Chapter 9
Pigments in Grape

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Introduction

Grapevine is the most valuable horticultural crop in the world. Significant grape acreage exists on all continents, save for Antarctica. Approximately 8 million ha of grapevine are currently planted and 60 million metric t of fruit are produced annually worldwide (Food and Agriculture Organization of the United Nations (FAO) production statistics). Spain, France, and Italy are the largest grape producers in the world, followed by many other European countries, the USA, Argentina, Chile, Australia, South Africa, and China. The majority of the fruit, in terms of yield and area, is used to produce wine, but the remaining is destined for fresh consumption, dried into raisins, processed into nonalcoholic juice, or distilled into spirits. The quality of wine and other grape products is the key to the crop's value, so sustainably maximizing quality is the primary goal of grape producers.

Most grape cultivars are used specifically in one market, but some cultivars may be used in several market classes. Premium wine and table grape cultivars are more specialized in their utilization than are raisin, juice, and concentrate varieties. For example, "Cabernet Sauvignon" is primarily used for wine but is not desirable as a table or raisin grape. "Sultanina" (known as "Thompson Seedless" in the USA) is the predominant raisin cultivar worldwide and also is an important table grape, wine grape, and concentrate cultivar. Wine grape cultivars usually have relatively small-seeded berries. Important wine cultivars include "Cabernet Sauvignon" and "Pinot Noir," used for red wine production, and "Chardonnay" and "sauvignon blanc," used for white wine production. Table grapes are consumed fresh. Table grape cultivars have relatively large berries, and seedlessness is valued by many consumers. Most dried grapes, usually called raisins, are made from seedless grapes. Unfermented juice is manufactured from cultivars with distinctive flavors and aromas. Varieties

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with relatively heat-stable flavors and aromas, such as "Concord" and "Niagara," are used in the production of pasteurized juices. Cultivars such as "Chasselas" with flavors and aromas that are noticeably altered by pasteurization are processed for unfermented juice production using ultrafiltration for juice sterilization. Jams, jellies, and other spreads are made from juice grape cultivars. Grape concentrate is juice with some water removed; it is used as a natural sweetener and coloring agent for beverages and foods. The concentrate market is an outlet for excess grapes in all market classes and is a target market for certain cultivars; "Rubired," a highly pigmented cultivar, is used in red concentrate.

The grape is a member of the Vitaceae, commonly called the grape family. The genus *Vitis* consists of about 60 species, plus some natural interspecific hybrids [1]. Nearly all grapes cultivated for fruit production are of the species *Vitis vinifera* or are hybrids that include *V. vinifera* in their parentage. *Vitis* species are found across the temperate zones of the Northern Hemisphere. The genus has the highest species diversity in east Asia and in eastern and southern North America, with about 30 species in each region. *Vitis* is separated into two subgenera, *Euvitis* and *Muscadinia*; some authorities treat the sections as the genera *Vitis* and *Muscadinia*. The subgenera are separated by morphological, anatomical, and cytological characteristics. Subgenus *Euvitis* species have $2n=2x=38$ chromosomes, forked tendrils, striate bark, pyriform seeds, and nodal diaphragms. These species and their hybrids are called "bunch grapes." Subgenus *Muscadinia* species have $2n=2x=40$ chromosomes, unforked tendrils, stellate bark, naviform seeds, and lack diaphragms at the nodes; they are known as muscadine grapes. Within a subgenus, species are maintained in nature by range and flowering time and can be considered ecospecies. Hybrids between species within a subgenus are typically fully fertile and many interspecific hybrids between *Euvitis* species have been developed as scion and rootstock cultivars. Hybrids between the subgenera are usually sterile due to the difference in chromosome number; two have been commercialized as rootstocks [2], and backcrossing with partially fertile intersubgeneric hybrids has led to the introduction of disease resistance from *Vitis rotundifolia* into bunch grape gene pools [3].

Subgenus *Euvitis* species (about 57 species) are the most important in viticulture. Most grape cultivars belong to the species *V. vinifera,* which is a native of the Mediterranean basin, southern and central Europe, northern Africa, and southwest and central Asia. *V. vinifera* cultivars are grown worldwide and account for the overwhelming majority of cultivated areas and grapes produced. Interspecific hybrid cultivars selected from crosses of *V. vinifera* with other species, including *Vitis labrusca, Vitis amurensis, Vitis riparia, Vitis rupestris,* and *Vitis aestivalis*, are locally important and account for a minor portion of world viticulture and enology. Rootstocks are used exclusively for bunch grape varieties, which are mostly interspecific hybrids or selections of North American *Euvitis* species.

The subgenus *Muscadinia* includes only three species. The range of the subgenus is limited to the southeastern USA and eastern Mexico. Muscadine grape cultivars, primarily *V. rotundifolia* and a few interspecific hybrids, are grown commercially only in the native region of *V. rotundifolia* in the southeastern USA.

Pigments in Grapes

The primary pigments in grapes are anthocyanins. The distribution and classification of anthocyanins within grape berries have been extensively studied. Anthocyanins are specific to red cultivars and localized in the berry skin of most cultivars. A small number of red-fleshed cultivars (also known as teinturier, Fig. 9.1) play a key role in producing highly pigmented juice for wine making. Anthocyanin profiles of many *V. vinifera* cultivars as well as several other *Vitis* species have been reported and previously reviewed [4–6]. Structurally, anthocyanins are glycosides and acyl-glycosides of anthocyanidins, and the aglycones and flavyliums differ in different hydroxyl or methoxyl substitutions in their basic structures [4]. The proportion of the primary individual anthocyanins is the 3-*O*-monoglucosides of delphinidin, cyanidin, peonidin, petunidin, and malvidin, with the proportion of 3′ and 3′, 5′ forms showing variation among cultivars as well as the contribution of acetylated forms [7]. In cultivars of *V. vinifera,* the glucose molecules can only be linked to the anthocyanidin through glycosidic bonds at the C_3 position to form 3-*O*-monoglucoside anthocyanins. In the other non-*V. vinifera* species, the 3,5-*O*-diglucoside anthocyanins can be present. Most cultivars possess acylated forms of the anthocyanins, but some have a much simpler profile, with the cultivar "Pinot Noir" being a notable example, possessing only the five basic anthocyanidin 3-glucosides. Some grape species, such as *V. rotundifolia,* are also known not to produce acylated forms of anthocyanins [8, 9]. It has recently been shown that the majority of anthocyanins within a cross section of North American grape species show a predominance of nonacylated forms of anthocyanins [10].

Further diversity in anthocyanin content is possible due to the presence of two distinct forms at vacuolar pH, the neutral quinonoidal anhydro base and the flavylium cation form [11]. The wide range in possible anthocyanin forms has led to a large amount of diversity in fruit color among cultivated grapes (Fig. 9.2). Because of this high level of diversity, grape cultivars have distinct anthocyanin profiles and it has been proposed as a method for the authentication of grape varieties and wine [12–14]. *V. vinifera* cultivars are characterized by the presence of only the monoglucoside forms of anthocyanins, while several of the wild *Vitis* species possess diglucosides. A double mutation occurring in an anthocyanin 5-*O*-glucosyltransferase within *V. vinifera* appears to be the cause for the loss of this enzymatic activity within this species [15].

Fig. 9.1 Anthocyanin accumulation within berry flesh of the teinturier cultivar "Bailey Alicante" during berry maturation
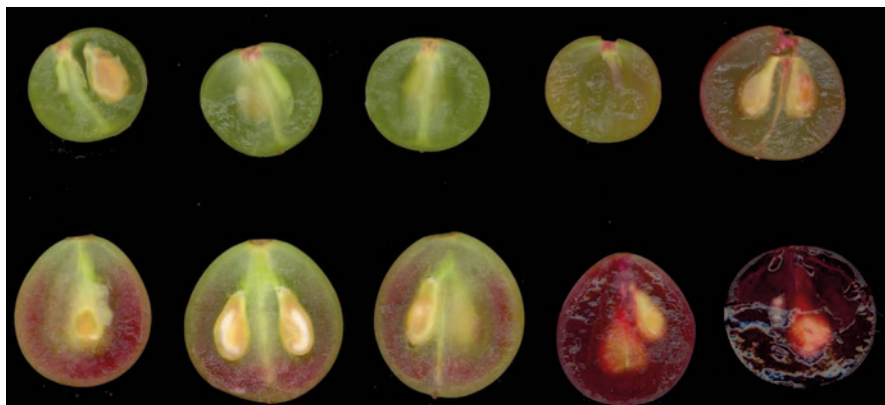
Fig. 9.2 Berry color diversity present within the cultivated grapevine *Vitis vinifera*

The production of red wine requires the maceration of the berries in order to extract the pigments from the berry skins. The concentration of anthocyanins begins to decrease after a few days of skin contact within the fermenting must [16]. During the course of wine ageing, polymeric pigments are known to form from reactions of anthocyanins with tannins [17], or from reactions with aldehydes [18]. Additionally, anthocyanin reactions that do not involve tannins are known to occur [19]. The resulting pigments include both anthocyanin polymers [20, 21] and small molecules such as pyranoanthocyanins [16, 22, 23], that are derived from the addition of yeast metabolites to the anthocyanins as well as caftaric acid–anthocyanin adducts that are formed through enzymatic reactions [24].

Anthocyanins are usually represented in the red flavylium cation form, the color of which shifts toward higher wavelengths (from orange to purple) as the number of substituents on the B ring increases. However, when dissolved in water, flavylium cations undergo proton transfer and hydration reactions, generating blue quinonoidal bases and colorless hemiketals, respectively [16]. At wine pH, grape anthocyanins occur mostly as the colorless, hydrated hemiketal form.

Red wine color is ensured through two stabilization processes: conversion of grape anthocyanins to other pigments, and association mechanism collectively called copigmentation. Anthocyanin-derived pigments show a wide range of colors from orange to blue. Tannin–anthocyanin adducts are red, like their anthocyanin precursors (λ_{max} 515–526 nm). Other reaction products include orange pyranoanthocyanins (λ_{max} 480–510 nm) [25, 26], purple ethyl-linked species (λ_{max} 528–540 nm) [18, 27], and blue flavanyl-vinylpyranoanthocyanins (λ_{max} 575 nm) [28]. These compounds may also change colors with the alternation of pH.

Color stabilization may also occur through copigmentation. The phenomenon of copigmentation is due to the molecular association between pigments and other nonpigmented organic molecules, leading to the exhibition of far greater color than would be expected by the pigment concentration [29]. Copigmentation can account for between 30 and 50% of the color in young wines and is vitally important for

determining wine color, the variation in color and pigment concentration between wines. Copigmentation both increases color intensity (the hyperchromic effect) and shifts the color toward purple (the bathochromic effect). Colored anthocyanins are planar structures that can interact with other planar species (copigments) to form molecular stacks from which water is excluded. The flavylium ion is thus trapped and protected from hydration. This is particularly important at wine pH, where hydrated forms predominate.

Genetic Control and Variability in Anthocyanin Accumulation

The genetic control and inheritance of fruit color or anthocyanin production in grapevine are not fully understood despite evidence that the primary determination of anthocyanin production in berries appears to be controlled by a single dominant locus in *V. vinifera* [30, 31] with white fruit being a recessive character. This observation is supported by numerous reports showing that controlled crosses between white-fruited vines universally result in white-fruited progeny [32–37]. Although fruit color in grape is frequently characterized as a qualitative trait, quantitative variation does exist within segregating populations for total anthocyanin and for anthocyanin content. Broad-sense heritability is typically high for total anthocyanin content, and the majority of the phenotypic variation localizes to a genetic loci containing a cluster of myeloblastosis (MYB) transcription factors [38–41]. A genetic association analysis with candidate genes from the anthocyanin biosynthetic pathway revealed many polymorphisms within five regulatory and ten structural genes to be positively associated with anthocyanin content [42].

The genetic regulation of the flavonoid biosynthetic pathways has been extensively studied. Work conducted primarily in *Arabidopsis* and maize has shown that the basic flavonoid pathway upstream of anthocyanin biosynthesis is under the control of several different families of regulatory genes, consisting of complexes of MYB, basic helix-loop-helix (bHLH), and WD40. These regulatory genes are connected to form a network to regulate the expression of the structural genes involved in flavonoid synthesis. Similarities in sequence homology have been used to isolate and characterize many of the flavonoid biosynthetic structural genes in grape [43–47].

In grapes, a series of R2R3-Myb transcription factors has been demonstrated to be involved in the control of different aspects of the phenylpropanoid pathway [48]. Despite the characterization of several MYB proteins and their role in grapevine anthocyanin regulation, characterization of additional members of the protein complexes is not as well described. One bHLH gene, *VvMYC1*, was characterized as a component of the transcriptional complex controlling anthocyanin biosynthesis in grapevine [49]. The first *Myb* transcription factors identified in grape were isolated from *V. labrusca* hybrids [50], with subsequent orthologs identified in *V. vinifera* [51].

White-fruited grapes are linked to the homozygous presence of *Gret1* in the promoter region of *Vvmyba1* as well as mutations in the tightly linked gene *Vvmyba2* [52, 53]. *Gret1* is inserted in the 5′ flanking region of *VvmybA1,* resulting in the loss of function of this transcription factor. In pigmented somatic mutants of white-fruited cultivars, the full *Gret1* insertion is absent from the *VvymbA1* gene, but a solo long terminal repeat (LTR) has been shown to remain [54, 55]. Pigmented cultivars possess at least one allele at the *VvmybA1* locus not containing this large insertion [56]. In pigmented cultivars, *VvmybA1* is expressed only after veraison and has been shown to regulate anthocyanin biosynthesis by controlling the expression of anthocyanin biosynthetic genes, particularly flavonoid-3-*O*-glucosyltransferase (UFGT). Further evidence suggested that *VvmybA1* is not expressed in the young leaves, tendrils, or stem of grape vines and is tissue-specific to the berry [54, 57], while ectopic expression of *Vlmyba1–2* was shown to induce the expression of many of the genes within the flavonoid biosynthetic pathway [58].

VvmybA1 belongs to a family of linked regulatory genes which have related sequence homology, *VvmybA2* and *VvmybA3*. Sequence analysis of *VvmybA2* in 55 white cultivars of *V. vinifera* shows that the existence of rare mutations in two adjacent regulatory genes, the insertion of *Gret1* in *VvmybA1* and two nonconservative mutations in *VvmybA2* are present in many white-fruited cultivars [59]. Although white-fruited somatic mutations appear to be independent developments of white-fruited cultivars [55], evidence shows that *VvmybA1* co-segregates with the morphological marker for berry color [60] and that mutations in *VvmybA1* are associated with the vast majority of white-fruited *V. vinifera* accessions and many pink and red accessions as well [53, 60]. Additional polymorphisms within this cluster of closely related *myb* genes are also significantly associated with quantitative variation in anthocyanin content of berries [61, 62]. Recent work, mapping gene expression quantitative trait loci (QTL), also shows that the majority of the phenotypic variation within a population derived from a cross between two pigmented cultivars, "Syrah" and "Grenache," colocated with the *VvmybA* gene cluster, while an additional large eQTL co-localized with *VvUFGT* [63].

Cellular Transport of Anthocyanins

The distribution of anthocyanins in the different branches of a grape cluster is highly variable depending on many environmental and physiological factors. Anthocyanins primarily accumulate in the hypodermal cell layers of the berry skin post-veraison. Anthocyanins are synthesized in the cytoplasm but accumulate in the vacuoles. Several glutathione S-transferase (GST) genes have been identified in grapes, which could function as anthocyanin transporters [64, 65]. In *Arabidopsis* and maize, GST proteins function with a glutathione S-conjugate pump and belong to the multidrug resistance-associated protein (MRP) family. To date, no MRP has been identified in grape involved with anthocyanin transport.

Two genes that encode multidrug and toxic compound extrusion (MATE) transporters have been identified in grape [66]. These genes were specifically expressed in fruit and showed expression patterns that correlated with anthocyanin accumulation. These genes have also been shown in vivo to be involved in vesicular anthocyanin transport in addition to GST [67]. Additionally, putative flavonoid translocators, which may be responsible for anthocyanin transport, and are similar to mammalian bilitranslocase, have been identified in ripening red- and white-fruited cultivars [68, 69].

Factors Affecting Variation in Anthocyanins

Variability in anthocyanin concentration and composition is known to be influenced by genotypes, berry developmental stages, environmental conditions, and cultural factors [7, 70].

The developmental stages of ripening have been shown to affect anthocyanin accumulation, with a two-stage accumulation, including a rapid increase of anthocyanins at early stages of development, closely correlated with sugar accumulation, followed by a second stage with slower accumulation [71]. These stages of ripening-related anthocyanin accumulation have been shown to be associated with vine vegetative conditions and climatic conditions [7]. The 3′-subsituted forms of anthocyanins have been observed to form earlier in the berry development than the 3′,5′ forms [72, 73].

Mineral nutrition is also known to influence variability in anthocyanin accumulation [70]. Higher concentrations of malvidin-3-O-glucoside and malvidin-3-O-coumarate glucoside in "Cabernet Sauvignon" vines that had been grafted on the high-vigor rootstock 1103P compared to those grafted on SO4 [74]. Heavy nitrogen application earlier in the season has been shown to delay ripening and to affect anthocyanin accumulation and composition [75].

Light and temperature also affect anthocyanin accumulation, with divergent effects depending on the ambient temperature [76–78]. Compositional changes in the constituent anthocyanins have also been observed in response to increases in solar radiation [76, 79, 80], while higher temperatures have also been reported to increase the proportion of acetylated to nonacetylated forms of anthocyanins [72, 76, 80]. Water deficits have also been showed to result in changes to anthocyanin concentrations as well as composition [81–83]. High nighttime temperatures have been shown to reduce the expression of several of the structural genes within the flavonoid biosynthetic pathway and also result in a reduction in the accumulation of anthocyanins [84–86]. Conversely, low storage temperatures have been shown to lead to an increase in expression of some of the flavonoid biosynthetic genes as well as an increase in anthocyanin accumulation [87, 88].

Considering the high value of the crop, extensive research has been conducted on utilizing viticultural practices to enhance fruit and wine quality, including the production of grape pigments. Cluster thinning, either by hand or mechanically,

early in the season, prior to fruit set, has been shown to have many effects on fruit quality, including an increase in anthocyanin accumulation [89]. Conversely, cluster thinning at veraison has been shown to have much less of an effect on fruit quality [90]. Numerous additional cultural factors are known to affect berry quality, including the accumulation of anthocyanins, such as girdling of stems, disease infection, or the use of partial root-zone drying [91–93].

Ultraviolet irradiation is known to increase the expression of anthocyanin biosynthetic genes in several plant species and also lead to an increase in the accumulation of anthocyanins [70, 94]. Research examining the structure of the promoter sequences of two of the structural genes involved in flavonoid biosynthesis in grapes revealed that these genes could be induced by exposure to ultraviolet-A light [95, 96]. Similarly, it has been shown that exposure of grape berries to ultraviolet irradiation leads to the accumulation of anthocyanins in the cultivar "Gros Colman" [97].

Phytohormones are also known to influence anthocyanin accumulation in grape berries and tissues. Abscisic acid (ABA) is a phytohormone involved in stress responses, especially in response to water stress. It is known that the application of ABA can increase the anthocyanin content in grape berry skin and that application of ABA can greatly enhance the color of grapes [98]. Addition of ABA to grape cell suspension cultures can also promote anthocyanin accumulation and increase the expression of chalcone isomerase [99]. Additional work has shown exogenous application of ABA leads to enhance the expression of several structural genes involved in flavonoid biosynthesis as well as the regulatory gene VvmybA1 [100, 101].

Ethylene is a phytohormone known to influence many aspects of fruit ripening [70]. Application of the ethylene-releasing compound, 2-chloroethylphosphonic acid (2-CEPA), can hasten the accumulation of anthocyanins in grape skin, and application of 2-CEPA has been shown to increase the expression of several genes involved in flavonoid biosynthesis [102]. Similarly, the postharvest application of ethylene and/or 1-methylcyclopropene (1-MCP) to grape berries has been shown to improve the stability of anthocyanins during storage [103].

The application of some phytohormones has been shown to have a negative impact on anthocyanin accumulation. Specifically, application of the auxins 2,4-dichlorophenoxyacetic acid (2,4-D) or 1-napthaleneacetic acid (1-NAA) to grape berries has been shown to reduce the expression of several structural genes in the flavonoid biosynthetic pathways, and decrease the expression of *Vvmyba1* as well [100, 101].

Several nonphytohormone chemicals have also been shown to influence the accumulation of anthocyanins in grape berries and other tissues. The accumulation of sugars is closely correlated with the accumulation of anthocyanins in developing grape berries, and some evidence shows that sugars can stimulate the expression of some of the structural genes involved in flavonoid biosynthesis as well as lead to an increase in the accumulation of anthocyanins [104, 105]. Similarly, the application of a 5% ethanol solution has been shown to enhance the accumulation of anthocyanins in grape berries at veraison as well as increase the expression of several of the structural genes involved in the flavonoid biosynthetic pathway [106].

Also, eutypine [4-hydroxy-3-(3-methyl-3-butene-1-ynyl)benzaldehyde], the toxin produced by *Eutypa lata,* the pathogen causing Eutypa dieback in grapevines, has been shown to reduce the gene expression of UFGT, but not additionally tested flavonoid structural genes, and also inhibits the accumulation of anthocyanins in developing grape berries [107].

Anthocyanin Production Using Cell Suspension Culture

There is significant interest in using cell suspension cultures as a means for producing anthocyanins as natural colorants in the food industry [108, 109]. The primary source of cells for suspension cultures for the production of grape anthocyanins come from the two intensely pigmented teinturier cultivars, "Gamay Freaux" or "Bailey Alicante," in which high osmotic potential has been shown to enhance anthocyanin production [110, 111]. Elevating the sucrose content in the cell culture medium can increase the external osmotic potential and lead to an increase in anthocyanin accumulation, presumably through a mechanism similar to the osmotic stress induced under water deficit. Similar increases in anthyocyanin accumulation are observed through the addition of other osmolytes, such as mannitol. The addition of nitrate has also been shown to increase anthocyanin levels in cell suspension cultures, presumably by removing an inhibitory effect on production and transport [111]. In contrast, high ammonium concentrations in the culture medium can lead to a reduction in the accumulation of anthocyanins [112]. Combined, the effect of high sugar and low nitrogen can lead to an increase in anthocyanin accumulation [111]. Similarly, phosphate deprivation has been shown to increase the expression of dihydroflavonol 4-reductase (DFR) and additional increase in the accumulation of anthocyanins in cell suspension culture [113]. Polysaccharide elicitors have also been shown to enhance the accumulation of anthocyanins in cell suspension culture [114].

Conclusions

Grapes are one of the world's most important horticultural crops, in which the quality of wine and other grape products is the chief determinant of its value and importance. Wine, juice, and grape color are critical in determining the maximum quality of grape products, and substantial research has been conducted into the diversity of grape anthocyanins, regulation, physiology, and environmental/cultural factors that affect the production of anthocyanins. Although the anthocyanin pigments are widely distributed in the plant kingdom and have been extensively studied in many plant species, including many cultivated fruit crops, grapevine anthocyanins are of extreme agricultural significance due to the value and worldwide distribution of the crop. Additionally, the diversity of anthocyanins present within cultivated grape

suggests the importance of these compounds for this crop and presents exciting opportunities to study the underlying processes leading to diversification of grape pigments over time.

References

1. Wen J (2007) Vitaceae. In: Kubitzki K (ed) Flowering plants-eudicots, vol 9. Springer-Verlag, Berlin, pp 467–479
2. Walker MA, Lider LA, Goheen AC, Olmo HP (1991) VR 039-16 grape rootstock. Hortscience 26(9):1224–1225. PubMed PMID: WOS:A1991GH45000049
3. Pauquet J, Bouquet A, This P, Adam-Blondon AF (2001) Establishment of a local map of AFLP markers around the powdery mildew resistance gene Run1 in grapevine and assessment of their usefulness for marker assisted selection. Theor Appl Genet 103(8):1201–1210. PubMed PMID: WOS:000173261300011
4. Mazza G (1995) Anthocyanins in grapes and grape products. Crit Rev Food Sci Nutr 35(4):341–371. PubMed PMID: WOS:A1995RM36300003
5. Liang Z, Owens CL, Zhong G-Y, Cheng L (2011) Polyphenolic profiles detected in the ripe berries of Vitis vinifera germplasm. Food Chem 129(3):940–950. PubMed PMID: WOS:000293726500034
6. Pomar F, Novo M, Masa A (2005) Varietal differences among the anthocyanin profiles of 50 red table grape cultivars studied by high performance liquid chromatography. J Chromatogr A 1094(1–2):34–41. PubMed PMID: WOS:000233150600005
7. Dai ZW, Ollat N, Gomes E, Decroocq S, Tandonnet J-P, Bordenave L et al (2011) Ecophysiological, genetic, and molecular causes of variation in grape berry weight and composition: a review. Am J Enol Vitic 62(4):413–425. PubMed PMID: WOS:000298125500001
8. Goldy RG, Maness EP, Stiles HD, Clark JR, Wilson MA (1989) Pigment quantity and quality characteristics of some native vitis-rotundifolia michx. Am J Enol Viti 40(4):253–258. PubMed PMID: WOS:A1989CC66100005
9. Pastrana-Bonilla E, Akoh CC, Sellappan S, Krewer G (2003) Phenolic content and antioxidant capacity of muscadine grapes. J Agr Food Chem 51(18):5497–5503. PubMed PMID: WOS:000184941500048
10. Liang Z, Yang Y, Cheng L, Zhong G-Y (2012) Polyphenolic composition and content in the ripe berries of wild Vitis species. Food Chem 132(2):730–738. PubMed PMID: WOS:000300475800008
11. Adams DO (2006) Phenolics and ripening in grape berries. Am J Enol Viti 57(3):249–256. PubMed PMID: WOS:000240934100002
12. Mattivi F, Guzzon R, Vrhovsek U, Stefanini M, Velasco R (2006) Metabolite profiling of grape: flavonols and anthocyanins. J Agr Food Chem 54(20):7692–7702. PubMed PMID: WOS:000240795400041
13. Edelmann A, Diewok J, Schuster KC, Lendl B (2001) Rapid method for the discrimination of red wine cultivars based on mid-infrared spectroscopy of phenolic wine extracts. J Agr Food Chem 49(3):1139–1145. PubMed PMID: WOS:000168967400011
14. Etievant P, Schlich P, Bertrand A, Symonds P, Bouvier JC (1988) Varietal and geographic classification of french red wines in terms of pigments and flavonoid compounds. J Sci Food Agr 42(1):39–54. PubMed PMID: WOS:A1988L932000005
15. Janvary L, Hoffmann T, Pfeiffer J, Hausmann L, Toepfer R, Fischer TC et al (2009) A double mutation in the anthocyanin 5-O-Glucosyltransferase gene disrupts enzymatic activity in *Vitis vinifera* L. J Agr Food Chem 57(9):3512–3518. PubMed PMID: WOS:000265896600018
16. Cheynier V, Prieur C, Guyot S, Rigaud J, Moutounet M (1997) The structures of tannins in grapes and wines and their interactions with proteins. In: Watkins TR (ed) Wine: nutritional and therapeutic benefits. ACS Symposium Series 661, pp 81–93

17. Salas E, Atanasova V, Poncet-Legrand C, Meudec E, Mazauric JP, Cheynier V (2004) Demonstration of the occurrence of flavanol-anthocyanin adducts in wine and in model solutions. Analytica Chimica Acta 513(1):325–332. PubMed PMID: WOS:000221718000043

18. Timberlake CF, Bridle P (1976) Interactions between anthocyanins, phenolic compounds, and acetaldehyde and their significance in red wines. Am J Enol Viti 27(3):97–105. PubMed PMID: WOS:A1976CM12400001

19. Cheynier V (2005) Polyphenols in foods are more complex than often thought. Am J Clin Nutr 81(1):223S–229S. PubMed PMID: WOS:000226401200003

20. Salas E, Duenas M, Schwarz M, Winterhalter P, Cheynier W, Fulcrand H (2005) Characterization of pigments from different high speed countercurrent chromatography wine fractions. J Agr Food Chem 53(11):4536–4546. PubMed PMID: WOS:000229405000035

21. Vidal S, Meudec E, Cheynier V, Skouroumounis G, Hayasaka Y (2004) Mass spectrometric evidence for the existence of oligomeric anthocyanins in grape skins. J Agr Food Chem 52(23):7144–7151. PubMed PMID: WOS:000225080100047

22. Fulcrand H, Benabdeljalil C, Rigaud J, Cheynier V, Moutounet M (1998) A new class of wine pigments generated by reaction between pyruvic acid and grape anthocyanins. Phytochemistry 47(7):1401–1407. PubMed PMID: WOS:000073714200040

23. Fulcrand H, Duenas M, Salas E, Cheynier V (2006) Phenolic reactions during winemaking and aging. Am J Enol Viti 57(3):289–297. PubMed PMID: WOS:000240934100006

24. Sarni-Manchado P, Cheynier V, Moutounet M (1997) Reactions of polyphenoloxidase generated caftaric acid o-quinone with malvidin 3-O-glucoside. Phytochemistry 45(7):1365–1369. PubMed PMID: WOS:A1997XL54600008

25. Benabdeljalil C, Cheynier V, Fulcrand H, Hakiki A, Mosaddak M, Moutounet M (2000) Evidence of new pigments resulting from reaction between anthocyanins and yeast metabolites. Sci Aliment 20(2):203–219. PubMed PMID: WOS:000088101400002

26. Sarni-Manchado P, Fulcrand H, Souquet JM, Cheynier V, Moutounet M (1996) Stability and color of unreported wine anthocyanin-derived pigments. J Food Sci 61(5):938–941. PubMed PMID: WOS:A1996VN17500018

27. Atanasova V, Fulcrand H, Le Guerneve C, Cheynier W, Moutounet M (2002) Structure of a new dimeric acetaldehyde malvidin 3-glucoside condensation product. Tetrahedron Lett 43(35):6151–6153. PubMed PMID: WOS:000177467500015

28. Mateus N, Silva AMS, Rivas-Gonzalo JC, Santos-Buelga C, De Freitas V (2003) A new class of blue anthocyanin-derived pigments isolated from red wines. J Agr Food Chem 51(7):1919–1923. PubMed PMID: WOS:000181706300027

29. Boulton R (2001) The copigmentation of anthocyanins and its role in the color of red wine: a critical review. Am J Enol Viti 52(2):67–87. PubMed PMID: WOS:000170693800001

30. Doligez A, Bouquet A, Danglot Y, Lahogue F, Riaz S, Meredith CP et al (2002) Genetic mapping of grapevine (*Vitis vinifera* L.) applied to the detection of QTLs for seedlessness and berry weight. Theor Appl Genet 105:780–795

31. Riaz S, Dangl GS, Edwards KJ, Meredith CP (2004) A microsatellite marker based framework linkage map of *Vitis vinifera* L. Theor Appl Genet 108(5):864–872. PubMed PMID: ISI:000220424400012

32. Madero E, Boubals D, Truel P (1986) Transmission hereditaire des principaux caracters des cepages Cabernet Franc, Cabernet Sauvignon et Merlot (*V. vinifera* L.). Vigne Vini 13(Suppl. 12):209–219

33. Barritt BH, Einset J (1969) Inheritance of 3 major fruit colors in grapes. J Amer Soc Hortic Sci 94(2):87–89. PubMed PMID: ISI:A1969D534400002

34. Hedrick UP, Anthony RD (1915) Inheritance of certain characters of grapes. New York State Agricultural College Technical Bulletin No 45, pp 3–19

35. Snyder E, Harmon FN (1939) Grape progenies of self-pollinated vinifera varieties. Proc Am Soc Hortic Sci 37:625–626

36. Snyder E, Harmon FN (1952) Grape breeding summary 1923–1951. Proc Am Soc Hortic Sci 60:243–246. PubMed PMID: ISI:A1952YB31100040

37. Wellington R (1939) The Ontario grape and its seedlings as parents. Proc Am Soc Hortic Sci 37:630–634

38. Liang Z, Sang M, Wu B, Ma A, Zhao S, Zhong G-Y et al (2012) Inheritance of anthocyanin content in the ripe berries of a tetraploid x diploid grape cross population. Euphytica 186(2):343–356. PubMed PMID: WOS:000304698100007

39. Fournier-Level A, Le Cunff L, Gomez C, Doligez A, Ageorges A, Roux C et al (2009) Quantitative genetic bases of anthocyanin variation in grape (*Vitis vinifera* L. ssp *sativa*) berry: a quantitative trait locus to quantitative trait nucleotide integrated study. Genetics 183(3):1127–1139. PubMed PMID: WOS:000272295800030

40. Bayo-Canha A, Ignacio Fernandez-Fernandez J, Martinez-Cutillas A, Ruiz-Garcia L (2012) Phenotypic segregation and relationships of agronomic traits in Monastrell x Syrah wine grape progeny. Euphytica 186(2):393–407. PubMed PMID: WOS:000304698100011

41. Viana AP, Riaz S, Walker MA (2013) Genetic dissection of agronomic traits within a segregating population of breeding table grapes. Genet Mol Res 12(2):951–964. PubMed PMID: WOS:000320030100009

42. Cardoso S, Lau W, Dias JE, Fevereiro P, Maniatis N (2012) A candidate-gene association study for berry colour and anthocyanin content in *Vitis vinifera* L. Plos ONE 7(9):e46021. PubMed PMID: WOS:000309973900073

43. Boss PK, Davies C, Robinson SP (1996) Analysis of the expression of anthocyanin pathway genes in developing *Vitis vinifera* L cv Shiraz grape berries and the implications for pathway regulation. Plant Physiol 111(4):1059–1066. PubMed PMID: WOS:A1996VD68800012

44. Bogs J, Ebadi A, McDavid D, Robinson SP (2006) Identification of the flavonoid hydroxylases from grapevine and their regulation during fruit development. Plant Physiol 140(1):279–291. PubMed PMID: WOS:000234492100025

45. Boss PK, Davies C, Robinson SP (1996) Expression of anthocyanin biosynthesis pathway genes in red and white grapes. Plant Mol Biol 32(3):565–569. PubMed PMID: WOS:A1996VY66300019

46. Ford CM, Boss PK, Hoj PB (1998) Cloning and characterization of *Vitis vinifera* UDP-glucose: flavonoid 3-O-glucosyltransferase, a homologue of the enzyme encoded by the maize Bronze-1 locus that may primarily serve to glucosylate anthocyanidins in vivo. J Biol Chem 273(15):9224–9233. PubMed PMID: WOS:000072990800091

47. Hall D, Yuan XX, Murata J, De Luca V (2012) Molecular cloning and biochemical characterization of the UDP-glucose: flavonoid 3-O-glucosyltransferase from Concord grape (*Vitis labrusca*). Phytochemistry 74:90–99. PubMed PMID: WOS:000300815700009

48. Deluc L, Bogs J, Walker AR, Ferrier T, Decendit A, Merillon J-M et al (2008) The transcription factor VvMYB5b contributes to the regulation of anthocyanin and proanthocyanidin biosynthesis in developing grape berries. Plant Physiol 147(4):2041–2053. PubMed PMID: WOS:000258184800051

49. Hichri I, Heppel SC, Pillet J, Leon C, Czemmel S, Delrot S et al (2010) The basic helix-loop-helix transcription factor MYC1 Is involved in the regulation of the flavonoid biosynthesis pathway in grapevine. Mol Plant 3(3):509–523. PubMed PMID: WOS:000278819900004

50. Kobayashi S, Ishimaru M, Hiraoka K, Honda C (2002) Myb-related genes of the Kyoho grape (*Vitis labruscana*) regulate anthocyanin biosynthesis. Planta 215(6):924–933. PubMed PMID: WOS:000178995100005

51. Kobayashi S, Goto-Yamamoto N, Hirochika H (2004) Retrotransposon-induced mutations in grape skin color. Science 304(5673):982. PubMed PMID: WOS:000221383300039

52. Walker AR, Lee E, Bogs J, McDavid DAJ, Thomas MR, Robinson SP (2007) White grapes arose through the mutation of two similar and adjacent regulatory genes. Plant J 49:772–785

53. This P, Lacombe T, Cadle-Davidson M, Owens CL (2007) Wine grape (*Vitis vinifera* L.) color associates with allelic variation in the domestication gene *VvmybA1*. Theor Appl Genet 114:723–730

54. Kobayashi S, Yamamoto NG, Hirochika H (2005) Association of VvmybA1 gene expression with anthocyanin production in grape (*Vitis vinifera*) skin—color mutants. J Jpn Soc Hortic Sci 74(3):196–203. PubMed PMID: WOS:000229191200003

55. Vezzulli S, Leonardelli L, Malossini U, Stefanini M, Velasco R, Moser C (2012) Pinot blanc and Pinot gris arose as independent somatic mutations of Pinot noir. J Exp Bot 63(18):6359–6369. PubMed PMID: WOS:000311645700006

56. Kobayashi S, Goto-Yamamoto N, Hirochika H (2004) Retrotransposon-induced mutations in grape skin color. Science 304:982

57. Jeong ST, Goto-Yamamoto N, Hashizume K, Esaka M (2006) Expression of the flavonoid 3†²-hydroxylase and flavonoid 3†²,5†²-hydroxylase genes and flavonoid composition in grape (*Vitis vinifera*). Plant Sci 170(1):61–69. PubMed PMID: WOS:000233340800008

58. Cutanda-Perez M-C, Ageorges A, Gomez C, Vialet S, Terrier N, Romieu C et al (2009) Ectopic expression of VlmybA1 in grapevine activates a narrow set of genes involved in anthocyanin synthesis and transport. Plant Mol Biol 69(6):633–648. PubMed PMID: WOS:000263899400001

59. Walker AR, Lee E, Bogs J, McDavid DAJ, Thomas MR, Robinson SP (2007) White grapes arose through the mutation of two similar and adjacent regulatory genes. Plant J 49(5):772–785. PubMed PMID: WOS:000244280300001

60. Lijavetzky D, Ruiz-Garcia L, Cabezas JA, De Andres MT, Bravo G, Ibanez A et al (2006) Molecular genetics of berry colour variation in table grape. Mol Genet Genom 276:427–435

61. Fournier-Level A, Le Cunff L, Gomez C, Doligez A, Ageorges A, Roux C et al (2009) Quantitative genetic bases of anthocyanin variation in grape (*Vitis vinifera* L. ssp *sativa*) berry: a quantitative trait locus to quantitative trait nucleotide integrated study. Genetics 183(3):1127–1139. PubMed PMID: ISI:000272295800030

62. Azuma A, Udo Y, Sato A, Mitani N, Kono A, Ban Y et al (2011) Haplotype composition at the color locus is a major genetic determinant of skin color variation in *Vitis xlabruscana* grapes. Theor Appl Genet 122(7):1427–1438. PubMed PMID: WOS:000289478500015

63. Huang Y-F, Bertrand Y, Guiraud J-L, Vialet S, Launay A, Cheynier V et al (2013) Expression QTL mapping in grapevine-revisiting the genetic determinism of grape skin colour. Plant Sci 207:18–24. PubMed PMID: WOS:000319488200004

64. Ageorges A, Fernandez L, Vialet S, Merdinoglu D, Terrier N, Romieu C (2006) Four specific isogenes of the anthocyanin metabolic pathway are systematically co-expressed with the red colour of grape berries. Plant Sci 170(2):372–383. PubMed PMID: WOS:000234732700020

65. Conn S, Curtin C, Bezier A, Franco C, Zhang W (2008) Purification, molecular cloning, and characterization of glutathione S-transferases (GSTs) from pigmented *Vitis vinifera* L. cell suspension cultures as putative anthocyanin transport proteins. J Exp Bot 59(13):3621–3634. PubMed PMID: WOS:000259973800012

66. Gomez C, Terrier N, Torregrosa L, Vialet S, Fournier-Level A, Verries C et al (2009) Grapevine MATE-type proteins act as vacuolar H^+-dependent acylated anthocyanin transporters. Plant Physiol 150(1):402–415. PubMed PMID: WOS:000265661700033

67. Gomez C, Conejero G, Torregrosa L, Cheynier V, Terrier N, Ageorges A (2011) In vivo grapevine anthocyanin transport involves vesicle-mediated trafficking and the contribution of anthoMATE transporters and GST. Plant J 67(6):960–970. PubMed PMID: WOS:000294866100002

68. Bertolini A, Peresson C, Petrussa E, Braidot E, Passamonti S, Macri F et al (2009) Identification and localization of the bilitranslocase homologue in white grape berries (*Vitis vinifera* L.) during ripening. J Exp Bot 60(13):3861–3871. PubMed PMID: WOS:000269609800021

69. Braidot E, Petrussa E, Bertolini A, Peresson C, Ermacora P, Loi N et al (2008) Evidence for a putative flavonoid translocator similar to mammalian bilitranslocase in grape berries (*Vitis vinifera* L.) during ripening. Planta 228(1):203–213. PubMed PMID: WOS:000256083200017

70. He F, Mu L, Yan G-L, Liang N-N, Pan Q-H, Wang J et al (2010) Biosynthesis of anthocyanins and their regulation in colored grapes. Molecules 15(12):9057–9091. PubMed PMID: WOS:000285709000036

71. Guidoni S, Ferrandino A, Novello V (2008) Effects of seasonal and agronomical practices on skin anthocyanin profile of Nebbiolo grapes. Am J Enol Viti 59(1):22–29. PubMed PMID: WOS:000253927900003

72. Downey MO, Dokoozlian NK, Krstic MP (2006) Cultural practice and environmental impacts on the flavonoid composition of grapes and wine: a review of recent research. Am J Enol Viti 57(3):257–268. PubMed PMID: WOS:000240934100003

73. Fournand D, Vicens A, Sidhoum L, Souquet J-M, Moutounet M, Cheynier V (2006) Accumulation and extractability of grape skin tannins and anthocyanins at different advanced physiological stages. J Agr Food Chem 54(19):7331–7338. PubMed PMID: WOS:000240465000056

74. Koundouras S, Hatzidimitriou E, Karamolegkou M, Dimopoulou E, Kallithraka S, Tsialtas JT et al (2009) Irrigation and rootstock effects on the phenolic concentration and aroma potential of *Vitis vinifera* L. cv. cabernet sauvignon grapes. J Agr Food Chem 57(17):7805–7813. PubMed PMID: WOS:000269376000028

75. Keller M, Arnink KJ, Hrazdina G (1998) Interaction of nitrogen availability during bloom and light intensity during veraison. I. Effects on grapevine growth, fruit development, and ripening. Am J Enol Viti 49(3):333–340. PubMed PMID: WOS:000076793300015

76. Tarara JM, Lee J, Spayd SE, Scagel CF (2008) Berry temperature and solar radiation alter acylation, proportion, and concentration of anthocyanin in Merlot grapes. Am J Enol Viti 59(3):235–247. PubMed PMID: WOS:000259247500002

77. Azuma A, Yakushiji H, Koshita Y, Kobayashi S (2012) Flavonoid biosynthesis-related genes in grape skin are differentially regulated by temperature and light conditions. Planta 236(4):1067–1080. PubMed PMID: WOS:000309229300010

78. Dokoozlian NK, Kliewer WM (1996) Influence of light on grape berry growth and composition varies during fruit development. J Am Soc Hortic Sci 121(5):869–874. PubMed PMID: WOS:A1996VF06300019

79. Chorti E, Guidoni S, Ferrandino A, Novello V (2010) Effect of different cluster sunlight exposure levels on ripening and anthocyanin accumulation in nebbiolo grapes. Am J Enol Viti 61(1):23–30. PubMed PMID: WOS:000275805400003

80. Spayd SE, Tarara JM, Mee DL, Ferguson JC (2002) Separation of sunlight and temperature effects on the composition of *Vitis vinifera* cv. Merlot berries. Am J Enol Viti 53(3):171–182. PubMed PMID: WOS:000178782800001

81. Castellarin SD, Pfeiffer A, Sivilotti P, Degan M, Peterlunger E, Di Gaspero G (2007) Transcriptional regulation of anthocyanin biosynthesis in ripening fruits of grapevine under seasonal water deficit. Plant Cell Environ 30(11):1381–1399. PubMed PMID: WOS:000249826400004

82. Olle D, Guiraud JL, Souquet JM, Terrier N, Ageorges A, Cheynier V et al (2011) Effect of pre- and post-veraison water deficit on proanthocyanidin and anthocyanin accumulation during Shiraz berry development. Aust J Grape Wine Res 17(1):90–100. PubMed PMID: WOS:000286626100011

83. Esteban MA, Villanueva MJ, Lissarrague JR (2001) Effect of irrigation on changes in the anthocyanin composition of the skin of cv Tempranillo (*Vitis vinifera* L) grape berries during ripening. J Sci Food Agr 81(4):409–420. PubMed PMID: WOS:000167217000006

84. Mori K, Goto-Yamamoto N, Kitayama M, Hashizume K (2007) Loss of anthocyanins in red-wine grape under high temperature. J Exp Bot 58(8):1935–1945. PubMed PMID: WOS:000248447500003

85. Mori K, Sugaya S, Gemma H (2005) Decreased anthocyanin biosynthesis in grape berries grown under elevated night temperature condition. Scientia Horticulturae 105(3):319–330. PubMed PMID: WOS:000229728500004

86. Yamane T, Jeong ST, Goto-Yamamoto N, Koshita Y, Kobayashi S (2006) Effects of temperature on anthocyanin biosynthesis in grape berry skins. Am J Enol Viti 57(1):54–59. PubMed PMID: WOS:000236618800006

87. Romero I, Sanchez-Ballesta MT, Maldonado R, Escribano MI, Merodio C (2008) Anthocyanin, antioxidant activity and stress-induced gene expression in high CO2-treated table grapes stored at tow temperature. J Plant Physiol 165(5):522–530. PubMed PMID: WOS:000254944100006

88. Sanchez-Ballesta MT, Romero I, Bernardo Jimenez J, Orea JM, Gonzalez-Urena A, Isabel Escribano M et al (2007) Involvement of the phenylpropanoid pathway in the response of table grapes to low temperature and high CO2 levels. Postharvest Biol Technol 46(1):29–35. PubMed PMID: WOS:000250077000004

89. Petrie PR, Clingeleffer PR (2006) Crop thinning (hand versus mechanical), grape maturity and anthocyanin concentration: outcomes from irrigated Cabernet Sauvignon (Vitis vinifera L.) in a warm climate. Aust J Grape Wine Res 12(1):21–29. PubMed PMID: WOS:000236875800003

90. Pena-Neira A, Caceres A, Pastenes C (2007) Low molecular weight phenolic and anthocyanin composition of grape skins from cv. syrah (Vitis vinifera L.) in the maipo valley (Chile): effect of clusters thinning and vineyard yield. Food Sci Technol Int 13(2):153–158. PubMed PMID: WOS:000248730900009

91. Bindon K, Dry P, Loveys B (2008) Influence of partial rootzone drying on the composition and accumulation of anthocyanins in grape berries (Vitis vinifera cv. Cabernet Sauvignon). Aust J Grape Wine Res 14(2):91–103. PubMed PMID: WOS:000257632600004

92. Parrado J, Escudero-Gilete ML, Friaza V, Garcia-Martinez A, Gonzalez-Miret ML, Bautista JD et al (2007) Enzymatic vegetable extract with bio-active components: influence of fertiliser on the colour and anthocyanins of red grapes. J Sci Food Agr 87(12):2310–2318. PubMed PMID: WOS:000249177500018

93. Brar HS, Singh Z, Swinny E, Cameron I (2008) Girdling and grapevine leafroll associated viruses affect berry weight, colour development and accumulation of anthocyanins in 'Crimson Seedless' grapes during maturation and ripening. Plant Sci 175(6):885–897. PubMed PMID: WOS:000261081300019

94. Park J-S, Choung M-G, Kim J-B, Hahn B-S, Kim J-B, Bae S-C et al (2007) Genes up-regulated during red coloration in UV-B irradiated lettuce leaves. Plant Cell Rep 26(4):507–516. PubMed PMID: WOS:000245896300013

95. Gollop R, Even S, Colova-Tsolova V, Perl A (2002) Expression of the grape dihydroflavonol reductase gene and analysis of its promoter region. J Exp Bot 53(373):1397–1409. PubMed PMID: WOS:000175955600003

96. Gollop R, Farhi S, Perl A (2001) Regulation of the leucoanthocyanidin dioxygenase gene expression in Vitis vinifera. Plant Sci 161(3):579–588. PubMed PMID: ISI:000170510400021

97. Kataoka I, Sugiyama A, Beppu K (2003) Role of ultraviolet radiation in accumulation of anthocyanin in berries of 'Gros Colman' grapes (Vitis vinifera L.). J Jpn Soc Hortic Sci 72(1):1–6. PubMed PMID: WOS:000180482600001

98. Kataoka I, Sugiura A, Utsunomiya N, Tomana T (1982) Effect of abscisic-acid and defoliation on anthocyanin accumulation in kyoho grapes (vitis-vinifera l x v labruscana bailey). Vitis 21(4):325–332. PubMed PMID: WOS:A1982QA03500004

99. Hiratsuka S, Onodera H, Kawai Y, Kubo T, Itoh H, Wada R (2001) ABA and sugar effects on anthocyanin formation in grape berry cultured in vitro. Sci Hortic 90(1–2):121–130. PubMed PMID: WOS:000172093200010

100. Ban T, Ishimaru M, Kobayashi S, Shiozaki S, Goto-Yamamoto N, Horiuchi S (2003) Abscisic acid and 2,4-dichlorophenoxyacetic acid affect the expression of anthocyanin biosynthetic pathway genes in 'Kyoho' grape berries. J Hortic Sci Biotechnol 78(4):586–589. PubMed PMID: WOS:000184479900025

101. Jeong ST, Goto-Yamamoto N, Kobayashi S, Esaka A (2004) Effects of plant hormones and shading on the accumulation of anthocyanins and the expression of anthocyanin biosynthetic genes in grape berry skins. Plant Sci 167(2):247–252. PubMed PMID: WOS:000222280600007

102. El-Kereamy A, Chervin C, Roustan JP, Cheynier V, Souquet JM, Moutounet M et al (2003) Exogenous ethylene stimulates the long-term expression of genes related to anthocyanin biosynthesis in grape berries. Physiol Plantarum 119(2):175–182. PubMed PMID: ISI:000185225200002

103. Bellincontro A, Fardelli A, De Santis D, Botondi R, Mencarelli F (2006) Postharvest ethylene and 1-MCP treatments both affect phenols, anthocyanins, and aromatic quality of Aleatico grapes and wine. Aust J Grape Wine Res 12(2):141–149. PubMed PMID: WOS:000239405400008

104. Zheng Y, Tian L, Liu H, Pan Q, Zhan J, Huang W (2009) Sugars induce anthocyanin accumulation and flavanone 3-hydroxylase expression in grape berries. Plant Growth Regul Jul;58(3):251–260. PubMed PMID: WOS:000266455600004

105. Gonzalez-sanjose ML, Diez C (1992) Relationship between anthocyanins and sugars during the ripening of grape berries. Food Chem 43(3):193–197. PubMed PMID: WOS:A1992HF29800004

106. El Kereamy A, Chervin C, Souquet JM, Moutounet M, Monje MC, Nepveu F et al (2002) Ethanol triggers grape gene expression leading to anthocyanin accumulation during berry ripening. Plant Sci 163(3):449–454. PubMed PMID: WOS:000178419800008

107. Afifi M, El-Kereamy A, Legrand V, Chervin C, Monje MC, Nepveu F et al (2003) Control of anthocyanin biosynthesis pathway gene expression by eutypine, a toxin from Eutypa lata, in grape cell tissue cultures. J Plant Physiol 160(8):971–975. PubMed PMID: WOS:000184874200016

108. Camire ME, Chaovanalikit A, Dougherty MP, Briggs J (2002) Blueberry and grape anthocyanins as breakfast cereal colorants. J Food Sci 67(1):438–441. PubMed PMID: WOS:000173893100077

109. Deroles S (2009) Anthocyanin biosynthesis in plant cell cultures: a potential source of natural colourants. In: Winefield C, Davies K, Gould K (eds) The anthocyanins. Springer-Verlag, New York, pp 107–167

110. Cormier F, Crevier HA, Do CB (1990) Effects of sucrose concentration on the accumulation of anthocyanins in grape (*vitis-vinifera*) cell-suspension. Can J Bot-Revue Canadienne De Botanique 68(8):1822–1825. PubMed PMID: WOS:A1990DZ76000029

111. Do CB, Cormier F (1991) Effects of low nitrate and high sugar concentrations on anthocyanin content and composition of grape (*vitis-vinifera* l) cell-suspension. Plant Cell Rep 9(9):500–504. PubMed PMID: WOS:A1991EU30300008

112. Do CB, Cormier F (1991) Effects of high ammonium concentrations on growth and anthocyanin formation in grape (*vitis-vinifera* l) cell-suspension cultured in a production medium. Plant Cell Tissue Organ Cult 27(2):169–174. PubMed PMID: WOS:A1991GR32000008

113. Dedaldechamp F, Uhel C, Macheix JJ (1995) Enhancement of anthocyanin synthesis and dihydroflavonol reductase (dfr) activity in response to phosphate deprivation in grape cell-suspensions. Phytochemistry 40(5):1357–1360. PubMed PMID: WOS:A1995TE27500005

114. Cai Z, Kastell A, Mewis I, Knorr D, Smetanska I (2012) Polysaccharide elicitors enhance anthocyanin and phenolic acid accumulation in cell suspension cultures of *Vitis vinifera*. Plant Cell Tissue Organ Cult 108(3):401–409. PubMed PMID: WOS:000301601600005