



## AROMA COMPOUNDS OF GRAPE AND WINE

I. Pipia\*, T. Nozadze

Agricultural University of Georgia, Institute of Molecular Genetics,  
Kakha Bendukidze University Campus, 240 David Aghmashenebeli Alley, 0159, Tbilisi, Georgia

Received: 12 September 2021 Accepted: 29 October 2021

### ABSTRACT

Aroma compounds represent the most important factors that play a crucial role in the formation of wine character. Generally, wine's aroma depends on the grape variety, the winemaking process and environmental factors, such as soil, weather, water, sunlight etc. Here we present a short review of the types of volatile aroma compounds (grape-derived aromas, aromas produced from the process of fermentation, maturation aromas), the chemistry of aromas, and the genetic bases of aroma formation.

**Keywords:** Aroma compounds, Grape, Wine

\*Corresponding Author: Dr. I. Pipia, E-mail address: [i.pipia@agruni.edu.ge](mailto:i.pipia@agruni.edu.ge)

### Introduction

From the ancient times the cultivated grape (*Vitis vinifera* ssp. *vinifera*) represents the most important horticultural crop worldwide. For human society, the importance of grapevines goes into two main usages: grapes as table fruits and as a source of wine or other products of grapes (i.e., juice, vinegar). Among sweetness, acidity, tannin levels, and wine body types (light, medium, full-bodied), aromas are the most important factors contributing to the formation of wine character. The terms "wine aroma" and "wine bouquet" have two independent meanings. The "aroma" corresponds to the smells unique to the grape variety, while "bouquet" represents the new smells formed as a result of winemaking process of fermentation and aging [1].

The main contributors to wine quality are volatile aroma compounds, which are grouped into three classes: grape-derived aromas (primary aromas, varietal aromas), aromas produced from the process of fermentation (secondary aromas, fermentative aromas), and maturation aromas (tertiary aromas, aging aromas) [2, 3, 4]. Besides, it should be

noted that there are several additional factors that are affecting grape aromas. Among them are soil, weather, sunlight, water, nitrogen fertilization, and fungicide treatment [5].

In general, it is very difficult to pinpoint the perception and characterization of wine aromas. This difficulty stems from the above-mentioned different origins of aromas as well as the perception of flavors defined by human sensory systems. The brain interprets the taste of wine through the gustatory system, which is responsible for a taste, and the olfactory system, responsible for a smell. The gustatory system is made up of the so-called taste cells in the mouth. These cells are responding to that chemical compound of food that makes all five known tastes: salty, sweet, bitter, sour, and umami. Olfaction activates when aroma compounds enter the nasal cavity (by inhalation through the nose or mouth). The molecules of the mentioned compounds bind to receptors that signal to the specific olfactory bulb, which initiates a cascade of neural signals responsible for smell recognition, memory, and emotion. According to some authors,

the flavor is not presented in the food - it is created by the brain from food. It is proposed that humans can differentiate more than 1 trillion olfactory stimuli. The human nose can perceive some of the compounds only at very high concentrations, while others are even at low levels [4, 6, 7]. In difference from the human sense of aromas, there are a number of laboratory methods that can accurately detect aromatic compounds at any concentration. Among them, the most usable is Gas-Chromatography coupled with Mass-Spectroscopy (GC-MS) and High-performance liquid chromatography (HPLC analyses) [8, 9].

## Grape derived aromas

Grape-derived aroma compounds are important contributors to the wine bouquet as they offer a unique set of wine aromas. These aromas are called as prime or varietal aromas of wine and are aromas associated with fruit (e.g., peach, blackberry), herbal (e.g., mint, oregano), and flower (e.g., roses, iris) flavors. In the overall aroma composition, grape varieties are mostly similar, differences lie in the rations of the compounds contributing to the aroma profiles [10].

It is determined that in grapes there are at least seven different systems or pools of aroma precursors, but not all of them are contributing to the formation of wine flavor (i.e., the Strecker amino acid system and the fatty acid/peroxygenase system) [11].

The actual aroma of grapes involves compounds in three related categories: 1). Free aromas – aroma compounds presented in the grape skins. This category represents very small amounts of compounds in most grape varieties, and displays weak, rather neutral odors and flavors; 2). Aroma molecules which are formed by enzymatic/catalytical processes triggered during the disruption of fruit tissues. A number of aldehydes, alcohols, and ketones formed as a result of the peroxidation of fatty acids are examples of this category. As the abundance of these molecules has 6 carbons, they are often called C6-compounds; 3). Aroma molecules which are made in the buccal cavity by the activity of salivary or bacterial enzymes. It has been shown that glutathione and cysteinyl precursors (odorless cysteine-S-conjugates) can release the aromatic thiol by the action of buccal microbiota [11]. It should be noted that the certain aromas originated from grapes are modified by the

fermentation process or aging.

Most aroma compounds are presented as non-volatile precursors, including glycosidic precursors, polyolic forms, cysteinylated and glutathionylated precursors, or 32 dimethyl sulfide (DMS) precursors [12]. From those compounds, the main quotative ones are glycosidic precursors. Some most popular aroma chemicals, such as linalool and geraniol (terpenoids, the major aroma compounds in both red and white grapes), eugenol and guaiacol (volatile phenols) are derived from the glycosidic precursors already existing in grapes. In muscat-related grapes, varietal wine aromas originated from the various isoprenoid monoterpenes (i.e., linalool, geraniol, nerol, and citronellol) [10].

## Aromas producing from the process of fermentation

Wine is the product of fermentation, which means the transformation of grape juice into an alcoholic beverage by yeast. During fermentation, yeasts transform the sugars of the juice into ethanol and carbon dioxide. The intensive smell of wine formed under the influence of yeast *Saccharomyces cerevisiae* (often referred to as “wine yeast”). But *S. cerevisiae* is not only responsible for the metabolism of grape sugar to alcohol and CO<sub>2</sub>. Grape must contain a mixture of yeast species and so fermentation is not a ‘single-species’ process [13]. In the early stages of fermentation, numerous yeast species may exist, but as the alcohol concentration increases, *Saccharomyces* species progressively take over [14]. Such non-saccharomyces species include: *Hanseniaspora*, *Hansenula*, *Candida*, *Pichia*, *Lachancea*, *Brettanomyces*, *Kluyveromyces*, *Schizosaccharomyces*, *Torulaspora*, *Zygosaccharomyces* and *Saccharomycodes*.

The major odor-active compounds that arrive from the process of fermentation are esters, higher alcohols, carbonyl, and sulfur compounds. In wines, esters are presented in the form of acetate and ethyl esters, which have different fruity perceptions. Acetate esters are the products of a condensation reaction between acetyl-CoA and higher alcohols produced by yeast from amino acid metabolism. Ethyl esters are the results of the esterification of ethanol, and acyl-CoA intermediates as a result of esterase and transferase enzyme activity. Higher alcohols are formed by yeasts as a result of amino acid metabolism (See below).

## Maturation aromas

During the fermentation process, yeasts transform sugars into alcohol, which is accompanied by the formation of secondary aromas. By this time, wine is still immature, it has to rest to harmonize aromas and balance acidity and tannins. The period between the end of fermentation till bottling represents a period of wine maturation or aging. Maturation partially changes the taste of wine and its bouquet. During wine storage, certain changes in wine aroma composition occur. For instance, many esters, formed by the yeast's metabolic activity, are hydrolyzed and a fresh and fruity aroma is lost. At the same time, a synthesis of new esters occurs (i.e., isoamyl acetate, diethyl succinate). In muscat varieties in which the main odor compounds are terpenes, the concentration of monoterpene alcohols declines, and monoterpene oxides are formed. In wine, the bound terpenes are slowly transformed to free volatile terpenes over time, and when this occurs the fruity aroma

of wine is enhanced during maturation [15]. It was shown that the chemical profiles of wines can be significantly changed by the influence of chips used for aging. In particular, in red wines aged with French oak chips smoky, licorice, and toasty aromas were noticed, while in wines aged with American oak chips vanilla, toasty and cacao aromas were detected [16].

## Chemistry of aromas

There are several types of chemical compounds that are the main contributors to the aroma composition generally for both grapes and wines. Among them are aliphatic alcohols, aliphatic acids, aliphatic esters, monoterpenes, norisoprenoids, volatile phenols and benzoids [4]. Table 1 presents the list of some key aroma compounds of grape and wine with the description of their corresponding flavors [summarized from 10, 16, 17, 18, 19, 20, 21].

**Table 1.** Some major aroma compounds of grape and wine with the description of their characteristic odors.

Compounds		Aroma
Aliphatic alcohols	C6-alcohols	“Green” aroma
Higher alcohols	3-methyl-butan-1-ol	Alcohol notes, nail varnish, malt
	Phenylethanol	Floral, rose, honey notes, peach notes
	Methionol	Crushed potatoes
	Propan-1-ol	Alcohol, ripe fruits
Esters	Ethyl butanoate	Pineapple, strawberries
	Ethyl propanoate	Cherries
	Ethyl hexanoate	Green apples, strawberries, blackberries
	2-phenylethyl acetate	Rose, fruity
	Hexyl acetate	Pears, plums, bananas, currants
Monoterpenes	Linalool	Floral aroma with spicy tones and lemon aroma
	Geraniol	Floral, fruity, Citrus
	$\alpha$ -terpineol	Floral, fruity, Citrus
	Citronellol	Floral, fruity
	Nerol	Sweet, fresh aromas
Volatile phenols	Guaiacol	Smokey, ashy aroma
	Eugenol	Spice, clove, smoke
	Vanillin	Smokey
Volatile thiols	3-sulfanylhexas-1-ol (3SH)	Fruity notes
	4-methyl-4-sulfanylpentan-2-one (4MSP)	Fruity notes
Benzenoids	Phenylethanol	Weak floral aroma
	Phenylacetaldehyde	Weak floral aroma
Sulphur compounds	Volatile thiols	Fruity, “green” aroma
	Methanethiol	Rotten Cabbage, Stagnant Water

Aliphatic alcohols can be originated from both grape and yeast fermentation. C6-alcohols which are formed from the corresponding C6-aldehydes are a group of plant volatiles with a “green” aroma, reminding of leaves and fresh-cut grass. The fusel short-chain alcohols are formed by yeasts during the fermentation process from amino acid catabolism. They can negatively impact wine aroma. Aliphatic alcohols also can act as precursors of esters – other types of aroma compounds. During the fermentation the yeasts produce: a). Long aliphatic acids with 6 and more carbon from fatty acids; b). Short and branched acids from amino acids, and c). Sugar-derived acetic acids. Aliphatic acids can be turned into esters and lactones [10].

As mentioned above, there are two main classes of esters in wines: ethyl esters and acetate esters. While the concentration of ethyl esters of medium-chain fatty acids depends on the concentration of the fatty acid precursor, its concentration does not regulate the concentration of acetate esters [10].

Terpenoids represent the most important organic compounds which are contributing to the formation of aromas of grape varieties and wine's bouquet [22]. They can be found in grapes, musts and wines [23]. Among the different classes of terpenoids (hemiterpenoids, diterpenoids, sesquiterpenoids, etc.) the monoterpenes (substances with 10 carbon atoms built from 2 isoprenoids units) and sesquiterpenes (substances with 15 carbon atoms built from 3 isoprenoids units) appear to be the most important aroma compounds of fruits [23, 24]. The chemical bases of the most floral and citrusy notes in wine are monoterpenes (a C<sub>10</sub> class of terpenes). These compounds are mainly derived from grape varieties and are predominantly glycosylated. In well-known aromatic grape varieties, such as Riesling, Muscat d'Alexandrie etc., the major monoterpenes are linalool, geraniol, nerol, citronellol and  $\alpha$ -terpineol [18]. Monoterpenes are products of terpene synthase enzymes (see below).

Like monoterpenes the floral or fruity notes have group of carotenoid-derived metabolites – norisoprenoids, which are synthesized by enzyme carotenoid cleavage dioxygenases. Wine norisoprenoids with important sensory properties are: 2,2,6-trimethylcyclohexanone (TCH), beta-damascenone, beta-ionone, vitispirane, actinidiol, 1,1,6-trimethyl-1,2-dihydronaphthalene (TDN), riesling acetal and 4-(2,3,6-trimethylphenyl)buta-

1,3-diene (TPB) [25].

Volatile phenols give to wine spicy aroma notes. They originated from ferulic acid or related metabolites. Most of these compounds are presented as glycosides in grapes, that can be hydrolyzed during the process of winemaking. The most often founded volatile phenols in wine are: 4-ethylguaiacol (4-EG), 4-ethylphenol (4-EP), 4-methylguaiacol, vinylphenols, guaiacol, eugenol, and vanillin. The last one from the list – vanillin can also originate from aging in oak barrels. Some volatile phenols are associated with the non-pleasant aroma. The example of such volatile phenol is guaiacol with smokey and ashy aroma [19].

Volatile thiols, such as 3-sulfanylhexan-1-ol (3SH) and 4-methyl-4-sulfanylpentan-2-one (4MSP), are also important contributions to the wine fruity aromas. Many of thiol compounds are found in Sauvignon blanc wines. The source of thiols is fermentation process [20, 21].

Benzenoid-derived metabolites (i.e., phenylethanol, phenylacetaldehyde) gives to wine floral and fruity flavors [21]. In comparison to grapes in wines the concentration of benzenoids is much higher, that means that the source of these compound are not only grapes, but also yeasts.

More than 800 volatile aroma compounds have been identified in wines [8]. In the standpoint of the source, the core volatile compounds of wines can be classified as follows [5]:

Pyrazines - Originate in grapes.

Terpenes - Usually originate in grapes, but can be made by some yeasts and molds (but not *Saccharomyces*).

Shikimic acid derivatives - Formed by aromatic amino acid metabolism, originate in the plants, microbes, oak barrels.

Lactones – Originated in grapes, microbes, and oak barrels.

Esters - Alcohol: ethanol or alcohol from the degradation of amino acids, purine, and pyrimidine, Acid: acetic acid or acid from the degradation of amino acids or biosynthesis of fatty acids.

Higher alcohols or fusel oils - Formed mostly by microbes, but can be made by plants.

Acids – Made from the plant or microbes

Phenolic compounds – Made by plants

Sulfur-containing compounds – i.e., thiols are made during the fermentation process.

## Genetic bases of aroma compounds

The varietal aromas originated in grape berries by a variety of enzymes (i.e., terpene synthases, carotenoid cleavage dioxygenases, O-methyl transferases, cytochromes P450). It is known that genetic variation in the genes associated with aroma biosynthesis cause differences in aromas between grapevine varieties. For instance, an allelic variant of a terpenoid biosynthetic gene – 1-deoxy-D-xylulose-5-phosphate synthase, is responsible for the accumulation of terpenoids especially in Muscat and Gewürztraminer grapes [4].

Martin et al., reported findings from the analysis of the updated 12-fold sequencing and assembly of the grapevine genome that place the number of predicted terpenoid synthase genes (VvTPS) at 69 putatively functional VvTPS, 20 partial VvTPS, and 63 VvTPS probable pseudogenes. This work included information about gene architecture and chromosomal location [26]. Possible variations in the relative expression of terpene synthase (TPS) genes that depend on the organ were studied by Matarese et al., [22]. Tabidze et. al., reported the resequencing results of four Georgian grape cultivars - Chkhaveri, Saperavi, Meskhuri mtsvane, and Rkatsiteli, belonging to different haplogroups [27]. Annotation of chromosomal DNA of Georgian grape cultivars by MEGANTE annotation system shows the existence totally 66,745 predicted genes in all four cultivars. Among detected coding sequences, 106 predicted genes and 43 pseudogenes of terpene synthase genes were found in chromosomes 12, 18 random (18R), and 19. It should be noted that four novel TPS genes not presented in reference to Pinot noir DNA were detected. Two of them - germacrene A synthase (Chromosome 18R) and (–) germacrene D synthase (Chromosome 19) can be identified as putatively full-length proteins.

Aromatic norisoprenoids (C9, C10, C11, C13 molecules) with the floral/fruity aromas in grapes and wines, are produced from the carotenoids through the cleavage of carotenoid cleavage dioxygenases (CCD). By recombinant expression studies of *VvCCD1* it was shown that the gene encoded a functional CCD [28, 29]. Two cDNA encoding O-methyltransferases were isolated from Cabernet Sauvignon. By recombinant studies it was shown that O-methyltransferases are able to methylate non-volatile hydroxypyrazine to produce methoxypyrazines - volatile, grape-derived aroma compounds with herbaceous flavors [30]. By using

of bioinformatical analyses Iiu et al., identified a sum of 236 *VvCYPs* (the cytochrome P450 (CYP) superfamily) divided into 46 families and clustered into nine clans [31].

## Conclusion

The wine character is made by complex interactions between, on the one hand, varietal aroma profiles, fermentation and maturation processes, and environmental factors (i.e., soil, water, sunlight), on the other. As aroma compounds are one of the most important parameters in determining the quality of grape-derived products, such as wine, grape juice, and vinegar, the understanding of the general profiles of aroma content, wine aroma sources, and molecular bases of varietal aroma formation are the most important for the human society as this knowledge can help to enhance the quality of wines and to derive certain flavors in them.

## References

- [1] Alvaro C. Jimenez, Understanding of Wine, A Brief Guide to Wine Exploration
- [2] Matarese F., Scalabrelli G., D'Onofrio C., Analysis of the expression of terpene synthase genes in relation to aroma content in two aromatic *Vitis vinifera* varieties, *Functional Plant Biology*, (2013) 40:552–565.
- [3] Belda I, Ruiz J, Esteban-Fernández A, et al. Microbial Contribution to Wine Aroma and Its Intended Use for Wine Quality Improvement. *Molecules*, (2017) 22(2):189. Published 2017 Jan 24. doi:10.3390/molecules22020189
- [4] Ilc T., Werck-Reichhart D. and Navrot N., Meta-Analysis of the Core Aroma Components of Grape and Wine Aroma. *Front. Plant Sci.*, (2016) 7:1472. doi: 10.3389/fpls.2016.01472
- [5] González-Barreiro C., Rial-Otero R., Cancho-Grande B., Jesús Simal-Gándara J., Wine Aroma Compounds in Grapes: A Critical Review, *Critical Reviews in Food Science and Nutrition*, (2015) 55:2, 202–218, DOI: 10.1080/10408398.2011.650336
- [6] Neuroenology: The Brain Science Behind Wine testing, By Emily Oleisky, <https://gravitywinehouse.com/blog/neuroenology-science-of-wine-tasting/> 2021
- [7] Bushdid C, Magnasco MO, Vosshall LB, Keller A. Humans can discriminate more

- than 1 trillion olfactory stimuli, *Science*, (2014) 343(6177):1370-2. doi: 10.1126/science.1249168. PMID: 24653035; PMCID: PMC4483192.
- [8] Toci, A. T., Crupi, P., Gambacorta, G., Dipalmo, T., Antonacci, D., and Coletta, A., Free and bound aroma compounds characterization by GC-MS of Negroamaro wine as affected by soil management. *J. Mass Spectrom.*, (2012) 47, 1104–1112. doi: 10.1002/jms.3045
- [9] Moroşanu, A.-M.; Luchian, C.E.; Niculaea, M.; Colibaba, C.L.; Tarţian, A.C.; Cotea, V.V. Assessment of Major Volatile and Phenolic Compounds from ‘Fetească Regală’ Wine Samples after Pre-fermentative Treatments using GC-MS Analysis and HPLC Analysis. *Not Bot Horti Agrobo*, (2018) 46(1):247-259. DOI:10.15835/nbha46110889
- [10] Styger G., Prior P., Bauer F.F., Wine flavor and aroma, *Journal of Industrial Microbiology and Biotechnology*, Vol. 38, Issue 9, (2011) pg. 1145, <https://doi.org/10.1007/s10295-011-1018-4>
- [11] Ferreira V, Lopez R., The Actual and Potential Aroma of Winemaking Grapes, *Biomolecules*, 2019; 9(12):818. Published 2019 Dec 3. doi:10.3390/biom9120818
- [12] Alegre Y, Arias-Pérez I, Hernández-Orte P, Ferreira V., Development of a new strategy for studying the aroma potential of winemaking grapes through the accelerated hydrolysis of phenolic and aromatic fractions (PAFs), *Food Res Int.* (2020) 127:108728. doi: 10.1016/j.foodres.2019.108728. Epub 2019 Oct 9. PMID: 31882095.
- [13] Neil P. Jolly, Cristian Varela, Isak S. Pretorius, Not your ordinary yeast: non-Saccharomyces yeasts in wine production uncovered, *FEMS Yeast Research*, Vol. 14, Issue 2, (2014), pg. 215–237.
- [14] Mas A, Guillamón JM and Beltran G Editorial: Non-conventional Yeast in the Wine Industry. *Front. Microbiol.*, (2016) 7:1494. doi:10.3389/fmicb.2016.01494
- [15] Wine Aging, M. Dharmadhikari, (2016) <http://www.extension.iastate.edu/wine/w-aging>
- [16] Dumitriu Gabur GD, Teodosiu C, Gabur I, Cotea VV, Peinado RA, López de Lerma N. Evaluation of Aroma Compounds in the Process of Wine Ageing with Oak Chips, *Foods*, (2019) 10;8(12):662. doi: 10.3390/foods8120662. PMID: 31835490; PMCID: PMC6963919.
- [17] Baron M., Prusova B., Tomaskova L., Kumsta M., Sochor J., Terpene content of wine from the aromatic grape variety ‘Irsai Oliver’ (*Vitis vinifera* L.) depends on maceration time, *Open Life Sciences*, vol. 12, no. 1 (2017) pp. 42-50. <https://doi.org/10.1515/biol-2017-0005>
- [18] Pardo E., Rico, J., Gil, J.V. et al., De novo production of six key grape aroma monoterpenes by a geraniol synthase-engineered *S. cerevisiae* wine strain, *Microb Cell Fact* 14, 136 (2015). <https://doi.org/10.1186/s12934-015-0306-5>
- [19] Parker M., Osidacz P., Baldock G.A., Hayasaka Y., Black C.A., Pardon K.H., Jeffery D.W., Geue J.P., Herderich M.J., Francis L.I., Contribution of Several Volatile Phenols and Their Glycoconjugates to Smoke-Related Sensory Properties of Red Wine, *J. Agric. Food Chem.* (2012) 60, 10, 2629–2637.
- [20] Helwi, P., Guillaumie, S., Thibon, C. et al. Vine nitrogen status and volatile thiols and their precursors from plot to transcriptome level. *BMC Plant Biol* 16, 173 (2016). <https://doi.org/10.1186/s12870-016-0836-y>
- [21] Renault, P., Coulon, J., Moine, V., Thibon, C., & Bely, M., Enhanced 3-Sulfanylhexan-1-ol Production in Sequential Mixed Fermentation with *Torulaspora delbrueckii*/ *Saccharomyces cerevisiae* Reveals a Situation of Synergistic Interaction between Two Industrial Strains, *Frontiers in microbiology*, (2016) 7, 293. <https://doi.org/10.3389/fmicb.2016.00293>
- [22] Matarese F., Cuzzola A.R., Scalabrelli G., D’Onofrio C., Expression of terpene synthase genes associated with the formation of volatiles in different organs of *Vitis vinifera*. *Phytochemistry* 105 (2014), DOI: 10.1016/j.phytochem.2014.06.007
- [23] Lengyel E., Primary aromatic character of wines, *Acta Universitatis Cibiniensis Series E: Food Technology* Vol. XVI, no.1 (2012).
- [24] Dunlevy J., Kalua C., Keyzers R., Boss P. The Production of Flavour & Aroma Compounds in Grape Berries. In: Roubelakis-Angelakis K.A. (eds) *Grapevine Molecular Physiology & Biotechnology*. Springer, Dordrecht, 2009
- [25] Mendes-Pinto MM., Carotenoid breakdown products the-norisoprenoids-in wine aroma,

- Arch Biochem Biophys. (2009) 483(2):236-45. doi: 10.1016/j.abb.2009.01.008. PMID: 19320050.
- [26] Martin D.M., Aubourg S., Schouwey M.B., Daviet L., Schalk M., Toub O., Lund S.T., Bohlmann J., Functional Annotation, Genome Organization and Phylogeny of the Grapevine (*Vitis vinifera*) Terpene Synthase Gene Family Based on Genome Assembly, FLeDNA Cloning, and Enzyme Assays. BMC Plant Biology (2010) 10(1):226, DOI: 10.1186/1471-2229-10-226
- [27] Tabidze V., Pipia I., Gogniashvili M., Kune-lauri N., Ujmajuridze L., Pirtskhalava M., Vishnepolsky B., Hernandez AG., Fields CJ., Beridze T., Whole genome comparative analysis of four Georgian grape cultivars, Mol. Genet. & Genomics, (2017) 292(6):1377-1389. doi: 10.1007/s00438-017-1353-x.
- [28] Mathieu S., Terrier N., Procureur J., Bigey F., Günata Z., A Carotenoid Cleavage Dioxygenase from *Vitis vinifera* L.: functional characterization and expression during grape berry development in relation to C13-norisoprenoid accumulation, Journal of Experimental Botany, Volume 56, Issue 420, (2005) pg. 2721–2731, <https://doi.org/10.1093/jxb/eri265>
- [29] Meng N, Wei Y, Gao Y, Yu K, Cheng J, Li X-Y, Duan C-Q and Pan Q-H (2020) Characterization of Transcriptional Expression and Regulation of Carotenoid Cleavage Dioxygenase 4b in Grapes. Front. Plant Sci. 11:483. doi: 10.3389/fpls.2020.00483
- [30] Dunlevy JD., Soole KL., Perkins MV., Dennis EG., Keyzers RA., Kalua CM., Boss PK., Two O-methyltransferases involved in the biosynthesis of methoxypyrazines: grape-derived aroma compounds important to wine flavour. Plant Mol Biol. 2010 Sep;74(1-2):77-89. doi: 10.1007/s11103-010-9655-y. Epub 2010 Jun 23. Erratum in: Plant Mol Biol. 2013 Mar;81(4-5):523. PMID: 20567880.
- [31] Jiu S., Xu Y., Wang J., Wang L., Liu X., Sun W., Sabir Ia, Ma C., Xu W., Wang S., Abdullah M., Zhang C., The Cytochrome P450 Monooxygenase Inventory of Grapevine (*Vitis vinifera* L.): Genome-Wide Identification, Evolutionary Characterization and Expression Analysis. Front. Genet. (2020) 11:44. doi: 10.3389/fgene.2020.00044