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Biochemistry

Analysis of Selected Terpenoids and their Genetic Bases in Georgian Grape Varieties and Wines

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Abstract. Selected volatile terpenoids associated with the aroma of six Georgian wines – Rkatsiteli, Meskhuri Mtsvane, Tsitska, Ojaleshi, Saperavi, and Chkhaveri – were investigated alongside the genetic basis of varietal aroma formation through terpene synthase (TPS) gene analysis were investigated using liquid–liquid extraction, gas chromatography with flame-ionization detection, and *in silico* genome analyses. Significant varietal differences in monoterpene composition were observed limonene was the dominant compound in Chkhaveri and Saperavi wines, while moderate levels of geraniol, terpinen-4-ol, and citronellol derivatives further contributed to cultivar-specific aroma characteristics. *In silico* genome analysis and PCR, using a *Vitis vinifera* reference, identified TPS gene homologs on chromosome 18 of Georgian grapevines, revealing variable homology. Partial TPS fragments were amplified in all cultivars, but full-length genes failed in some, likely due to sequence polymorphisms. Phylogenetic analysis of predicted TPS proteins showed that Rkatsiteli, Meskhuri Mtsvane, and Chkhaveri cluster closely, while Saperavi diverges. Overall, the results reveal a clear link between varietal differences in Georgian wine terpenoid composition and structural variation in the TPS gene among Georgian grapevine cultivars. This study represents the first interdisciplinary attempt to investigate the chemical and genetic foundations of aroma formation in these cultivars. © *2026 Bull. Natl. Acad. Sci. Georg.*

Keywords: Georgian grapes and wines, TPS genes, aroma

Introduction

The country of Georgia recognized as “the cradle of viticulture” is home to more than 500 indigenous grapevine cultivars and the earliest archeological evidence of grape domestication. The discovery of early sixth millennium BC grape wine in this region is vital to the later history of wine in Europe and the rest of the world (Imazio et al., 2013; McGovern et al., 2017). Wine aroma is one of the most critical factors influencing wine quality, typicity, and consumer preference. Volatile compounds from grape metabolism, fermentation, and aging (e.g., terpenoids, C_{13}-norisoprenoids, and higher alcohols) shape wine aroma, and are influenced by grape genetics, environment, viticulture, and winemaking (Escudero et al., 2007; Ferreira & López, 2019; Robinson et al., 2014; Pipia &

Nozadze, 2022). Terpenoids, including linalool, geraniol, nerol, terpineol, and citronellol, are key contributors to grape flavor and wine aroma and serve as important metabolite markers in viticulture and enology (Martin et al., 2010). During the past decade, several studies have emerged in the literature aiming to identify aroma-related genes in grapevine genomes (Lin, Massonnet & Cantu, 2019; Li et al., 2023; Wu et al., 2025). From this standpoint, valuable work was conducted by Tabidze et al. (2017) on Georgian grape varieties. Their resequencing of four Georgian grape cultivars – Chkhaveri, Saperavi, Meskhuri Mtsvane, and Rkatsiteli – provided important data on TPS genes, identifying a total of 106 predicted TPS genes and 43 TPS pseudogenes on chromosomes 12, 18, and 19, which encode enzymes catalyzing reactions in grape terpene biosynthesis pathways (Tabidze et al., 2017).

The main objectives of the present research were 1) to detect selected volatile terpenoids in six Georgian wine samples produced using the classic European winemaking technique, employing liquid–liquid extraction followed by gas chromatography with flame-ionization detection; and 2) to perform *in silico* analyses of structural differences in TPS nucleotide sequences and their corresponding amino acid sequences among Georgian grape varieties and to assess how these differences are reflected in the phylogenetic relationships of TPS-associated proteins.

Materials and Methods

Six wine samples made from Georgian grape varieties were selected for the research: white wines (Rkatsiteli, Meskhuri Mtsvane, and Tsitska) and red wines (Ojaleshi, Saperavi, Chkhaveri). All wines in this study were produced from the 2023 grape harvest at the National Centre for Grapevine and Fruit Tree Propagation in Mtskheta, eastern Georgia, using classic European winemaking technology. Volatile aroma compounds were extracted from the wines using a liquid-liquid extraction method (Lopez & Gomez, 2000). Diethyl ether-pentane (1:2) was used as a solvent. All chemicals were of analytical grade. Six terpenoids were used as standards: (-)-citronellol, β-citronellol, (-)-linalool, (S)-limonene, (+)-terpinen-4-ol, and geraniol. A Perkin Elmer Clarus 500 gas chromatograph (GC) equipped with a flame ionization detector and a Supelcovax-10 fused-silica capillary column (30 m x 0.32 mm x 0.25 µm film) was used to perform the GC analysis. Nitrogen was used as the carrier gas. All experiments were performed in triplicate.

Total genomic DNA extraction was performed using the OxGEn DNA purification kit. PCR amplification was carried out with the Qiagen Taq PCR Master Mix Kit targeting the DNA sequence retrieved from the NCBI database corresponding to the TPS gene located on chromosome 18 of Pinot Noir (NCBI ID: 100267145). Primer design and synthesis were performed at the Laboratory Services Division of the University of Guelph (ON, Canada). PCR conditions were as follows: initial denaturation at 94°C for 3 min.; 40 cycles of denaturation at 94°C for 30 s, annealing at 57°C for 40 s, and extension at 72°C for 2 min; followed by a final extension at 72°C for 10 min. PCR products were visualized using 1% (w/v) agarose gel electrophoresis. For *in silico* analyses of TPS gene sequences and their corresponding proteins online platforms NCBI, MEGANTE and Mafft were used (Numa & Itoh, 2014).

Results and Discussion

Analyses of several terpenoids of Georgian wines. GC analysis of Rkatsiteli, Meskhuri Mtsvane, Tsitska, Ojaleshi, Saperavi, and Chkhaveri wines revealed notable variations in the concentration and distribution of key monoterpenes, reflecting both varietal specificity and enological influences (Table 1).

It has been shown that Chkhaveri and Saperavi wines exhibited the highest overall terpene concentrations, particularly of (-)-limonene (1726.9

Table 1. Terpenoid content (μg/L) in the analyzed wines

Standards	RT (min)	Diethyl ether-Pentane fractions (μg/L)					
		Tsitska	Ojaleshi	Meskhuri Mtsvane	Saperavi	Rkatsiteli	Chkhaveri
(S)- (-)-Limonene	1.93	16.62	93.45	16.82	1284.38	529.64	1726.9
Geraniol	10.4	-	409.11	-	106.83	221.64	157.58
(+)-Terpinen-4-ol	6.94	-	746.11	-	13.84	-	24.88
(-)-Citronellol	5.24	-	-	-	18.26	-	-
(-)-β-Citronellol	9.25	13.54	-	12.17	15.13	-	12.53

and 1284.4 μg/L, respectively), a well-established contributor to wine aroma (Swiegers & Pretorius, 2007). Such elevated levels suggest a strong varietal potential for expressing citrus and floral aromatic notes. In the literature, some studies have reported that monoterpene concentrations above 400-500 μg/L can significantly influence the sensory perception of wines (Guth, 1997; Ferreira & López, 2019). Therefore, the limonene content detected in these wines likely contributes prominently to their aromatic intensity and typicity. In contrast, Tsitska, Meskhuri Mtsvane, and Ojaleshi wines displayed lower total terpene levels, with more moderate amounts of limonene (16-93 μg/L) and the presence of specific compounds such as terpinen-4-ol (746 μg/L in Ojaleshi). Terpinen-4-ol, known for its woody and herbal nuances, has been associated with complex aromatic character in white wines (Rapp & Mandery, 1986). Its abundance in Ojaleshi wine, made from a red variety, suggests a unique volatile profile distinct from the other cultivars. Rkatsiteli wine showed a balanced monoterpene composition with moderate amounts of geraniol (221 μg/L) and limonene (530 μg/L). Geraniol contributes rose-like notes and can act as a precursor for *β*-citronellol and linalool under acidic or oxidative conditions. The observed geraniol levels are comparable to those reported for other neutral white cultivars such as Pinot Gris and Chardonnay (González-Barreiro et al., 2015), suggesting that Georgian Rkatsiteli wines may share certain aromatic traits with these internationally recognized types. Citronellol and *β*-citronellol were detected in Tsitska, Meskhuri Mtsvane, Saperavi, and Chkhaveri wines, although at relatively low levels (<20 μg/L). Despite their modest concentrations, these compounds are known for their low odor thresholds and can impart pleasant floral or citrus nuances even at trace levels. Their occurrence in Saperavi and Rkatsiteli wines is consistent with earlier reports showing that fermentation-derived transformations of geraniol can generate citronellol, especially under warm fermentation conditions (Swiegers & Pretorius, 2007). Linalool, a key terpenoid marker of Muscat-type varieties that imparts floral and sweet notes (Etievant, 1991), was detected only in trace amounts in the studied wines. Its minimal presence here reinforces the idea that the analyzed wines belong primarily to the non-Muscat aromatic group, characterized by subtler, more balanced terpene expression rather than overtly floral profiles.

Overall, the diversity of the monoterpene composition among the analyzed wines reflects the distinct varietal identity of Georgian cultivars. The high limonene content of Chkhaveri and Saperavi may be associated with their sensory distinctiveness and potential for aromatic branding, whereas the moderate but complex terpene profiles of Rkatsiteli and Ojaleshi wines suggest a nuanced aroma balance suited to classic European wine-making styles.

In silico analyses and PCR amplification of TPS genes and their corresponding amino acid sequences of Georgian grape varieties. At the initial stage of the *in silico* analysis, the reference TPS sequence located on chromosome 18 of *Pinot Noir* was retrieved from the NCBI database (NCBI ID:

100267145). To identify the homologs of this sequence in the genomes of the Georgian grapevine cultivars from which the analyzed wines were produced, we utilized whole-genome sequencing data from Tabidze et al., specifically the chromosome 18 sequences of Rkatsiteli, Meskhuri Mtsvane, Saperavi, and Chkhaveri (Tabidze et al., 2017). For comparative genomic analysis, the MEGANTE platform was employed, using the chromosome 18 DNA sequences of the aforementioned cultivars were provided. As a result, MEGANTE successfully identified homologous TPS sequences within all analyzed genomes. Moreover, comparative BLAST analyses revealed high-quality homologies among these sequences and with the reference Pinot Noir, as summarized in Table 2.

Table 2. TPS gene location and homology with reference *Pinot noir* (NCBI ID: 100267145)

Grape varieties	Genome position on chr. 18	Homology with reference TPS
Rkatsiteli	4200119-4202384	67%
Meskhuri Mtsvane	4206381-4208650	82%
Saferavi	3792733-3878253	99%
Chkhaveri	4206203-4208472	82%

After the preliminary *in silico* analysis confirmed the presence of the reference TPS gene in the target genomes, PCR-based detection was planned. For this purpose, genomic DNA was extracted from young leaves of Rkatsiteli, Meskhuri Mtsvane, Tsitska, Ojaleshi, Saperavi, and Chkhaveri, the grape varieties used for the wines in the liquid-liquid extraction analyses. PCR primers were designed based on the reference sequence of the TPS gene on chromosome18 of Pinot Noir, which is 2,245 base pairs in length. To ensure efficient amplification of the sequence, several primer pairs were designed. Among them, F1/R1 was intended for the amplification of the full-length gene sequence (2,245 bp), while F1/R3, F2/R2, and F3/R1 were designed to individually amplify fragments of 1048 bp, 1023 bp, and 862 bp, respectively (Table 3).

Table 3. Primer sequences designed based on the TPS gene sequence located on the reference Pinot Noir chromosome 18 (NCBI ID: 100267145)

Primer name	Sequence (5' – 3')
Vitis-vinifera-tps-F1	AAGAAGTGTTCTACTACCATTCC
Vitis-vinifera-tps-R1	CAATCAACTACTCCATTTGG
Vitis-vinifera-tps-F2	CAATGAGTTCAAGGATGAAA
Vitis-vinifera-tps-F3	ACAGCATAGATCAGCTTCC
Vitis-vinifera-tps-R2	GCCTCAGCAAAGTAAGCT
Vitis-vinifera-tps-R3	GATCAGCATACAGGAAAGTG
Vitis-vinifera-tps-R4	TATCACCTTCCATATCATCG

PCR was performed using all primer pairs on the genomes of all studied grapevine genomes, with specific positive amplification observed in each variety. As shown in Fig. 1, the full-length gene PCR fragment (2,245 bp) was amplified only from the Rkatsiteli genome using the primer pair F1/R1, as well as with all three additional primer combinations (F1/R3, F2/R2, and F3/R1). In contrast, in Saperavi, Meskhuri Mtsvane, and Chkhaveri, amplification was obtained only for the F1/R3, F2/R2, and F3/R1 fragments.

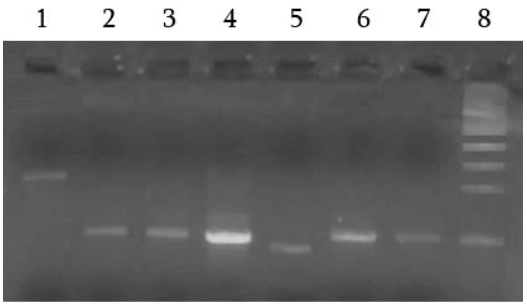

Fig. 1. 1% agarose gel-electrophoresis of PCR-amplified genomic fragments. Lines: 1) Rkatsiteli F1R1; 2) Rkatsiteli F2R2; 3) Saperavi F2R2; 4) Rkatsiteli F2R2; 5) Rkatsiteli F3R1; 6) Meskhuri Mtsvane F2R2; 7) Chkhaveri F2R2; 8) 1kb DNA Ladder.

The results likely reflect genomic differences (SNPs) and suggest that amplifying the full TPS gene requires designing shorter primers within the gene and assembling the complete sequence from

these fragments. The proposed assumption regarding the presence of structural differences among the TPS nucleotide sequences is partly supported by the differences identified between the amino acid sequences of the proteins generated from these sequences using the MAFFT program (Katoh et al., 2019). Specifically, it was observed that mentioned amino acid sequences highly similar in Rkatsiteli, Meskhuri Mtsvane, and Chkhaveri, but show strong divergence between Rkatsiteli and Saperavi TPS proteins. These differences are clearly illustrated in the phylogenetic tree presented in Fig. 2.

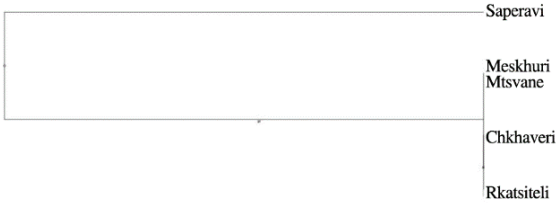

Fig. 2. Phylogenetic tree constructed using Archaeopteryx based on MAFFT alignment of TPS-associated amino acid sequences from Rkatsiteli, Saperavi, Meskhuri Mtsvane, and Chkhaveri.

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CLUSTAL format alignment by MAFFT (v7.511)
Rkatsiteli MSGQVLASPLGQFPELENRPVVKYHPSIWGDQFMSYTPEDEVTRACKEKQLEDLKEEIRR
Saperavi   MSGQVLASPLGQFPELENRPVVKYHPSIWGDQFLSYTPEDEVTRACKEKQLEDLKEEIRR
           ************************************:**************************
Rkatsiteli KLMNTAGNTSQKLKFIDAVQRLGVAYHFEREIEEVLQHIYDSYPNGDDMEGGIYNVALQF
Saperavi   KLMNTAGNTSQQLKFIDAVQRLGVAYHFEREIEEVLQHIYDSYPNGDDMEGDIYNVALQF
           ***********:****************************************.********
Rkatsiteli RLLRQAGFNISCGLFNEFKDEKGNFKKALVSDVRGMLGLYEAAHLRVHGEDILDEALAFT
Saperavi   RLLRQAGFNISCGLFNEFKDEKGNFKKALVSDVRGMLGLYEAAHLRVHGEDILAKALAFT
           ************************************************** :*****
Rkatsiteli TTHLRSMVEHLEYPFAEQVAHALKQPIRKGLERLEARWYISIYQDETSHDRTLLKLAKLD
Saperavi   TTHLKAMVESLGYHLAEQVAHALNRPIRKGLERLEARWYISVYQDEAFHDKTLLELAKLD
           ****::*** * * :********::*****************:****: **:***:*****
Rkatsiteli FNLVQSLHKEELSNITRWWKQLNFATKLPFARDRLVEGYFWILGVFFEPQYAWARRIVTK
Saperavi   FNLVQSLHKEELSNLARWWKELDFATKLPFARDRLVECYFWMLGVYFEPQYLRGRRILTK
           **************::****:*:*************** ***:***:*****  .***:**
Rkatsiteli TIAMTSTMDDIYDAYGTFEELELFTEAIERWDINSIDHLPEYMKHFYVALLDVYKEIEEE
Saperavi   VIAMISILDDIHDAYGTPEELKLFIEAIERWDINSIDQLPEYMKLCYAALLDVYKEIEEE
           .*** * :***:***** ***:** ************:******  *.************
Rkatsiteli MEKEGNQYRVQYAIEAMKKQVRAYFHEAKWLHEGRIPTMEEYMSIARVSSGYPMLTATSF
Saperavi   MEKEGNQYRVHYAKEVMKNQVRAYFAEAKWLHEEHVPTFEEYMRVALVSSGYCILATTSF
           **********:** *.**:****** ******* ::**:**** :* ***** :*::***
Rkatsiteli IGMGKIVTKEAFDWVISDPKIVTASAVIARLMDDITSHKFEQKRGHVASGVECYMKQYGA
Saperavi   VGMGEIATKEAFDWVTSNPKIMSSSNFIARLMDDIKSHKFEQKRRHVASAVECYMKQYGV
           :***:*.******** *:***:::* .********.******** ****.*********.
Rkatsiteli SEEEVYDKFQKQVVDAWKDTNEEFLRPTAVPMPLLMRVLNLSRVMYVIYTGGDGYTHVGK
Saperavi   SEEQVYSEFQKQIENAWLDINQECLKPTAVSMPLLARILNLTRTADVFYKEQDSFTHVGK
           ***:**.:****: :** * *:* *:****.**** *:***:*.  *:*.  *.:*****

Rkatsiteli VMKNNVASLLIHPIA
Saperavi   VMRDNIASVFINAVI
           **::*:**::*:.:
```

Fig. 3. Cluster format alignment (MAFFT (v7.511)) of the predicted amino acid sequences of Rkatsiteli and Saperavi.

In the tree, the predicted amino acid sequences of Rkatsiteli, Meskhuri Mtsvane, and Chkhaveri form a single clade, whereas Saperavi occupies a relatively distant position. The pronounced differences between the Saperavi sequence and the other cultivars are clearly illustrated by the pairwise comparison of the amino acid sequences for Saperavi and Rkatsiteli, as shown in Fig. 3.

It should be noted that the variations shown in the figure cannot be regarded as random, since an amino acid substitution in a protein is generated only when a missense mutation occurs within the gene sequence *in vivo*. This, in turn, excludes the possibility of mechanical translation of amino acid sequences by the MEGANTE program and, consequently, rules out any machine-related errors.

Conclusions

Overall, based on the findings from this study, the following conclusions can be drawn:

- Georgian wines exhibit significant varietal differences in monoterpene composition, with limonene identified as the dominant aroma compound in Chkhaveri and Saperavi.
- The identified terpenoid profiles reflect both the genetic background and the use of classic European winemaking practices, which together shape the aromatic features of Georgian grape cultivars.
- *In silico* genome analysis confirmed the presence of TPS gene homologs on chromosome 18 across the Georgian grape varieties, with varying levels of sequence homology relative to Pinot Noir.
- PCR amplification successfully identified partial TPS gene fragments; however, amplification of the full-length gene in all studied genomes was not achieved, likely due to DNA-sequence divergence among cultivars.
- Future studies should focus on designing shorter, overlapping primers and performing fun-

ctional validation of TPS genes to fully elucidate their contribution to wine aroma and to support the conservation of Georgian grapevine biodiversity.

- Phylogenetic analysis confirmed that the amino acid sequences of Rkatsiteli, Meskhuri Mtsvane, and Chkhaveri cluster together, whereas Saperavi occupies a phylogenetically distant position.

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ბიოქიმია

ზოგიერთი ტერპენოიდისა და მათი გენეტიკური საწყისების კვლევა ქართული ვაზის ჯიშებსა და ღვინოებში

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(წარმოდგენილია აკადემიის წევრის თ. სადუნიშვილის მიერ)

შესწავლილ იქნა არომატების ფორმირებასთან დაკავშირებული ტერპენოიდების შემცველობა და მისი გენეტიკური საწყისები ქართულ ღვინოებსა და ვაზის ჯიშებში. ტერპენოიდების იდენტიფიცირებისათვის გამოყენებულ იქნა თხევად-თხევადი ექსტრაქციის მეთოდი გაზური ქრომატოგრაფით, არომატების ფორმირებასთან ასოცირებული ტერპენ სინთაზას გენებისა (TPS) და მათი შესაბამისი ამინომჟავური თანმიმდევრობების ანალიზისათვის კი *in silico* კვლევის მეთოდები. მონოტერპენების შემადგენლობაში მნიშვნელოვანი ჯიშობრივი განსხვავებები დაფიქსირდა ჩხავერისა და საფერავის ღვინოებში ლიმონენის დომინანტურობით და გერანიოლის, ტერპინენ-4-ოლის და ციტრონელოლის საშუალო შემცველობით. პარალელურად, in silico გენომური ანალიზით ქართული ვაზის ჯიშების გენომების მე-18 ქრომოსომაში დადასტურდა TPS გენების ჰომოლოგების არსებობა. PCR ამპლიფიკაცია წარმატებული აღმოჩნდა TPS გენების ნაწილობრივი ფრაგმენტების დეტექციისათვის ყველა შესწავლილ

გენომში. სრული სიგრძის გენის ამპლიფიკაცია არსებული პრაიმერების საშუალებით დაფიქსირდა რქაწითელის გენომში, რაც შესწავლილი გენომური თანმიმდევრობების პოლიმორფიზმზე მიანიშნებს. კვლევის ფარგლებში, ასევე, განხორციელდა TPS გენებიდან ტრანსლირებული ცილების ამინომჟავური თანმიმდევრობების *in silico* და ფილოგენეტიკური ანალიზი. ნაჩვენები იქნა, რომ რქაწითელის, მესხური მწვანესა და ჩხავერის TPS გენებთან ასოცირებული ცილები ფილოგენეტიკურ ხეზე ერთ კლასტერად ჯგუფდებიან, საფერავის შესაბამისი ცილა კი ცალკე, დამოუკიდებელ ჯგუფს ქმნის. ჩატარებული სამუშაო ქართული ღვინოების ტერპენოიდული შემადგენლობისა და ვაზის ჯიშების TPS გენებისა და მათი შესაბამისი ამინომჟავური თანმიმდევრობების სტრუქტურული მრავალფეროვნების შესწავლის პირველ ინტერდისციპლინურ მცდელობას წარმოადგენს.

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