisp flesh, thin skin and a pleasantly strong muscat aroma. As a popular table grape cultivar, ‘Shine Muscat’ is widely planted and consumed in Asian areas, especially in China and Japan, due to its exceptional fresh-eating quality [4].

Rootstock grafting, a practice widely used to enhance adaptability in viticulture, not only improves scion growth habits and fruit quality but also significantly enhances resistance caused by biotic and abiotic stress, as demonstrated by the fact that grafting saved the European grape and vine industry from the terrible impacts of phylloxera (*Daktulosphaira vitifoliae* Fitch) from the year 1864 [5]. Although the mechanism of the biochemical interaction between scions and rootstocks is still unresolved, numerous studies have reported the effects that various rootstocks have on the quality and stress resistance of grapevines [6–8]. Research on the effects of grafting on grapevines has primarily focused on flavor compound accumulation [9,10], antioxidant properties [11–14] and stress resistance traits [15–18], while research on the effects of grafting on table grapes has mainly focused on yield [19–21], postharvest storage quality [22] and fruit maturity [23]. In addition, previous reports have studied the use of wild grape resources from the East Asian group as rootstocks for grafting and their effects on the growth and quality of scion varieties including Shanputao (*V. amurensis*), Spine grape (*V. davidii*) and *V. heyneana* grape [24–26]. These wild grape species constitute vital genetic resources for rootstock cultivation and breeding programs targeting desirable agronomic traits [27]. Our team previously conducted grafting trials using *V. heyneana* var. *adenoclada* grapes as rootstocks and found that the critical greenwood grafting period can improve the survival rate. However, research remains relatively limited regarding how *V. heyneana* var. *adenoclada* grapes modify scion fruit quality, particularly berry sensory attributes and aroma compounds, when used as rootstocks.

Terpenes, especially monoterpenes, have been identified as the source of the characteristic aroma of table grapes. Further studies have indicated that compounds such as linalool, nerol and geraniol provide the characteristic aromas of ‘Shine Muscat’ grape [28,29]. Terpenes are produced through two distinct biosynthetic pathways: the cytosol-localized mevalonic acid (MVA) pathway and the plastid-localized 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway [30]. While rootstocks have been utilized primarily in response to biotic and abiotic challenges in specific vineyards in the past, it has been demonstrated that rootstocks can also alter the aroma quantity and components of grapes, with growing consumer emphasis on the quality traits of table grapes [31–33]. Aromatic compound distribution and composition vary significantly across grape varieties and genetics. Since a rich aroma is an important quality characteristic in grapes, numerous studies have emerged on the aroma of table grapes. However, the mechanisms of how rootstocks influence the volatile profiles of grapes are still unknown.

To improve both the stress resistance and quality of berries, we used five rootstock varieties—‘Beta’, ‘SO4’, ‘5C’, ‘Fercal’ and ‘Yeniang No.2’ (‘YN2’)—for grafting with ‘Shine Muscat’ (SM) grape. In the present study, we document the effects of different rootstocks on the physicochemical properties and volatile profiles of ‘Shine Muscat’ grape, using headspace solid-phase microextraction (HS-SPME) combined with gas chromatography–mass spectrometry (GC-MS) to determine their volatile aromas. This study provides a theoretical and practical reference for enhancing the fruit edible value and flavor quality of ‘Shine Muscat’ grapes in humid subtropical regions in southern China.

2. Materials and Methods

2.1. Plant Materials and Treatment

Grafted and own-rooted SM grapes were grown at the Mingyang vineyard of the Guangxi Academy of Agricultural Sciences (108°14' E, 22°50' N), Nanning, China, which is situated in a low-latitude zone characterized by a subtropical monsoon climate. The vineyard is on improved neutral yellow soil with medium fertility. Healthy SM grape buds were grafted as greenwood onto five different rootstocks ('Beta', 'SO4', '5C', 'Fercal' and 'YN2') (Table 1), and SM grape own-rooted vines were used as the control group. On 9 May 2023, SM grape was grafted with five rootstocks through cleft grafting, and the grafting site was wrapped with biodegradable eco-friendly rice paper grafting film [34]. When performing greenwood grafting, the length of the scion was about 4–5.5 cm. The grafting cleft of the rootstock and the whole scion were wrapped so that the vascular cambium of the rootstocks and scions were tightly united and attached symbiotically. After the grafting treatment was completed, irrigation was conducted immediately until the soil was completely moist. Each scion–rootstock combination contained six vines with uniform growth. Three biological replicates are set for each treatment, with two vines constituting one biological replicate. All experimental SM vines were grown in a horizontal trellis system with a spacing of 1 m × 3 m. The vineyard adopts simple rain-shelter cultivation, with the ground surface covered by horticultural ground cloth, and uses integrated water and fertilizer method.

Table 1. Information on five grape rootstock varieties.

Rootstock Varieties	Species
Beta	<i>Vitis riparia</i> × <i>Vitis labrusca</i>
SO4	<i>Vitis berlandieri</i> × <i>Vitis riparia</i>
5C	<i>Vitis berlandieri</i> × <i>Vitis riparia</i>
Fercal	<i>Vitis berlandieri</i> × <i>Vitis vinifera</i>
YN2	<i>Vitis heyneana</i> var. <i>adenoclada</i>

Experimental berries were collected when they reached physiological maturity. Thirty berries were collected for each biological replicate, totaling 90 berries per treatment. All samples were collected from the top, middle and bottom parts of the clusters, and both sides of the trellis were taken into account. For each treatment, nine berries were randomly taken from every biological replicate for the determination of grape physicochemical indexes, and the remaining berries were frozen in liquid nitrogen and then stored at −80 °C for qRT-PCR and metabolomics analysis.

2.2. Measurement of Physicochemical Index

Berry weight and longitudinal/transverse diameters were measured using an analytical balance and a fruit diameter measuring ruler, respectively. The total soluble solids (TSS) content and pH value were determined using a handheld digital refractometer (PAL-1, ATAGO, Tokyo, Japan) and a pH meter (AZ8601, AZ Instrument, Taiwan, China), respectively. Titratable acidity (TA) was quantified through acid–base titration, and the results are expressed as grams per liter of tartaric acid equivalent (g/L). Fruit color parameters (L^* , a^* , b^*) were analyzed using a chromatic aberration meter (CR-10, Konica Minolta, Tokyo, Japan). Specifically, the L^* value represents luminance on a scale of 1–100, where a higher value indicates greater pericarp brightness. The a^* value quantifies red–green chromaticity ($+a^*$ = red, $-a^*$ = green), while the b^* value measures yellow–blue chromaticity ($+b^*$ = yellow, $-b^*$ = blue). All measurements were conducted in triplicate for each treatment group, and the results are expressed as the mean ± standard deviation.

2.3. Metabolomics Analysis

2.3.1. Extraction of Volatile Aroma Compound from Berries

Grape berries were deseeded and thoroughly ground in liquid nitrogen. The homogenized berry tissues were vortex-mixed, and approximately 500 mg of each powdered sample was transferred to 20 mL headspace vials and mixed with saturated NaCl solution and 20 μ L of 10 μ g/mL 3-Hexanone. All vials were equilibrated at 60 °C for 5 min with constant agitation (700 rpm) using headspace solid-phase microextraction (HS-SPME). A pre-conditioned 120 μ m SPME fiber (DVB/CWR/PDMS, Agilent, CA, USA) was subsequently exposed to the vial headspace for 15 min of volatile adsorption. Thermal desorption was performed in the GC inlet at 250 °C for 5 min, followed by GC-MS chromatographic separation and identification. For each treatment, three sample extractions were performed corresponding to biological replicates.

2.3.2. Gas Chromatography/Mass Spectrometry Analysis

The volatile compounds were identified and quantified in an Agilent 8890 gas chromatograph coupled with a 7000D mass spectrometer equipped with a DB-5MS chromatographic column (30 m $\times$ 0.25 mm $\times$ 0.25 μ m, Agilent, CA, USA). High-purity helium was employed as the carrier gas, with a constant flow rate of 1.2 mL/min, while the injection port temperature was maintained at 250 °C. The GC oven temperature was programmed initially at 40 °C with a 3.5 min hold, followed by three successive ramps—an increase first to 100 °C at 10 °C/min, then up to 180 °C at 7 °C/min and finally up to 280 °C at 25 °C/min—concluding with a 5 min isothermal phase at 280 °C. The mass spectrometer operated in electron ionization (EI) mode at 70 eV, with optimized temperature parameters for the ion source, quadrupole and transfer line at 230 °C, 150 °C and 280 °C, respectively. The acquisitions were performed with selected ion monitoring (SIM). Three analytical tests were performed for each treatment, corresponding to three biological replicates.

2.3.3. OAV Analysis

The odor activity values (OAVs) were calculated by dividing the relative concentration of a compound by its odor threshold from the literature [35,36].

2.3.4. qRT-PCR Analysis

Total RNA was extracted from grape berries using the TIANGEN, Beijing, China RNApure Pure Plant Kit (Polysaccharides & Polyphenolics), and cDNA synthesis was performed via reverse transcription with the PrimeScript™ FAST RT Kit (Takara, Shiga, Japan). The expression levels of key enzyme-encoding genes involved in aroma biosynthesis pathways (MEP and MVA pathways), including *DXS1*, *DXS3*, *DXR*, *GPPS*, *FPPS*, *LIS* and *TPS*, were quantitatively analyzed using quantitative real-time PCR (qRT-PCR), with *EF1- α* serving as the reference gene. Gene expression quantification was performed using the $2^{-\Delta\Delta C_t}$ method. The primer sequences for qRT-PCR amplification are detailed in Table 2. Three extractions and detections were performed for each treatment, corresponding to three biological replicates.

Table 2. Primer sequences for qRT-PCR amplification.

Gene	Forward Primer 5' $\rightarrow$ 3'	Reverse Primer 5' $\rightarrow$ 3'
<i>DXS1</i>	F: CTCATTTCCTGCCCATTTTAGC	R: CTTACTCCTTTGCTGGGATTGG
<i>DXS3</i>	F: GAAGGCTCTGTTGGAGGGTTT	R: TCCTCTGGTGATGCCTGTTCT
<i>DXR</i>	F: AGAGGCTTTGGCTGACTGTGA	R: AACCTGCGCAACCTACTATTCC

Table 2. Cont.

Gene	Forward Primer 5' → 3'	Reverse Primer 5' → 3'
GPPS	F: AGAATCTGGGATTGGCATTCC	R: TGGCGGATGTCAGACAATGA
FPPS	F: ATTGCTTATGGCAGGCGAAA	R: CCGTTCCGATCTTACCAATCAC
LIS	F: TGGGATTCTCTCCTGCCTTTT	R: GCAGTAGGCACAAGCACAACA
TPS	F: TGAAGGGAATGCTCTGCTTGT	R: TGTTTTGCTCAAGGCCCTTT
EF1- α	F: GAACTGGGTGCTTGATAGGC	R: AACCAAAATATCCGGAGTAAAAGA

2.4. Statistical Analysis

The experimental data were analyzed using Microsoft Excel 2019 for statistical calculations. One-way analysis of variance (ANOVA) was performed using the Metware Cloud, a free online platform for data analysis (<https://cloud.metware.cn>) to assess intergroup differences, followed by Duncan's new multiple range test ($p < 0.05$). All the data in this experiment are presented as the average of three biological replicates.

3. Results

3.1. Effects of Rootstocks on 'Shine Muscat' Berry Basic Physicochemical Parameters

Five scion–rootstock combinations had significant effects on the physicochemical indexes of 'Shine Muscat' grapes (Table 3). SM-YN2 exhibited the highest berry weight and largest transverse diameter, and increased by 21.96% and 10.29% compared with SM self-rooted seedling, followed by SM-Beta. SM-Beta, SM-5C and SM-YN2 significantly reduced the fruit shape index by increasing the transverse diameter of the berries while not changing or reducing the longitudinal diameter of the fruit. The total soluble solids (TSS) content of grapes from SM-5C and SM-YN2 showed no significant differences compared to own-rooted vines. In contrast, SM-Beta, SM-SO4 and SM-Fercal demonstrated a significantly lower TSS content than own-rooted vines. Furthermore, pH values and titratable acid (TA) content showed no significant differences between most grafted combinations and own-rooted vines, with the exception of SM-SO4. SM-SO4 and SM-Fercal significantly reduced the TSS/TA ratio, while the other treatments showed no significant difference compared to the self-rooted seedlings. These results indicate that grafting onto '5C' or 'YN2' rootstocks could better maintain the basic physicochemical indicators of the fruit. For color coordinates, all combinations had similar L^* and a^* values, displayed lustrous yellow-green pericarps, and had no significant differences compared with own-rooted grapevines. In addition, SM-Beta, SM-5C and SM-YN2 showed similar and higher b^* values compared with the rest of the combinations (Table 3). In summary, the SM-YN2 combination is most conducive to stabilizing and increasing yield, as well as achieving good fruit maturity.

Table 3. Basic physicochemical parameters of the berries of different scion–rootstock combinations.

Combinations	SM	SM-Beta	SM-SO4	SM-5C	SM-Fercal	SM-YN2
Berry weight (g)	9.49 c $\pm$ 0.38	10.60 b $\pm$ 0.21	9.18 c $\pm$ 0.18	9.48 c $\pm$ 0.31	9.15 c $\pm$ 0.08	12.16 a $\pm$ 0.34
Longitudinal diameter (cm)	3.10 ab $\pm$ 0.06	3.03 bc $\pm$ 0.05	2.95 c $\pm$ 0.02	2.96 c $\pm$ 0.05	3.00 bc $\pm$ 0.08	3.18 a $\pm$ 0.06
Transverse diameter (cm)	2.43 cd $\pm$ 0.06	2.53 b $\pm$ 0.01	2.40 cd $\pm$ 0.05	2.46 c $\pm$ 0.03	2.36 d $\pm$ 0.02	2.68 a $\pm$ 0.02
Fruit shape index	1.28 a $\pm$ 0.04	1.20 b $\pm$ 0.02	1.23 ab $\pm$ 0.02	1.20 b $\pm$ 0.02	1.27 a $\pm$ 0.04	1.19 b $\pm$ 0.03
TSS ($^{\circ}$ Brix)	19.27 a $\pm$ 0.91	16.87 b $\pm$ 0.47	15.57 c $\pm$ 0.80	18.93 a $\pm$ 0.46	17.53 b $\pm$ 0.47	18.90 a $\pm$ 0.89
pH	4.06 ab $\pm$ 0.07	4.16 a $\pm$ 0.01	3.77 c $\pm$ 0.10	3.98 b $\pm$ 0.04	3.97 b $\pm$ 0.06	4.01 b $\pm$ 0.05
TA (g/L)	3.46 bc $\pm$ 0.02	2.81 c $\pm$ 0.22	4.59 a $\pm$ 0.77	3.61 b $\pm$ 0.16	3.98 ab $\pm$ 0.28	3.35 bc $\pm$ 0.13
TSS/TA ratio	55.65 a $\pm$ 2.88	60.38 a $\pm$ 6.35	34.70 c $\pm$ 6.88	52.53 ab $\pm$ 3.46	44.26 b $\pm$ 4.09	56.55 a $\pm$ 4.40
L^*	35.63 ab $\pm$ 0.47	36.75 a $\pm$ 0.50	35.14 b $\pm$ 0.57	34.93 b $\pm$ 0.54	35.66 ab $\pm$ 0.41	36.55 a $\pm$ 1.12
a^*	−1.87 ab $\pm$ 0.05	−1.81 a $\pm$ 0.10	−2.16 b $\pm$ 0.18	−1.99 ab $\pm$ 0.04	−1.87 ab $\pm$ 0.20	−2.14 ab $\pm$ 0.19
b^*	7.87 c $\pm$ 0.37	9.41 a $\pm$ 0.51	8.06 bc $\pm$ 0.92	8.96 abc $\pm$ 0.53	7.87 c $\pm$ 0.76	9.17 ab $\pm$ 0.62

Different letters after the mean values in the same column indicate statistically significant differences ($p < 0.05$).

3.2. Volatile Profiles in ‘Shine Muscat’ Berry

The volatile compound compositions of five different scion–rootstock combinations and own-rooted vines were analyzed using the GC-MS platform, and a total ion current chromatogram of volatile compounds in SM grape berries was obtained (Figure S1). A total of 841 volatile compounds were identified in these samples, and these compounds were classified into 15 categories, including terpenoids, esters, ketones, heterocyclic compounds, alcohols, hydrocarbons and aldehydes, with total concentrations ranging from 0.78 to 217.54 µg/g (Figure 1B, Table S1). Among these compounds, terpenoids contributed the most to the aroma (18.43%), followed by esters (17.24%) (Figure 1B).

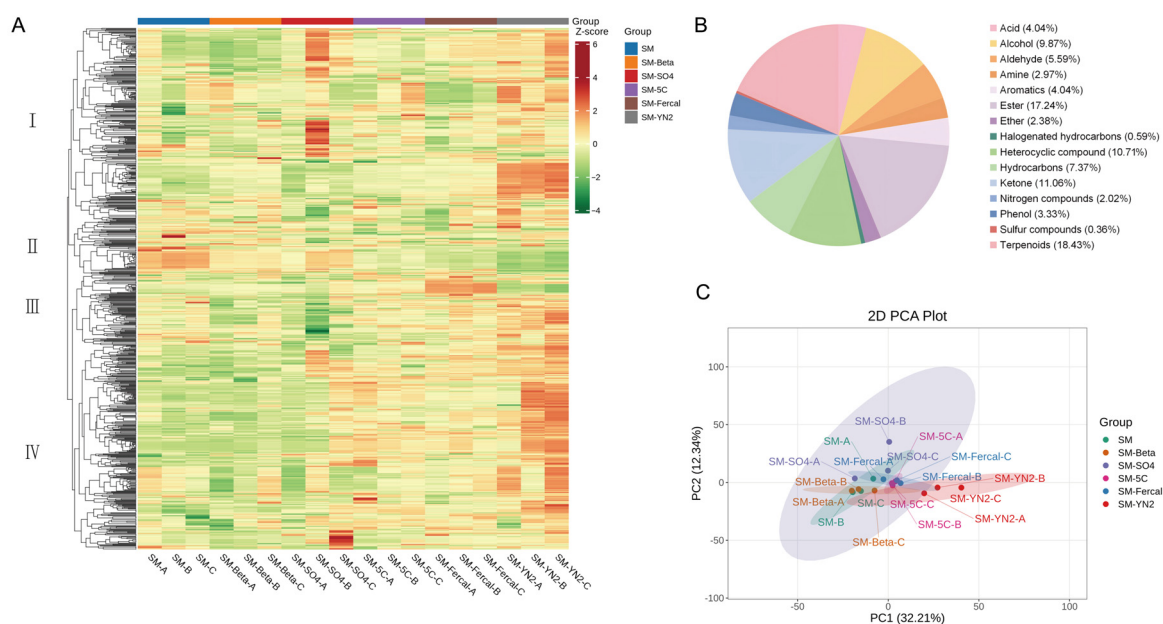


Figure 1. Overview of metabolomics changes in grape berries from different treatments. Hierarchical cluster analysis (A); classification and proportion of 841 volatile compounds detected in grape berries (B); principal component analysis (PCA) (C).

A hierarchical cluster analysis of volatile compounds in SM, SM-Beta, SM-SO4, SM-5C, SM-Fercal and SM-YN2 berries was performed. As shown in Figure 1A, all the identified metabolites were divided into four groups through horizontal clustering. The concentration of volatile compounds in Cluster I was highest in SM-SO4 and SM-YN2, the concentration of volatile compounds in Cluster II was highest in SM own-rooted vines, and the concentration of volatile compounds in Clusters III and IV was highest in SM-YN2. Therefore, the concentration of the most volatile compounds was higher in SM-YN2 than in the other treatments. The above research results indicate that YN2 as a rootstock is conducive to the accumulation of aroma substances in ‘Shine Muscat’ grapes.

The results of the PCA showed that the first two principal components explained 32.21% and 12.34% of the total variance, respectively (Figure 1C). The first principal component effectively separated SM-YN2 from the own-rooted vine (SM) and the rest of the combinations (Figure 1C), which indicated that the overall volatile metabolites of SM-YN2 differed significantly from SM and the other combinations.

3.3. Characteristic Aroma and Odor Profiles in ‘Shine Muscat’ Berry

To determine the effects of rootstocks on the characteristic aroma of grapes, the volatile terpenoids in berries from five combinations and own-rooted vines were examined. In total, 22 major terpenoids were identified in these samples, and Table 4 shows significant differences in the terpenoids of the five combinations. Linalool, (*E*)-linalool oxide (furanoid),

menthol, neral, β -cyclocitral, γ -terpinene, 6,10-dimethyl-5,9-undecadien-2-one, β -pinene, (+)-4-carene and ionone had a relatively higher abundance in the five combinations and in 'Shine Muscat' own-rooted vines, in which their concentration exceeded 10 ng/g. Linalool had the highest concentration among all terpenoids in 'Shine Muscat' fruit. Notably, the concentration of linalool in the 'YN2' rootstock combination increased by 31.96% compared to the control group, and was significantly higher than in other treatments. The concentrations of (*E*)-linalool oxide (furanoid), β -pinene, (+)-4-carene, citral, geranyl isobutyrate and α -isomethyl ionone in the fruits from the 'YN2' rootstock grafting treatment were also significantly higher than those in the control. In addition to 'YN2', the 'Fercal' rootstock was able to significantly increase the concentration of some terpenoids, such as linool, (*E*)-linalool oxide (furanoid), β -pinene, (+)-4-carene, geranyl isobutyrate and limonene oxide. '5C', 'Fercal' and 'YN2' rootstocks significantly reduced the concentration of p-cymene in 'Shine Muscat' fruit, and the total concentration of characteristic aroma was significantly higher in the SM-YN2 and SM-Fercal combinations compared to other treatments and the control group, with SM-YN2 exhibiting the highest concentration among all treatments. No significant differences were observed between the other treatments and the control, indicating that 'YN2' and 'Fercal' rootstocks exclusively demonstrated a positive effect on terpene enhancement, both for individual compounds and for the total concentration.

Though hundreds of volatile terpenoids were detected in each grape sample, not all of these components had a major impact on the overall aroma character of these fruits. To evaluate the contribution of various volatile compounds to the olfactory characteristics of this fruit, OAVs of terpenoids in the combinations were calculated from the averages of analytical relative concentrations and published odor thresholds (Table 5) in water. In general, only compounds whose OAVs are above 1 can be considered to directly contribute to grape aroma (Table 6). It should be noted that there were only three odor-active volatiles with OAVs higher than 1 in SM grapes. The OAVs of ionone and β -cyclocitral were above 9 and 22, with the former contributing primarily to sweet and floral aromas and the latter contributing to herbal and rose aromas. The third, with an OAV above 100, was linalool, which contributes to floral and green aromas. It is worth noting that the OAV value of SM-YN2 increased by 31.96% compared to the control group. Other terpenes with OAVs greater than 0.1 but less than 1 were p-cymene, (*E*)-linalool oxide (furanoid), citronellol, geranyl isobutyrate and α -isomethyl ionone, which are classified as background flavor compounds. Although they do not dominate the overall flavor profile, these compounds contribute to sensory qualities through a nuanced modulation of complexity and layered perception.

We statistically analyzed the proportional contribution of 16 characteristic aroma-active compounds with calculable OAVs and visualized the data using bar chart. As illustrated in Figure 2, linalool consistently constituted over 70% of the characteristic aroma profile across all sample groups, with the SM-YN2 group in particular exhibiting the highest linalool proportion at 77.53%. (*E*)-linalool oxide (furanoid) represented the second highest proportion compared to the rest of the quantified compounds. Significantly, the compounds (*E*)-linalool oxide (furanoid), menthol, neral, β -cyclocitral, p-cymene, citronellol and ocimene had decreased levels in the SM-YN2 combination compared to the control group. The proportion of (*E*)-linalool oxide in the YN2 combination was significantly lower than in the control and other treatments, with a value of 8.67%. These results indicate that linalool is the primary contributor to the characteristic aroma of 'Shine Muscat' grape berries, and that this compound was present in a higher proportion within the SM-YN2 group. Therefore, YN2 as the rootstock not only helps to increase the total aroma, but also contributes to the accumulation of the characteristic aroma of 'Shine Muscat' grapes.

Table 4. Concentrations (ng/g) of terpenoids in the berries of different scion–rootstock combinations. Data are means (n = 3). The aroma compounds are listed on the left of the concentration arrays, and the color scale is shown at the bottom. The highest concentrations for each compound are presented in red; otherwise, green is used.

Compounds	RI	SM	SM-Beta	SM-SO4	SM-5C	SM-Fercal	SM-YN2
Linalool	1101	657.62 cd	708.73 bc	648.13 d	713.70 bc	754.17 b	867.79 a
(E)-linalool oxide (furanoid)	1075	86.70 c	87.79 bc	85.01 c	88.87 bc	93.09 ab	97.00 a
Menthol	1177	30.82 ab	30.60 ab	28.96 b	30.10 ab	30.63 ab	31.39 a
Neral	1240	25.79 a	23.52 a	23.75 a	24.49 a	26.58 a	25.65 a
β-cyclocitral	1227	23.64 a	22.95 a	24.78 a	23.16 a	24.72 a	24.23 a
γ-terpinene	1060	16.27 a	16.22 a	18.13 a	17.84 a	17.69 a	19.86 a
6,10-dimethyl-5,9-undecadien-2-one	1452	15.29 a	16.86 a	18.03 a	23.68 a	22.22 a	20.10 a
β-pinene	980	12.79 b	11.38 b	16.33 a	17.04 a	17.18 a	18.35 a
(+)-4-carene	1009	12.22 b	12.83 ab	11.99 b	12.54 b	14.00 a	14.04 a
Ionone	1435	9.22 a	9.94 a	9.22 a	10.82 a	10.40 a	10.41 a
Citronellol	1228	6.51 a	5.78 a	4.44 a	4.30 a	4.40 a	2.88 a
p-cymene	1026	6.03 a	5.48 ab	5.37 ab	4.50 bc	4.69 bc	4.26 c
Citral	1273	3.10 c	3.40 c	4.02 bc	4.72 ab	3.31 c	5.16 a
Ocimene	1049	2.92 a	3.04 a	3.19 a	3.14 a	3.23 a	3.11 a
Geranic acid	1356	2.33 a	2.26 a	1.93 a	2.46 a	2.64 a	2.26 a
(E)-geranic acid methyl ester	1322	2.24 b	2.22 b	2.62 ab	3.17 a	2.87 ab	2.75 ab
Geranyl isobutyrate	1514	2.09 c	2.08 c	2.30 bc	3.22 a	2.99 ab	3.46 a
D-limonene	1031	1.71 b	1.93 ab	2.31 a	2.16 ab	2.19 ab	2.14 ab
α-isomethyl ionone	1480	1.21 c	1.17 c	1.70 bc	2.17 ab	1.85 abc	2.50 a
Terpinen-4-ol	1181	1.04 ab	1.03 ab	0.28 b	1.53 a	1.54 a	1.16 ab
Limonene oxide	1133	0.78 b	1.11 ab	1.19 ab	1.11 ab	1.22 a	1.10 ab
(Z)-3,7-dimethyl-2,6-octadien-1-ol, acetate	1365	0.26 a	0.27 a	0.34 a	0.36 a	0.38 a	0.38 a
Total		920.60 cd	970.61 bcd	914.01 d	995.07 bc	1042.00 b	1159.99 a



relative
row min row max

Different letters after the mean values in the same column indicate statistically significant differences ($p < 0.05$).

Table 5. Aroma description and odor threshold of terpenoids [37–39].

Compounds	Odor Description	Threshold (μg/g)
Citral	Sharp, lemon, sweet	0.1
(+)-4-carene	-	-
(E)-geranic acid methyl ester	Flowery, green, fruity	-
D-limonene	Citrus	0.034
β-pinene	Dry, woody, resinous, pine, hay, green	0.14
p-cymene	Gasoline, citrus	0.0114
Geranic acid	Green	-
Geranyl isobutyrate	Sweet, floral, fruity, green, peach, apricot, rose	0.013
Neral	Sweet, citral, lemon, peel	1
β-cyclocitral	Tropical, saffron, herbal, clean, rose, sweet, tobacco, damascone, fruity	0.003
γ-terpinene	Oily, smoky	2.1
α-isomethyl ionone	Floral, fruity, powdery, violet, woody, tea	0.01
Citronellol	Floral, rose, lime	0.04
Linalool	Floral, green	0.006
(E)-linalool oxide (furanoid)	Flowery	0.19

Table 5. Cont.

Compounds	Odor Description	Threshold (µg/g)
Ionone	Sweet, woody, floral, violet, orris, tropical, fruity	0.00378
Ocimene	Sweet, herbal	0.034
Menthol	Minty	0.9
Limonene oxide	Fresh, citrus, minty, spearmint, herbal	0.1
(Z)-3,7-dimethyl-2,6-octadien-1-ol, acetate	Floral, rose, soapy, citrus, dewy, pear	2
6,10-dimethyl-5,9-undecadien-2-one	Fresh, rose, leafy, floral, green, magnolia, aldehydic, fruity	-
Terpinen-4-ol	Turpentine	1.2

Table 6. OAVs of terpenoids in ‘Shine Muscat’ grape berries.

Compounds	SM	SM-Beta	SM-SO4	SM-5C	SM-Fercal	SM-YN2
Linalool	109.60	118.12	108.02	118.95	125.70	144.63
β-cyclocitral	7.88	7.65	8.26	7.72	8.24	8.08
Ionone	2.44	2.63	2.44	2.86	2.75	2.75
p-cymene	0.53	0.48	0.47	0.39	0.41	0.37
(E)-linalool oxide (furanoid)	0.46	0.46	0.45	0.47	0.49	0.51
Citronellol	0.16	0.14	0.11	0.11	0.11	0.07
Geranyl isobutyrate	0.16	0.16	0.18	0.25	0.23	0.27
α-isomethyl ionone	0.12	0.12	0.17	0.22	0.19	0.25
β-pinene	0.09	0.08	0.12	0.12	0.12	0.13
Ocimene	0.09	0.09	0.09	0.09	0.09	0.09
D-limonene	0.05	0.06	0.07	0.06	0.06	0.06
Menthol	0.03	0.03	0.03	0.03	0.03	0.03
Citral	0.03	0.03	0.04	0.05	0.03	0.05
Neral	0.03	0.02	0.02	0.02	0.03	0.03
Limonene oxide	0.01	0.01	0.01	0.01	0.01	0.01
γ-terpinene	0.01	0.01	0.01	0.01	0.01	0.01

3.4. Integrated Analysis of Aroma Biosynthetic Pathways and Related Gene Expression

Gene expression analyses of seven terpene biosynthesis genes were performed using qRT-PCR across the six different samples. The expression levels of six genes from the MEP pathway and one from the MVA pathway are shown in Figure 3. The results show that SM-Beta, SM-SO4 and SM-Fercal significantly downregulated *DXS3* expression levels, while other rootstocks showed no significant differences compared to own-rooted vines. SM-Beta and SM-SO4 markedly downregulated *DXR* expression levels, with SM-SO4 additionally downregulating *GPPS*. SM-5C significantly downregulated *FPPS* expression, while SM-SO4, SM-5C and SM-Fercal downregulated *TPS* expression. None of the grafted combinations significantly affected *DXS1* or *LIS* expression. These results demonstrate that all scion–rootstock combinations except SM-YN2 variably downregulated key enzyme genes in the terpenoid biosynthesis pathway, suggesting that most rootstocks may reduce the synthesis of floral–fruity aroma compounds in SM grapes, potentially compromising flavor quality. Notably, the ‘YN2’ rootstock exhibited neutral effects on terpenoid-related gene expression, preserving the aromatic profile of grapes.

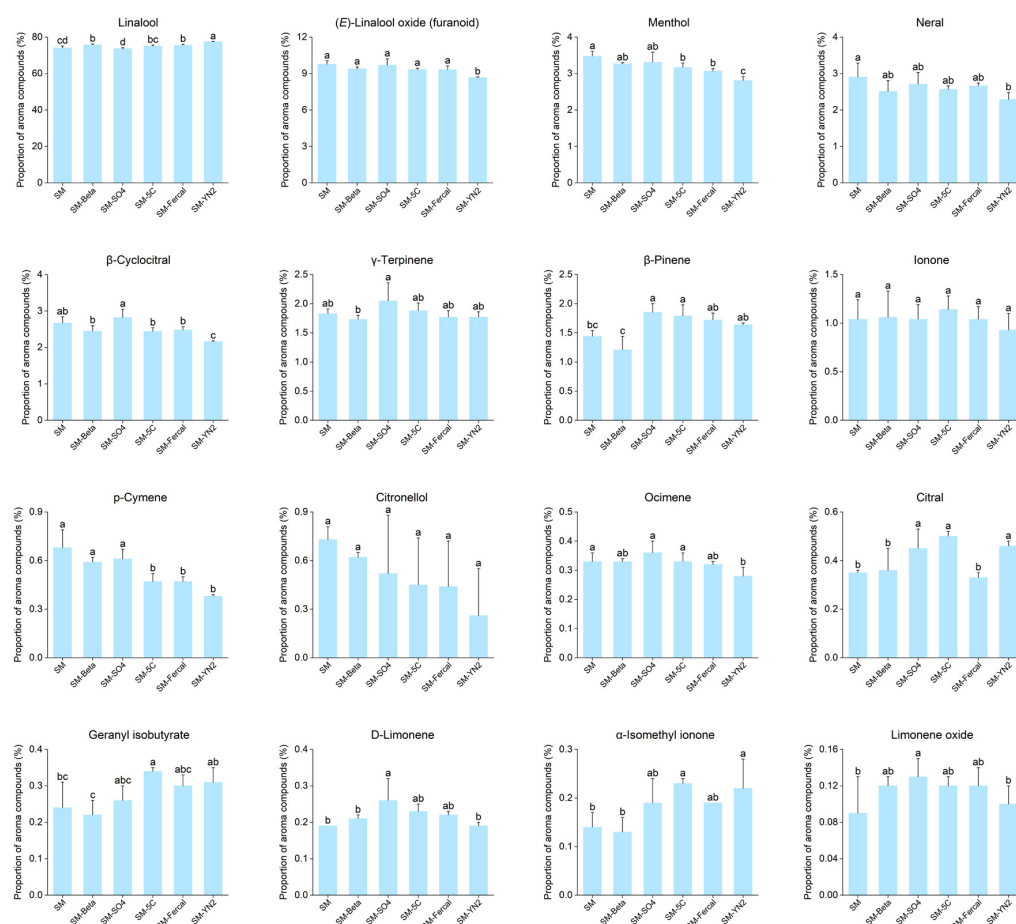


Figure 2. Proportions of 16 characteristic aroma compounds. Different letters indicate statistically significant differences ($p < 0.05$).

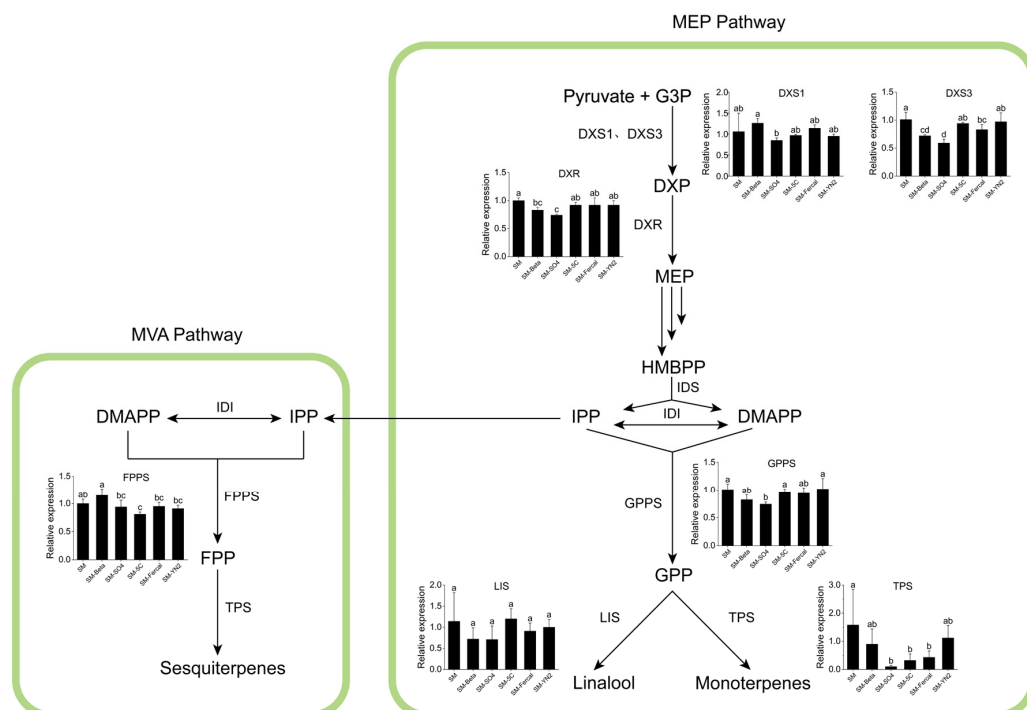


Figure 3. Expression levels of aroma synthesis-related genes in SM grape berries from different rootstocks. Different letters indicate statistically significant differences ($p < 0.05$).

4. Discussion

Grafting grapevines onto resistant rootstocks is an effective method for improving berry quality and overcoming biotic and abiotic stress constraints [23]. In this study, we investigated the performance of ‘Shine Muscat’ table grapes on five rootstocks: ‘Beta’, ‘SO4’, ‘5C’, ‘Fercal’ and ‘Yeniang No.2’ (YN2). Previous studies have indicated that rootstock selection can affect berry weight in grafted grapevines [40]. Chen et al. [33] speculated that the berry fresh weight might increase when using *V.vinifera* × *V.labrusca* varieties as rootstocks, while Klimek et al. [13] found that the ‘125AA’ rootstock significantly exerted the best effect on the yield [8]. Lin et al. [26] clarified that using ‘Kyoho’ as a rootstock for grafting ‘Shine Muscat’ can increase the weight of fruit clusters and berries. In the present study, ‘YN2’ and ‘Beta’ rootstocks exhibited a higher berry weight than the own-rooted vines, while significantly reducing the fruit shape index. This indicates that selecting a suitable rootstock can improve the fruit characteristics and increase the yield of the scion variety. Sugar and acid profiles determine, to a great extent, the sensory attributes and flavor complexity in table grapes, and rootstocks can change the sugar and acid content of berries. Research has shown that the ‘1103P’ rootstock promoted the ripening of ‘Merlot’ berries, and the total soluble solids content and titratable acid content were 29.33 g/L and 0.95 g/L higher, respectively, than those of Merlot own-rooted vines [31]. ‘110R’, ‘SO4’ and ‘Kangzhen 3’ rootstocks optimized the sugar–acid balance and enhanced oenological quality in ‘Cabernet Sauvignon’ berries by elevating NAD-MDH enzyme activity and upregulating its gene expression, thereby promoting malic acid accumulation while reducing oxalic and citric acid contents [41]. Wang et al. [42] found that ‘1103P’ and ‘5BB’ as rootstocks significantly increased the soluble solids content of ‘Shine Muscat’ fruit, while significantly decreasing the titratable acidity content. In the present study, ‘5C’ and ‘YN2’ rootstocks could better maintain TSS, TA, TSS/TA and pH levels, whereas ‘Beta’, ‘SO4’ and ‘Fercal’ rootstocks reduced TSS in grape berries. The above results indicate that rootstock grafting can have positive or negative effects on fruit maturity and basic physicochemical indicators. For this study, the ‘YN2’ rootstock increased fruit weight but also maintained maturity without adverse effects, demonstrating that the use of *V. heyneana* var. *adenoclada* grapes as rootstocks can ensure the preservation of ‘Shine Muscat’ fruit flavor quality.

Terpenoids, mainly synthesized via the MEP and MVA pathways, have been recognized as one of the most important groups of volatile compounds in the aroma of most table grapes [30]. In particular, the characteristic ‘muscat’ aroma in ‘Shine Muscat’ berries primarily originates from monoterpenoid compounds, including linalool, citronellol, neral, terpineol and geraniol [43,44]. These volatile constituents not only impart floral and fruity notes to the berries, but their concentrations and compositional profiles critically dictate the intensity and typicality of ‘muscat’ aroma in grapes. In cold climate regions, some studies have found that grafting on rootstocks such as ‘SO4’ and ‘Beta’ has a positive effect on the synthesis and accumulation of aromatic substances for ‘Shine Muscat’ [45,46]. Wang et al. [45] demonstrated that ‘Shine Muscat’ grafted onto ‘Beta’ rootstock conferred an increase in the concentration of volatile aroma compounds in the berry juice, whereas the use of ‘3309C’ rootstock resulted in a reduction in these compounds. Research by Liu et al. [46] indicated that ‘SO4’ and ‘Beta’ rootstocks played a promotive role in the development of berry aroma in ‘Shine Muscat’ grape. The ‘YN2’ grape (*V. heyneana* var. *adenoclada*), native to Guangxi province of China, is adapted to tropical and subtropical climates and has strong resistance to heat and humidity [47]. In this study, ‘YN2’ rootstock significantly increased the concentrations of the majority of aroma compounds in grafted ‘Shine Muscat’ grape berries, and ‘Beta’ rootstock had no significant promoting effect on aromatic substances. Therefore, for humid and hot southern regions, ‘YN2’ as a native grape resource may be superior to rootstock varieties screened from cold regions in improv-

ing the aromatic profile of scion varieties. Sun et al. [48] demonstrated that ‘1103P’, ‘110R’, and ‘SO4’ rootstocks significantly increased the total content of free terpene compounds in ‘Ruiduxiangyu’ grape berries from northern China, such as linalool, myrcene, cis-rose oxide, linalool oxide, D-limonene, β -cis-ocimene, nerolidol, geraniol, citral, β -selinene, α -terpineol and dehydro-linalool. In the present study, ‘SO4’ rootstock significantly increased D-limonene concentration, while ‘YN2’ and ‘Fercal’ rootstocks significantly increased the concentration of linalool, (*E*)-linalool oxide (furanoid), β -pinene, (+)-4-carene and geranyl isobutyrate. Therefore, the same rootstocks have different effects on the aroma quality of the scion in different regions, and selecting appropriate rootstocks can enhance the terpene content of specific grape varieties. In addition, in the SM-YN2 combination, the key aroma compound linalool was found to have the highest proportion among all quantified aroma compounds, demonstrating that grafting ‘Shine Muscat’ grapevines onto ‘YN2’ rootstock leads to superior flavor quality.

The mechanisms underlying the rootstock-mediated modulation of scion fruit aroma quality remain incompletely elucidated. Chen et al. [33] reported that ‘Summer Black’ and ‘Couderc 3309’ as rootstocks significantly upregulated the expression level of genes related to the MEP pathway in ‘Shine Muscat’ grapes. In the present study, ‘Beta’, ‘SO4’, ‘5C’ and ‘Fercal’ downregulated one or more structural genes in the MVA and MEP pathways, particularly ‘SO4’, which simultaneously reduced the expression levels of DXS3, DXR, GPPS and TPS. Notably, the ‘YN2’ rootstock exhibited neutral effects on terpenoid-related gene expression, and increasing the content of characteristic aroma compounds, especially linalool. Combined with the analysis of metabolites and gene expression, this indicates that the effect of the rootstock on terpenoid metabolism may also be subject to the co-regulation of related upstream pathways.

Continuous high temperatures are considered a critical abiotic stressor, severely affecting plant growth and development. Grafting cultivation is predominantly adopted in viticultural production, and grafting technology can confer enhanced thermotolerance in horticultural crops [49,50]. Tao et al. [51] demonstrated that grafting cucumber onto momordica charantia rootstock significantly enhances thermotolerance by modulating photosynthetic performance and activating the antioxidant defense system. Hu et al. [52] evaluated 15 rootstocks and found that ‘Shanhe 2’ and ‘Fercal’ had strong heat tolerance, while ‘5C’, ‘Beta’ and ‘SO4’ had weak heat tolerance. In this study, the observed enhancement in volatile compounds, particularly the significant accumulation of linalool in ‘Shine Muscat’ grape grafted onto ‘YN2’ and ‘Fercal’ rootstocks, may be attributed to their superior thermotolerance. In fact, the rootstock will shape different aromatic characteristics of the same variety in different climatic regions. Wang et al. [45] conducted research on the aroma components of ‘Shine Muscat’ grape grafted on different rootstocks in cold regions of northern China, and the results showed that ‘Beta’ rootstock had the highest total terpene content, and the ‘5BB’ rootstock combination had a high content of ester compounds. In the present research, the positive effects of ‘YN2’ on the basic physicochemical indexes and flavor compounds of ‘Shine Muscat’ were confirmed. Therefore, ‘YN2’ can be applied as a rootstock in grape production in hot regions in the future. Furthermore, the previous studies have confirmed that different rootstocks can significantly affect the growth vigor, yield, and quality indicators of grapes by regulating root architecture, nutrient absorption, water efficiency, and hormone balance [7,53,54]. Therefore, subsequent studies can further investigate the mechanism of root–soil interaction in heat-tolerant rootstocks such as ‘YN2’, and explore heat tolerance of the root systems of *V. heyneana* var. *adenoclada* grape rootstocks.

5. Conclusions

Grafting onto rootstocks significantly influences fruit quality and volatile aroma profiles in ‘Shine Muscat’ grape berries. The ‘5C’ and ‘YN2’ rootstocks effectively maintained TSS, TA, TSS/TA and pH in the berries, while ‘Beta’, ‘SO4’ and ‘Fercal’ rootstocks consistently reduced TSS. In addition, the ‘YN2’ rootstock yielded the highest berry weight, and increased by 21.96% compared with SM self-rooted seedling. ‘YN2’ and ‘Fercal’ rootstock could enhance the aromatic profile of ‘Shine Muscat’ berries with the ‘YN2’ rootstock exhibiting the most pronounced improvement. Linalool emerged as the most abundant volatile compound, constituting the highest proportion and serving as the predominant contributor to the characteristic muscat aroma. Notably, the SM-YN2 combination exhibited 31.96% and 4.61% higher concentration and proportion of linalool compared to own-rooted vines. Among all the experimental rootstocks, only ‘YN2’ maintained the expression level of structural genes in the terpenoid metabolic pathway consistent with that of the control. Our integrated analysis of physicochemical and aromatic attributes revealed that grafting onto the ‘YN2’ rootstock produced berries with a superior overall quality, likely attributable to the enhanced thermotolerance conferred by this rootstock. This study provides critical insights for optimizing rootstock selection in humid subtropical regions of southern China, demonstrating that the ‘YN2’ rootstock effectively maintains or enhances fruit quality in ‘Shine Muscat’ grapes. As a local wild resource in Guangxi, *V. heyneana* var. *adenoclada* grape can be utilized as a rootstock in the production of grapes in southern hot and humid regions in the future.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12070842/s1>, Figure S1: Total ion current chromatogram of volatile compounds in SM grape berries; Table S1: Concentrations of all metabolites identified in SM grape berries of five different scion–rootstock combinations.

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Data Availability Statement: The data used for the analysis in this study are available within the article and the Supplementary Materials.

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Conflicts of Interest: The authors declare no conflicts of interest.

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