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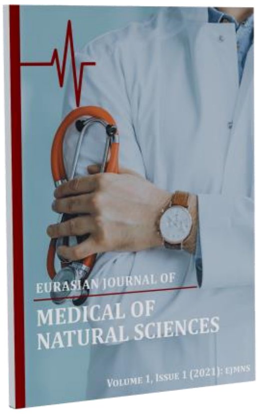

ANALYSIS OF GENETIC MATERIAL IN RAISIN GRAPE VARIETIES

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ABSTRACT

Grapes are one of the oldest and most important horticultural crops. Various products are made from grapes, grape has long been of cultural and scientific interest. The diverse compound classes comprising aroma result from multiple biosynthetic pathways. Only fairly recently have researchers begun to elucidate the genetic mechanisms behind the biosynthesis and metabolism of grape volatile compounds. This review summarizes current findings regarding the genetic bases of grape and wine aroma with an aim towards highlighting areas in need of further study. From the literature, we compiled a list of functionally characterized genes involved in berry aroma biosynthesis and present them with their corresponding annotation in the grape reference genome.

With nearly 8 million hectares of vineyards worldwide and a global annual production of around 90 million tons, the grapevine is one of the most important horticultural crops. The majority of cultivated grapes belong to *Vitis vinifera* subsp. *vinifera* (hereafter *V. vinifera*); however, cultivars and hybrids of other *Vitis* species, as well as the related genus *Muscadinia* are also grown, particularly in regions where climate and/or disease pressure preclude the cultivation of *V. vinifera* (1). Over its long history of domestication and usage for wine and consumption as fresh and dried fruit, *V. vinifera* has undergone selection for desirable traits such as hermaphroditism, sugar content, berry color, and berry size (2). Attempts to utilize wild non-*vinifera* species, whether as interspecific crosses with *V. vinifera* or as selected cultivars, to overcome environmental and biotic limitations on grape cultivation have been complicated by the presence of negatively perceived flavors, especially in wine production (3). On the other hand, there is enormous genetic diversity in cultivated and wild species of grape and with it the potential to generate novel flavor combinations by utilizing that diversity(4).

The aroma, i.e., the olfactory component of flavor, of grapes and wine has been an area of intense interest for many decades. Much has been written regarding topics such as the volatile profiles of different cultivars, the sensory significance of individual compounds, environmental effects on the accumulation of aroma compounds, and the impacts of viticultural and enological treatments on fruit and wine aroma. Advances in analytical techniques together with sensory methodologies have dramatically increased our understanding of the composition and interactions within the complexity that is grape and wine aroma(5). While variations in aromatic potential between cultivars have long been documented, for many reasons the study of genetic explanations for these differences has lagged behind our knowledge of grape volatile constituents.

Only fairly recently have we been able to unravel the role of specific genes in the origins of grape and wine aroma. Molecular markers have been invaluable in helping researchers understand the inheritance of a number of viticulturally and enologically significant traits including those related to flavor and aroma(1). Expressed sequence tags (ESTs) have also been instrumental in the identification of genes involved in secondary metabolism (3). More recently, the publication of the Pinot noir and PN40024 genomes has greatly facilitated the identification and characterization of genes involved in many metabolic pathways (5). Ongoing technological advances in sequencing, omics, biotechnology, and phenotyping will further enable researchers to understand the genetic mechanisms behind grape and wine aromas.

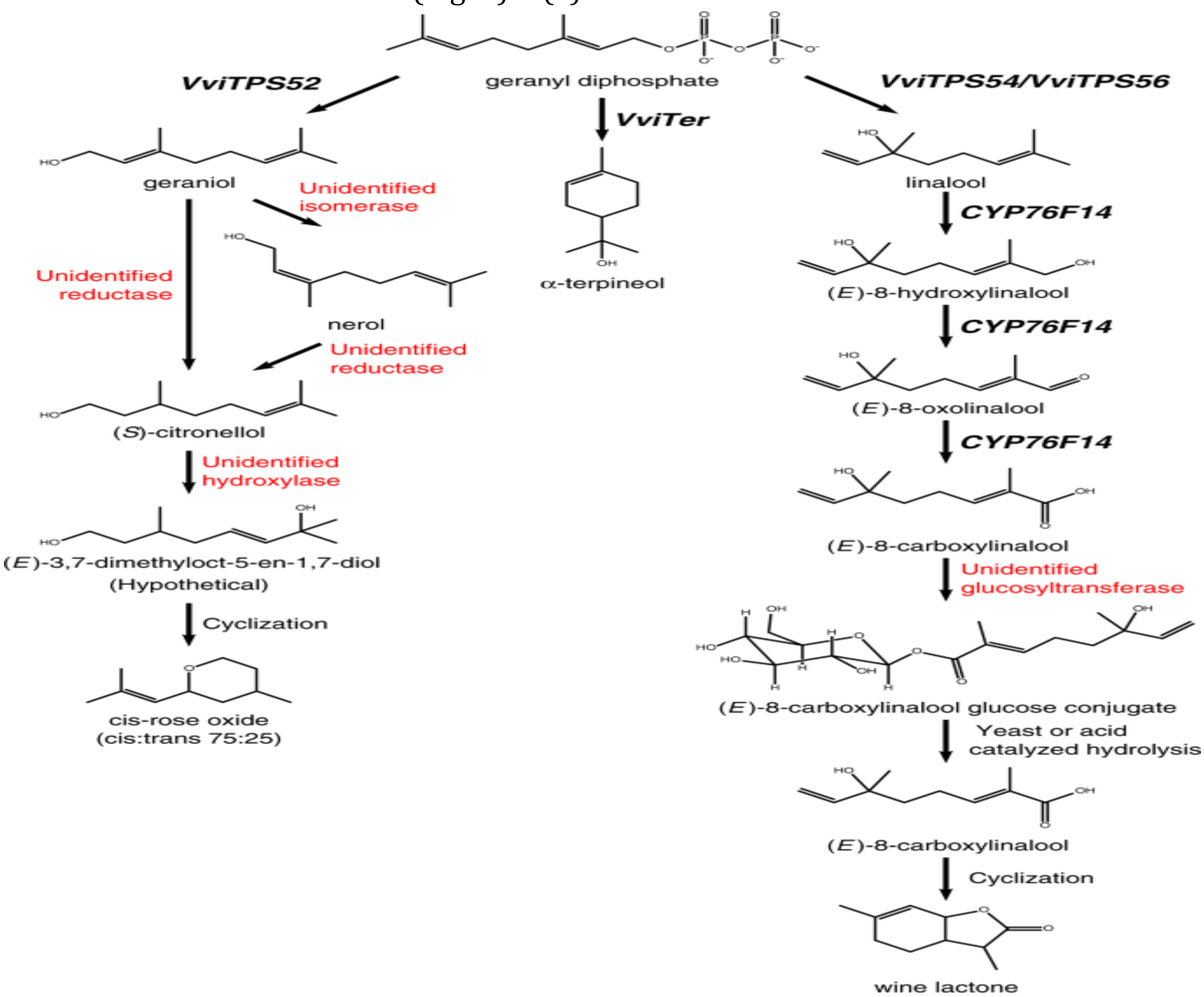
The purpose of this review is to summarize the state of our knowledge regarding grapevine genetics in relation to the biosynthesis and modification of volatile compounds. The current review is not intended to be a complete listing of the volatile compounds found in wine but to inform the reader on what has so far been elucidated regarding their genetic basis and to highlight areas that need further study. Although the impact of environmental conditions on the biosynthesis and metabolism of volatile compounds can be considerable, genotype by environment interactions have not yet been thoroughly explored in grape. A number of excellent reviews have been written regarding the diversity of wine and grape aroma compounds, environmental impacts on their biosynthesis, and their chemistry, to which we refer the reader for more information in those areas(2). An emphasis has been made here on genes that have been functionally characterized in grapevine. Where little study has been conducted on grapevine, comparable systems in other plants have been provided.

Monoterpene synthesis and modifications

With 69 putative genes identified, the terpene synthase (*TPS*) gene family is greatly expanded in *Vitis vinifera* and represents all of the angiosperm terpene synthase subfamilies except for *TPS-f*. Seventeen *VviTPS* belonging to the *TPS-b* and *TPS-g* subfamilies have been functionally characterized as monoterpene synthases. The majority are multi-product enzymes(6). In this section, we describe the genes functionally characterized as involved in the synthesis, i.e., VviTPS, and/or modification of the major monoterpenes geraniol, α-terpineol, and linalool.

In aromatic cultivars, geraniol concentrations peak early in berry development followed by a decline until véraison, at which point the concentration increases dramatically(3). *VviTPS52*, a geraniol synthase characterized by Martin et al(1), was shown to correlate with geraniol accumulation in ripening *V. vinifera* cv. Aleatico berries and to a smaller extent in Muscat blanc, indicating its importance in the biosynthesis of geraniol in ripe fruit(5). Experiments with deuterium-labeled geraniol in *V. vinifera* cv. Scheurebe berries revealed that geraniol can be converted to nerol by an unknown isomerase. In addition, geraniol can be enzymatically reduced to (*S*)-citronellol by an unidentified reductase (Fig. 1). (*S*)-citronellol then undergoes hydroxylation and cyclization to form *cis* and *trans*-rose oxide(6). *Cis*-rose oxide predominates in Gewürztraminer and Scheurebe wines and is a key component of the varietal character of Gewürztraminer(1).

Fig. 1: Proposed biosynthetic pathways of a selection of monoterpenes and monoterpene-derived metabolites in grapevine.



Although no enzymes responsible for the formation of rose oxides from (*S*)-citronellol have been identified, the process may occur in a similar manner as in rose geranium (*Pelargonium*) and roses (*Rosa damascena*)(4). Wüst et al. proposed a mechanism of diol formation via a cytochrome oxidase with low specificity followed by acid-catalyzed cyclization of two of the four resulting diols as shown in Fig(5). Enantiomeric ratios of *cis*-rose oxides in grape, rose geranium, and rose all indicate the action of as yet unidentified enzymes. It is interesting to note that during fermentation, yeast can also produce both (−) and (+) enantiomers of *cis*-rose oxide from citronellol in sufficient quantities to impact wine aroma(1). Therefore, the final impact of *cis*-rose oxide in wine depends not only on the amount synthesized by the grape but also on the level of citronellol present at harvest. The conversion rate of geraniol to citronellol increases in late berry development, indicating that the final stages of ripening are important in developing the characteristic aroma of Gewürztraminer and Scheurebe(2).

As one of the more abundant monoterpenes in grape, α-terpineol is an important component of the character of aromatic varieties(6). In addition to contributions from the rearrangement of other monoterpenes, α-terpineol is synthesized in the grape berry: a *TPS-b* subfamily α-terpineol synthase (*VviTer*) was one of the first monoterpene synthases identified and functionally characterized in grape(2). A candidate gene association study of 61 grape cultivars found two SNPs in coding regions of the *VviTer* gene correlated with higher α-terpineol concentrations. These mutations result in non-synonymous amino acid substitutions (I38S and T519I); however, additional studies are needed to establish the sensory impact of these point mutations(6).

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