Ecophysiological, Genetic, and Molecular Causes of Variation in Grape Berry Weight and Composition: A Review

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Abstract: Berry fresh weight and composition are under the control of complex interactions among genotype, environmental factors, and viticulture practice, which all affect not only the mean value but also the ranges of variation in berry traits. Both mean values and variation range in berry composition play a role in berry quality and, subsequently, wine typicity. This review examines recent ecophysiological, genetic, and molecular knowledge to provide better understanding of the mechanisms that influence variability in berry weight and composition. We specifically reviewed the variation range in berry weight and composition (including sugars, organic acids, and anthocyanins) among *Vitis* genotypes, the environmental and viticulture practices that cause variability for a given cultivar, the genetic clues underlying the genotypic variation, and the putative genes controlling berry weight and composition. Despite numerous studies comparing differences in the mean value of a berry trait among different environment conditions and viticulture practices, very few studies have explored the level of variation in response to those factors. Present genetic and molecular studies are mainly focused on identifying genes involved in the control of berry weight and composition, with few considerations of environmental factors that affect their expression. In the future, more effort should be directed toward integration of genetic and molecular work with ecophysiological approaches in an effort to gain novel insights into the cause of variability in grape fresh weight and composition.

Key words: *Vitis*, genetic diversity, phenotypic plasticity, berry composition, fruit quality

Variability is an intrinsic property of all biological systems, including grapevine, and may occur at different levels. Genotype is an important source of variability, taking into consideration the great diversity within the *Vitis* genus (This et al. 2006). Within a given genotype (cultivar or clone), variability is the result of plasticity, defined as "the amount by which the expression of individual characteristics of a genotype are changed by different environments" (Bradshaw 1965). Environmental factors (e.g., temperature, light, and soil moisture) and viticulture practices (e.g., pruning, irrigation, and cluster thinning) are known to cause variability within berries, among berries within a cluster, among clusters on a vine, and among vines within a vineyard (Gray 2002, Keller 2010). The existing variability can be a benefit or a burden (Tijskens et al. 2003). On the one hand, genetic variability and plasticity offer the advantages to adapt existing cultivars to a specific growing region, to produce a wide range of different wines from the same cultivar, or to breed new cultivars well-adapted to a different specific growing area. On the other hand, the plasticity of a given genotype in response to environmental conditions and viticulture practices may be considered a disadvantage, because it may cause uneven maturity (Selvaraj et al. 1995) and large interseasonal fluctuations (Clingeleffer 2010). Moreover, wine quality and complexity result not only from the average berry composition but also from the range of variation within a population of berries (Kontoudakis et al. 2011, Singleton et al. 1966). Despite an acceptable average maturity, the heterogeneity in berry maturity may increase the potential for green (from immature berries) or jamlike (from overmature berries) tastes in the final wine (Long 1987). Therefore, uniform grape composition is usually regarded as desirable for winemaking (Keller 2010). A better understanding of the underlying causes of variation in grape berry may help to reduce the heterogeneity of a given cultivar within a vineyard and among vintages and to use the best-suited cultivar in a given growing region.

The need to evaluate grape variability (both genetic diversity and phenotypic plasticity) is further increased by ongoing climate change. First, climate change may alter the adaption of a cultivar to a specific growing season (Bindi et al. 1996, Duchêne et al. 2010, Jones 2006, Jones et al. 2005, Schultz 2000, Webb et al. 2007). Second, climate change has been predicted to modify the mean grape yield and variability for a given cultivar (Bindi et al. 1996). Overall, climate change will modify the whole physiology of grapevine, with strong effects on wine quality and typicity (Jones et al. 2005, Schultz 2000). This raises challenges for producing berries of optimal enological quality potential and consistent stability in current winegrowing regions in the next decades

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with the current genotypes (both scions and rootstocks) and agronomical practices.

The causes of grape variability, especially plasticity, have been extensively studied by the use of physiological approaches. Genetic and molecular approaches provide further information about the genes that contribute to the variability due to genotype and/or environment. The genomic information has significantly increased in the last 10 years, from expressed sequence tag (EST) sequencing programs (Iandolino et al. 2004) to the release of the Pinot noir genome sequence and annotation (Jaillon et al. 2007). Several generations of microarrays have been created and used, from the first 3,500 unigene Qiagen/Operon chips (Terrier et al. 2005) to the newly developed genomewide slides bearing up to 30,000 unigenes (Bellin et al. 2009). Most recently, the grapevine research community gained access to massive parallel signature sequencing-based transcriptome analysis, the so-called deep RNA sequencing approach (Zenoni et al. 2010). These genomic and transcriptomic approaches provide high-throughput tools to identify and integrate the function of candidate genes that contribute to the natural genetic variation for specific traits such as berry development, ripening, and abiotic stress response and to understand the nature and effects of their allelic differences (Martinez-Zapater et al. 2010). Ultimately, such genes could be used in future breeding programs to produce scions with improved fruit.

The aim of this review is to distill physiological, genetic, and molecular knowledge in order to provide a better understanding of the mechanisms that regulate variability in berry weight and composition. The information about the range of variation in berry weight and composition (including sugars, organic acids, and anthocyanins) among *Vitis* genotypes is summarized. Physiological parameters that cause variability for a given cultivar are then analyzed. Genetic clues underlying the genotypic variation, which is mainly identified from quantitative trait loci (QTL) analysis and whole genome association genetic analysis, are described, and the putative underlying genes for berry weight and composition are reviewed. To conclude, a systems biology approach that would integrate physiological, genetic, and molecular approaches is recommended to gain novel insights into the cause of variability in berry weight and composition.

Berry Fresh Weight

Variation in berry weight can be caused by altering cell number and/or cell volume, which are determined by cell division and cell expansion, respectively (Fernandez et al. 2006b). Intrinsic and extrinsic factors such as genotype (Boursiquot et al. 1995, Fernandez et al. 2006b, Houel et al. 2010, Mejia et al. 2011), seed number within a berry (Cawthon and Morris 1982, Walker et al. 2005), source-sink ratio, and environmental parameters such as water supply (Ojeda et al. 2001, Shellie 2010, van Leeuwen et al. 2009) exert their effects on berry weight through modifying cell division and/or cell expansion.

Genetic variability. Grape berry weight shows high genetic diversity within the *Vitis* genus, ranging from <0.5 to >10 g (Boursiquot et al. 1995, Houel et al. 2010, Shellie 2007). In addition to the variation between cultivars, berry weight also varies among clones of a given cultivar. For example, a reduction of 49 to 90% in berry weight has been reported among clones of lower berry weight and their reference wild-type clones of cvs. Grenache, Mourvèdre, and Ugni blanc (Fernandez et al. 2006b). The smaller berries of some Grenache and Mourvèdre clones were a result of reduced cell enlargement, whereas the smaller berries of some Ugni blanc clones resulted from the decrease in both cell division and enlargement (Fernandez et al. 2006c). In particular, the Ugni blanc mutant "fleshless berry" (flb) shows a 20-fold reduction in berry weight and lacks flesh. The *flb* mutant has become a valuable material for screening genes that control berry weight in grapevine (Fernandez et al. 2006a, 2006c, 2007, Houel et al. 2010).

Ecophysiological parameters underlying fresh weight plasticity. All published data recorded on single berries for a given cultivar, within or among clusters, displayed a high variation in berry weight. The weight of seeded berries may differ by a factor of 2 within a cluster (Friend et al. 2009, Ollat et al. 2002). The coefficient of variation (CV) of berry weight has been reported at ~25 to 30% at maturity in Merlot berries (Shellie 2010). The CV of berry weight varied between 41 and 53% during the development of Syrah berries (Gray and Coombe 2009). Furthermore, the variability is generally higher within clusters than between clusters or vines at maturity (Pagay and Cheng 2010, Sato et al. 2000). Therefore, factors that might cause intracluster variation are focused on in the following paragraphs.

Seed number is an important determinant of berry weight (Cawthon and Morris 1982, May 2000, Walker et al. 2005), especially within a grape cluster. Many authors have shown that berry weight is correlated to seed weight (Coombe 1959, Ebadi et al. 1996, Friend et al. 2009, Gray and Coombe 2009). Results from Thompson stenocarpic seedless berries showed a CV of berry weight ~25 to 30% (Kasimatis et al. 1975), comparable to Merlot (Shellie 2010). This suggests that the major role of seeds for berry development may be qualitative rather than quantitative. Other factors such as assimilate supply and/or environmental conditions (e.g., water stress) are probably also involved in generating these variations. Although water stress is known to inhibit berry growth, a recent study performed on cv. Merlot demonstrated that berry growth in a cluster was homogenously inhibited by water stress, ruling out, or at least limiting, its role in causing intracluster variation in berry weight (Shellie 2010).

Berry fresh weight within a cluster depends on berry position within the cluster. Berries at the tip (distal end) of a cluster weigh significantly less than berries at the center or shoulder (proximal part and wing) (Pagay and Cheng 2010, Tarter and Keuter 2005). This position effect may arise from sink competition. It is well known that source-sink relationships affect berry weight (Kliewer 1970, Ollat and Gaudillere 1998). Usually, source limitation during berry development induces a reduction in individual berry weight. However, its role in affecting the level of intracluster variability needs

further investigation. It may be hypothesized that the berries of different positions may not equally access the assimilate pool. The berries from the proximal part of clusters might have a higher priority for receiving assimilate supply, as indicated in banana (Jullien et al. 2001a, 2001b). Overall, the potential roles in berry weight variation of seed number, berry position within a cluster, and within-cluster assimilate supply should be investigated jointly in both seeded and seedless cultivars in order to better explain this variability.

Genes that control genetic diversity or plasticity of weight. The regions of the grapevine genome that contain genes that influence berry weight have been mainly identified using two kinds of plant materials: seedless- or *flb*-related progenies. According to QTL analyses on seedless-originated progenies, berry weight would be controlled by three genomic regions related to seedlessness, two on linkage group 18 (LG18) and one on LG4 (Cabezas et al. 2006, Doligez et al. 2002, Fanizza et al. 2005). Additionally, at least four genomic regions (LG5, LG11, LG13, and LG15) would affect berry weight independently of the presence of seeds (Cabezas et al. 2006). Among these potential genomic regions, only one locus named *seed development inhibitor* (*SDI*) is commonly detected on LG18 by multiple authors, among different years, and for different progenies (Cabezas et al. 2006, Doligez et al. 2002, Mejia et al. 2007). This major QTL can explain 43 to 67% of the total berry weight variation, depending on the mapping population (Cabezas et al. 2006, Doligez et al. 2002). Recently, the *SDI* locus was characterized precisely by integrating genetic and physical maps and adding new codominant markers (Mejia et al. 2011). One candidate gene, *VvAGL11*, an ortholog of the *AGAMOUS-like 11* gene of *Arabidopsis* (*AGL11*), was further studied. In fact, *AGL11* belongs to the D-lineage MADS box family that is known for its role in ovule identity in *Arabidopsis*. Sequence characterization, association analyses, and transcriptional analysis provide evidence that *VvAGL11* plays a major control role in seedlessness and berry weight. However, whether this gene regulates berry weight by exerting its effect indirectly through modifying seed development or directly on berry development is still an open question and needs further functional evaluation (Mejia et al. 2011). On the same LG18, a locus associated with fleshless berry *(FLB)* is also detected by studying the *flb*-related progenies (Fernandez et al. 2006a). This *FLB* locus does not colocalize with the *SDI* locus. Four candidate gene fragments, including *WC2966A*, *W05786A*, *W05777A*, and *W05775A*, have been recently determined by evaluating the sequence polymorphism in the *FLB* locus in different grapevine cultivars (Houel et al. 2010). In addition, several genes potentially involved in berry development were identified by comparing gene expression between the *flb* mutant and its wild-type counterpart, Ugni blanc (Fernandez et al. 2007). For example, MADS-box, HDZip, and BURP domain proteins are underexpressed during *flb* berry growth compared to wild-type ones. Despite the active progress in identifying genes regulating berry weight, further investigations are needed to better characterize and screen all the proposed candidate genes, especially through a genetic transformation approach (Houel et al. 2010, Mejia et al. 2011). Once the roles of a gene in controlling berry weight are confirmed under standard growth conditions, its response to different environmental factors should be assessed to help understand the plasticity of berry weight.

Sugar Concentration

Sugar concentration in grape berry plays an important role in shaping berry sensory properties, determining alcohol concentration after fermentation, and providing precursors for synthesis of organic acids, phenolics, and aroma compounds. Among various fruit species, grape berries contain at maturity one of the highest concentrations of sugar. This concentration may be higher than 1 M glucose and 1 M fructose (Coombe 1976). Sugars accumulated in berry originate from sucrose that is imported from photosynthesizing leaves (Hale and Weaver 1962, Swansom and Elshishiny 1958). Sugar composition in grape berry is mainly determined by genotype (Liu et al. 2006, 2007, Shiraishi 2000, Shiraishi et al. 2010), while sugar concentration varies with berry development (Coombe 1992), environment, and viticulture practices (Clingeleffer 2010, Jackson and Lombard 1993, Kliewer and Dokoozlian 2005, Reynolds and Vanden Heuvel 2009).

Genetic variability. There is a high genetic variability in both sugar composition and sugar concentration within the *Vitis* genus. Total sugar concentration, usually measured as total soluble solids (TSS), varies from 18.7 to 27 Brix at maturity among 78 *Vitis vinifera* cultivars, including table grape and red and white winegrape cultivars (Kliewer 1967b). Among 26 species of *Vitis* including species from North America and Middle East regions, Kliewer (1967a) reported a wider range of variation in TSS at maturity, ranging from 13.7 Brix (*V. champini*) to 31.5 Brix (*V. riparia* from Wyoming). Among different sugars, all the reported *V. vinifera* cultivars accumulate predominantly glucose and fructose (each range from 46 to 164 g/L) with very low traces of sucrose (Hawker et al. 1976, Liu et al. 2006, Shiraishi et al. 2010). In contrast, *V. labrusca* and *V. rotundifolia* cultivars and interspecific hybrids produced with these species are consistently characterized by the accumulation of non-negligible levels of sucrose (from 5 to 58.28 g/L), together with moderate amounts of glucose and fructose (from 35 to 54 g/L) (Carroll et al. 1971, Carroll and Marcy 1982, Liu et al. 2006, Shiraishi 2000, Shiraishi et al. 2010). The glucose-fructose ratio is reported to vary from 0.47 to 1.12, with only two species containing more glucose than fructose (*V. champinii* and *V. doaniana*). Most winegrapes from *V. vinifera* have a glucose-fructose ratio of 1 at maturity (Kliewer 1967b).

Physiological parameters underlying sugar concentration plasticity. Berry sugar concentration is a relatively stable trait for a given cultivar, being less responsive to environmental conditions and viticulture practices than organic acids (Keller et al. 2005) and anthocyanins (Keller et al. 1998, Sadras et al. 2007). The environmental effects in germplasm screening studies are usually derived from pluriannual experiments, with years differing in climatic conditions. Berry sugar concentration was assessed at maturity (estimated as

TSS) among 98 cultivars during two consecutive years (Liu et al. 2006) and among 29 cultivars during four consecutive years (Shellie 2007) and no statistically significant year effect on sugar concentration was recorded for a given cultivar. No significant year effect was detected on TSS of 14 *Vitis* species (paired *t*-test, $p = 0.11$) by reevaluating the results from Kliewer (1967a). Although the year effect on TSS was reported as significant in a study dealing with 129 grape cultivars among three years, its contribution of variance to total variance of TSS was only 1.5% (Shiraishi et al. 2010).

The response of sugar concentration to viticulture practices, including crop-load manipulation and irrigation, is more complex. Many inconsistent results have been reported (Clingeleffer 2010, Keller et al. 2005, Nuzzo and Matthews 2006, Reynolds and Vanden Heuvel 2009). Reducing crop load (either by pruning or cluster thinning) generally reduces yield and increases berry TSS compared to high crop-load vines (Chorti et al. 2010, Guidoni et al. 2002, Ollat and Gaudillere 1998, Petrie and Clingeleffer 2006, Petrie et al. 2000, Reynolds et al. 1994). Other studies showed that cluster thinning or defoliation has little or no influence on soluble solids at harvest (Keller et al. 2005, Nuzzo and Matthews 2006, Tardaguila et al. 2010). The response of berry sugar concentration to water supply depends on the intensity and timing of water stress applied to vines (Roby and Matthews 2004, Sadras et al. 2007), exhibiting increases (Cramer et al. 2007, van Leeuwen and Seguin 1994), decreases (Esteban et al. 1999, Santesteban and Royo 2006), or no change at all (Esteban et al. 2002, Sivilotti et al. 2005). The observed large discrepancy in the sugar response to fruit load and water supply may be due to experimental conditions, variety, using relatively over- or undercropped vines, and timing of water limitation.

An alternative but frequently overlooked explanation might be the differences in sampling strategies used among experiments to investigate sugar response to growing conditions. There are two main strategies: one is to harvest all treatments on the same date (Chorti et al. 2010, Guidoni et al. 2002, Ollat and Gaudillere 1998, Petrie and Clingeleffer 2006, Petrie et al. 2000, Reynolds et al. 1994) and the other is to harvest each treatment when a targeted sugar concentration is reached (Bates 2008, Garcia de Cortazar-Atauri et al. 2009, Keller et al. 2005, Kliewer and Dokoozlian 2005, Nuzzo and Matthews 2006). Almost all studies that reported a significant modification in sugar concentration in response to altered water supply and crop load used the first sampling strategy (Chorti et al. 2010, Guidoni et al. 2002, Ollat and Gaudillere 1998, Petrie and Clingeleffer 2006, Petrie et al. 2000, Reynolds et al. 1994). When the second sampling strategy was used, it was shown that water supply and crop load did not affect the final sugar concentration, but did modify the duration of accumulation (Bates 2008, Keller et al. 2005, Kliewer and Dokoozlian 2005, Nuzzo and Matthews 2006). It is clearly demonstrated that the duration of sugar accumulation interacts with the rate of sugar accumulation to determine the final sugar concentration at a given date (Garcia de Cortazar-Atauri et al. 2009, Sadras and McCarthy 2007). Many authors have pointed out that, for a given cultivar, high crop levels delay the date when berries reach a given Brix value, whereas the rate of sugar accumulation is less affected (Esteban et al. 2002, Nuzzo and Matthews 2006, Petrie and Clingeleffer 2006). Berries from thinned vines reached 16 Brix at least 9 days earlier than those from unthinned vines, while the sugar accumulation rate was very similar for all treatments with a value of ~0.182 Brix per day (Petrie and Clingeleffer 2006). That is most likely due to a change in veraison date between thinned and unthinned vines (Petrie and Clingeleffer 2006, Petrie et al. 2000). Nuzzo and Matthews (2006) showed that an approximately identical sugar concentration might be reached for three different crop loads if ripening duration increased. However, situations where accumulation duration and rate were both significantly modified have also been reported (Bates 2008, Kliewer and Dokoozlian 2005). The underlying reasons for these inconsistent results deserve further research. Moreover, the determination of these ripening parameters is crucial to compare cultivars that are not ripening over the same period and should be taken into account in any experiments aiming to describe genetic variability.

Despite numerous studies on the effect of environmental conditions and viticulture practices on the average sugar concentration, only a limited number have explored the level of variation (usually illustrated by distribution) in sugar concentration in response to those factors. In Thompson Seedless, it was demonstrated that the distribution of sugar concentration skews toward lower-value berries at maturity (Kasimatis et al. 1975). In addition to a modified average sugar concentration, the extent of skewness and kurtosis of sugar concentration distribution can be modified by shoot origin and exposure (Wolpert and Howell 1984, Wolpert et al. 1983). Moreover, the variation in sugar concentration among clusters was greater in immature than in mature berries in Pedro Ximénez, Riesling, Semillon, and Shiraz cultivars (Rankine et al. 1962). These authors also showed that variation in sugar concentration is greater for berries from vines grown with irrigation than those grown without irrigation. Recently, hand thinning was shown to increase the uniformity of sugar concentration in comparison with unthinned and machine-thinned vines (Petrie and Clingeleffer 2006). It seems mostly likely that environmental factors such as light, temperature, and humidity and viticulture practices not only modify the mean value of a berry trait but also affect the distribution or variation of that trait. Therefore, further efforts are needed to investigate the effect of environmental conditions and viticulture practices on the level of variation of berry traits, including sugar concentration.

Genes that control genetic diversity or plasticity of sugar concentration. Liu et al. (2007), studying inheritance of sugar concentration in three intra-*vinifera* progeny populations of different cross-combinations from the same maternal parent, observed that this trait exhibited quantitative inheritance. Broad sense heritabilities of glucose, fructose, and total sugars varied between 0.6 and 0.7 depending on progenies and year. This level is consistent with other published data (Wei et al. 2002). No QTL analyses for berry

sugar concentration have been published to date (Martinez-Zapater et al. 2010).

Three main families of proteins are believed to be involved in accumulation of glucose and fructose in grapevine berries. Two of them are sucrose metabolic enzymes: the acidic (vacuolar or cell wall associated) and neutral (cytosolic) invertases and sucrose synthases. The third family consists of sugar transporters (Agasse et al. 2009, Zhang et al. 2006). In grapevine, at least six sucrose synthase-encoding genes have been reported, but their expression patterns during berry ripening do not clearly support a role for these enzymes in sucrose cleavage in mesocarp cells (Zhang et al. 2006). Conversely, reports linking acidic invertase activities and hexose accumulation during berry ripening can be found in the literature. A cell wall invertase gene expression is induced just before the onset of veraison (Hayes et al. 2007, Zhang et al. 2006) and two vacuolar invertase transcripts (*VvGIN1* and *VvGIN2)* peak at veraison in Shiraz berries (Davies and Robinson 1996). The natural reduction of vacuolar invertase activity in berries from hybrid Steuben grapevine berries led to a decrease in vacuolar hexose accumulation and an increase in sucrose storage (Takayanagi and Yokotsuka 1997). Abscisic acid (ABA) upregulates both hexose transporters (Cakir et al. 2003) and vacuolar invertase (Giribaldi et al. 2010) activities. Taken together, these data suggest that acidic invertases are crucial for hexose accumulation in ripening berries, even though they are most certainly not the only enzymes involved.

The third family of proteins involved in sugar accumulation in the berries has received considerable attention in the past few years: the sugar transporters. Currently, three cDNAs encoding for disaccharide transporters have been isolated and characterized as proton-dependent sucrose transporters—*VvSUC11*, *VvSUC12,* and *VvSUC27* (for *V. vinifera* sucrose carrier 11, 12, and 27: Ageorges et al. 2000, Manning et al. 2001, Zhang et al. 2008)—with a fourth putative gene present in the Pinot noir genome sequence. Expression of *VvSUC11* and *VvSUC12* increases simultaneously with postveraison sugar accumulation, suggesting a role of the corresponding proteins in sucrose acquisition by berry cells, before its cleavage by sucrose-metabolizing enzymes (Davies et al. 1999). In comparison, the grapevine monosaccharide transporter (MST) gene family is much broader than the sucrose one, with no less than 59 putative MST genes identified in the Pinot noir genome (Agasse et al. 2009, Jaillon et al. 2007). Among them, six were isolated as cDNA from various grapevine cultivars and labeled *VvHT1* to *6* (for *V. vinifera* hexose transporters 1 to 6: Hayes et al. 2007, Vignault et al. 2005). All six *VvHTs* transcripts with different expression patterns can be detected in berries, although *VvHT1* transcript and protein levels are much higher at preveraison stages; *VvHT3* expression is important at both green and ripening stages but sharply decreases at veraison; *VvHT5* expression is mostly associated with late ripening days; and *VvHT2* transcript level remains rather constant throughout berry development, with a moderate increase around veraison (Conde et al. 2006, Hayes et al. 2007, Terrier et al. 2005). Most interesting is the case of *VvHT6*, with transcripts that are highly accumulated at veraison (Deluc et al. 2007, Vignault et al. 2005). The corresponding protein is presumably targeted to the tonoplast membrane, but has not been functionally characterized for its transport activity. *VvHT6* might mediate the massive import of hexoses at the inception of berry ripening.

Apart for the structural genes mentioned above, the search for genes coding for proteins controlling sugar transport activity has also been initiated. *VvMSA*, which is induced by ABA and sugars, is a transcriptional regulator controlling *VvHT1* expression (Cakir et al. 2003). Recently, a cDNA encoding a GK3/shaggy-like protein kinase, *VvSK1* (*V. vinifera* shaggy-like protein kinase 1) has been isolated and functionally characterized in our laboratory (Lecourieux et al. 2010). *VvSK1* is strongly expressed postveraison, when the berries accumulate hexoses, and in grapevine cell suspensions, *VvSK1* transcript abundance is increased by sucrose or ABA treatments. The overexpression of the *VvSK1* gene in transgenic 41b grapevine cells enhances the expression of four monosaccharide transporters (*VvHT3-6*) and leads to a three- to five-fold increase in glucose uptake by the cells, doubling the amounts of glucose and sucrose in the cells. Altogether, these data suggest that VvSK1 protein might be a key element for the regulation of hexose accumulation in flesh cells of berries (Lecourieux et al. 2010).

Organic Acids

Tartaric and malic acids typically account for 90% of total acids in grapevine berries (Conde et al. 2007, Kliewer 1967a, Kliewer et al. 1967). These organic acids are synthesized in the grape berry and accumulate during the first growth period. Tartaric acid is accumulated in berry cell vacuoles shortly after anthesis during cell division (Rüffner 1982). During ripening, tartaric acid concentration decreases mostly through dilution. Malate accumulates in the berry cell vacuoles during the first growth period. The content and concentration of malate reaches a maximum and decreases throughout ripening. Malate concentration is higher in the flesh than the skin during the first growth period and in the skin than the flesh during ripening (Iland and Coombe 1988). The acidity of grapes and wine depends on the ratio of concentrations between free organic acids and their potassium salted forms. This ratio increases throughout ripening and constitutes an important trait for quality and longevity of wines because it impacts must and wine pH (Kliewer 1965b, 1966, Ribéreau-Gayon et al. 2006).

Genetic diversity of berry tartaric and malic acid concentration. There is high genetic diversity for grape berry organic acid concentration (Kliewer 1965a, 1965b, 1967a, Liu et al. 2006, Shiraishi et al. 2010). In mature berry, tartaric acid represents generally between 5 and 40% of the total tartrate and malic acid usually between 30 and 70% of the total malate (Kliewer et al. 1967). A range of concentration at maturity from 4 to 9.4 g/L for tartrate and 1.5 to 6.8 g/L for malate for 78 *V. vinifera* table and winegrape cultivars has been reported (Kliewer et al. 1967). On a set of 98 varieties including interspecific hybrids, a range of 1.6 to 9.1 g/L for tartrate and 0.36 to 7.06 g/L for malate was recorded (Liu

et al. 2006). Total acid and malic acid concentrations were lower in hybrid cultivars from crosses between *V. labrusca* and *V. vinifera* than in *V. vinifera* cultivars. Within *V. vinifera*, winegrapes had significantly higher acid concentrations than table grapes (Liu et al. 2006). Gora Chirine, a cultivar originating from Iran (Boubals et al. 1971), accumulates very low concentrations of malate and tartrate compared to other *V. vinifera* varieties and is characterized by a much higher pH of its berry juice, but it has an identical vacuolar pH at veraison (Diakou et al. 1997). Among wild *Vitis* species, the range in concentration reported at maturity for tartrate is 3.1 g/L in *V. rufotomentosa* to 11.9 g/L in *V. solonis* (Kliewer 1967a). For malate, the range in concentration is 2.5 g/L for wild species from Afghanistan to 27.2 g/L for an accession of *V. berlandieri*.

In parallel with variation in concentration, the tartrate-malate ratio, which has been labeled the b ratio (Shiraishi 1995), also exhibits extensive genetic variability. In one population, the b ratio varied from 0.64 (Pinot St. George) to 3.41 (Palomino) (Kliewer 1967a). The same range of variation was reported within a set of varieties, including interspecific hybrids (Shiraishi et al. 2010). With varieties according to various criteria, seedless cultivars and *V. labrusca* x *V. vinifera* hybrids were characterized by the highest b ratio (~3.0) and *V. vinifera* table grapes by the lowest ratio (between 1.5 and 2) (Liu et al. 2006). In wild *Vitis* species, a wider range of variation is found for the b ratio, ranging from 0.34 (*V. berlandieri*) to 5.85 (*V. labrusca*).

Physiological parameters underlying the plasticity of tartaric and malic acid concentration. Berry organic acid concentration is influenced by environmental parameters and viticulture practices affecting source-sink relationships and cluster microclimate (Jackson and Lombard 1993). However, reports describing variability in acid concentration at the vine or cluster level and the direct effect of leaf to fruit ratio are scarce in the literature. For Cabernet Sauvignon cultivated in a growth chamber, a low leaf to fruit ratio applied shortly after fruit set on fruiting cuttings induced a significant decrease in berry weight and malate concentration before veraison (51 days after anthesis, when the amount of malate peaked in control berries) (Ollat and Gaudillère 1998). Malate concentration was correlated with berry weight for the low leaf to fruit treatment, and not for the control, indicating a possible link between malate concentration and ontogeny. Moreover, the onset of veraison was also delayed and there was a negative correlation between berry weight and the veraison date. On the contrary, tartrate concentration at this date was unaffected by the treatment. At maturity, the malate and tartrate concentrations were significantly higher in a low leaf to fruit ratio treatment (Ollat and Gaudillere 1998). Environmental factors are also known to affect malate concentration of the berries during ripening. Elevated temperature clearly decreases the concentration of malic acid, whereas grapevines grown in cool climates have a higher malic acid concentration in their berries (Keller et al. 2005, Koundouras et al. 2006, Pereira et al. 2006). The impact of water stress on berry malic acid concentration is less clear, and increases (Lòpez et al. 2007), decreases (Koundouras et al. 2006, Salon et al. 2005), or even no change (Esteban et al. 1999) have been reported. Tartaric acid concentration, on the other hand, does not appear to be significantly affected by temperature or water stress (Parra et al. 2010).

Genes that control genetic diversity or plasticity of tartaric and malic acid concentration. There are few genetic studies on berry acid concentration in the literature. Liu et al. (2007) reported that broad sense heritability for malate ranged from 0.73 to 0.89 in three cross offspring populations during two successive growing seasons. In comparison, the heritability of tartrate concentration varied from 0.59 to 0.84. According to Shiraishi et al. (2010), the b ratio was not affected by annual effects. To our knowledge, no result for QTL identification for organic acid concentration has been published, but some work is in progress (Duchêne and Romieu, personal communication, 2010).

Conversely, molecular data regarding the genes that control berry acid concentration have appeared in the literature during the past decade. Tartaric acid is thought to be synthesized from L-ascorbic acid through a five-step pathway; however, there is only scarce data to support the proposed reactions (Loewus 1999). It is only recently that a combination of transcript profiling, EST database surveys, and metabolic profiling led to the identification of the gene coding for L-idonate dehydrogenase (L-IdnDH), the enzyme that catalyzes the proposed rate-limiting step in tartaric acid biosynthesis from vitamin C (DeBolt et al. 2006). Subsequent transcriptomic studies demonstrated that the expression levels of three different transcripts coding for L-IdnDH closely follow variations in tartrate levels during development of Cabernet Sauvignon berries, further supporting the role of these genes in tartaric acid biosynthesis (Deluc et al. 2007). In contrast to tartaric acid, the metabolic pathways of malate biosynthesis and degradation in grapevine berries, although complex, are rather well documented, with most of the enzymes involved identified (for a recent review see Sweetman et al. 2009). However, relatively few genes involved in malate accumulation in berries have been formally identified, as there is little obvious correlation between transcript abundance and malate levels. The noticeable exceptions are two cytosolic and two mitochondrial malate dehydrogenases, with expression levels that increase during the ripening phase, when the malate concentration declines in the berries (Deluc et al. 2007). Additional studies, based on an integrated approach combining genetic, transcriptomic, proteomic, and metabolomics, are required to reach a more comprehensive view of the molecular parameters involved in berry malate concentration regulation.

Anthocyanin Composition

Among the grape secondary metabolites that are important for wine quality, this review will focus only on anthocyanins because of their essential roles in the color of grape and wine (Adams 2006, Boss and Davies 2009, Downey et al. 2006, He et al. 2010, Jackson and Lombard 1993, Kennedy et al. 2006, Mazza and Francis 1995). Anthocyanins are a class of crucial phenolic compounds that are synthesized via the flavonoid

pathway. In addition to controlling grape and wine color, they also play a major role in protection due to their free radical scavenging and antioxidant activity (He et al. 2010). The amount and composition of the anthocyanins present in red grapes are largely dependent on cultivar and species (Mazza and Francis 1995), stage of ripening (Fournand et al. 2006, Holt et al. 2010), and environmental and viticulture practices such as light exposure, temperature, and water and nitrogen availability (Downey et al. 2006, He et al. 2010, Kappel 2010, Ollé et al. 2011). The variability in anthocyanin composition influences the hue and color stability, with blueness and redness directly affected by the pattern of hydroxylation and methylation, respectively. There are also differences in their extractability (Downey et al. 2006) and their sensitivity to oxidation (reported in He et al. 2010), with major effects on wine characteristics (Cortell et al. 2007b, 2008, Fournand et al. 2006, Kontoudakis et al. 2011, Torchio et al. 2010).

Genetic variability. Anthocyanin profiles of numerous *V. vinifera* cultivars and *Vitis* species have been reviewed (Mazza and Francis 1995). Each grape cultivar is characterized by a distinct set of anthocyanins, and therefore anthocyanin analysis has been proposed for the varietal authentication of grapes and wine (Mattivi et al. 2006, Roggero et al. 1988). In *V. vinifera* cultivars, the principal individual anthocyanins are 3-*O*-monoglucosides of delphinidin, cyanidin, petunidin, peonidin, and malvidin. The proportion of the 3'-substituted to the 3',5'-substituted forms may change, as well as the contribution of acetylated forms. For example, Cabernet Sauvignon, Merlot, Syrah, and Tempranillo are characterized by a major proportion of malvidin derivatives, while Nebbiolo, an Italian variety, typically has peonidin-3-glucoside as the most prevalent one (Guidoni et al. 2008). Pinot noir is known for not synthesizing acetylated anthocyanins (Mazza and Francis 1995). *Vitis vinifera* cultivars are characterized by the presence of monoglucoside anthocyanins only, whereas wild *Vitis* species accumulate di-glucosides in non-negligible quantities. In a recent work where the grape variety Norton, with *V. aestivalis* background, was compared to Cabernet Sauvignon (Ali et al. 2011), 35 different anthocyanin forms were detected using LC–MS chromatography in the two cultivars. Eight of the 35 were common in both cultivars and 16 were detected only in Norton. These genetic differences between cultivars in anthocyanin composition are related to the modification of some enzymatic activities along the biosynthetic pathway. Flavonoid 3'hydroxylases, flavonoid 3',5' hydroxylases and *O*-methyl-transferases are probably the key enzymes involved (Mattivi et al. 2006). According to Boss and Davies (2009), these differences have to be considered for a better understanding of physiological responses to other cultural and environmental parameters.

Physiological parameters regulating anthocyanin composition. Mineral nutrition, yield and vigor, developmental stages, and environmental conditions have a strong impact on grape anthocyanin accumulation and composition. The accumulation of phenolics appears to be more susceptible to adverse environmental conditions than that of sugars (Keller et al. 1998). While quantifying the phenotypic plasticity of both anthocyanins and sugars in berries of Cabernet Sauvignon, sugar accumulation was shown as more strictly associated to thermal time, whereas anthocyanin accumulation was also affected by other sources of variations (water, yield, and climatic conditions) (Sadras et al. 2007). Consequently, under the experimental conditions tested, the amount of anthocyanins displays a much wider range of variation (148%) than that of sugars (37%). Developmental stages have an impact on anthocyanin concentration and composition. Guidoni et al. (2008) demonstrated that anthocyanins accumulate in a two-phase process, with an initial phase of rapid increase strongly correlated to sugar accumulation and a second phase where anthocyanins and sugars are uncoupled. This fact may explain why anthocyanin concentration does not always correlate with sugar concentration at maturity. The first phase is influenced mainly by vine vegetative conditions and cultural practices (photosynthetic conditions) and the second phase is strongly affected by climatic conditions. The 3'-substituted forms are synthesized earlier during berry development than the 3'-5'-substituted forms (Downey et al. 2006, Guidoni et al. 2008, Keller et al. 1998). Moreover, in one study, the 2-methoxylated forms (cyanidin and delphinidin) reached a maximum concentration earlier than the 3-methoxylated forms (malvidin and peonidin) (Fournand et al. 2006).

The effects of mineral nutrition and vine vigor on anthocyanin composition and concentration have also been investigated (Cortell et al. 2007a, Downey et al. 2006, Keller et al. 1998). Heavy N fertilization at flowering delayed ripening and anthocyanin accumulation, with malvidin-3-glucoside enhanced in proportion to the other forms (Keller et al. 1998). The most likely mechanism that explains nitrogen effect is the excess of vigor. One study reported that a reduction of vine vigor increased anthocyanin accumulation, but variations of composition were not clear regarding year and site (Cortell et al. 2007a). Koundouras et al. (2009) observed a higher concentration of malvidin-3-*O*-glucoside and malvidin-3-*O*-coumarate glucoside for Cabernet Sauvignon vines grafted onto the high-vigor rootstock 1103P than those grafted on SO4. In most cases, it is uncertain whether the vigor affects directly the biosynthetic pathway through carbon availability or has an indirect effect via changes in canopy architecture and light and thermal microclimate (Downey et al. 2006, He et al. 2010). Light and temperature appear to have a synergistic effect at moderate temperature and an antagonistic effect at high temperature (Tarara et al. 2008). Exposure to solar radiation increases the proportion of dihydroxylated anthocyanins in comparison to trihydroxylated ones (Chorti et al. 2010, Kappel 2010, Keller et al. 1998, Spayd et al. 2002, Tarara et al. 2008). High temperatures are mainly reported to increase the proportion of acetylated to nonacetylated forms (Downey et al. 2006, Spayd et al. 2002, Tarara et al. 2008). Water deficit results in an increase in anthocyanin concentration and the proportion of trihydroxylated anthocyanins as malvidin and *p*-coumaroylated derivatives (Castellarin and Gaspero 2007, Koundouras et al. 2009, Ollé et al. 2011).

Genes involved in control of genetic diversity and plasticity of berry anthocyanin composition. Numerous

structural genes coding for anthocyanin biosynthetic pathway enzymes have been identified (reviewed by Boss and Davies 2009). In *Arabidopsis* and other model plants, ternary complexes formed by MYB, bHLH, and WD40 proteins are responsible for the transcriptional activation of the anthocyanidin and anthocyanin biosynthetic genes (Baudry et al. 2004, Hichri et al. 2010, Morita et al. 2006). In grapevine, the first reported gene encoding for MYB transcription factors were *VvMYBA1* and *VvMYBA2* (Kobayashi et al. 2002). The expression profiles of *VvMYBA1* in various berry tissues match the changes in expression levels seen for several structural genes of the anthocyanin pathway (Ageorges et al. 2006). Apart from *VvMBYA1*, two other MYB genes, *VvMYB5a* and *VvMYB5b,* have been cloned and functionally characterized (Deluc et al. 2006, 2008). Both genes are able to transactivate promoters of several structural genes of the flavonoid pathway, but their expression is different: *VvMYB5a* is highly expressed before veraison and its transcript level declines after veraison, whereas *VvMYB5b* transcripts strongly accumulate after veraison, during the ripening stages, supporting the idea of complementary roles for these two genes in anthocyanin accumulation. The identification of MYB protein partners (bHLH and WD40 protein) for anthocyanin biosynthesis regulation has long been elusive in grapevine. *VvMYC1*, a gene coding for a bHLH transcription factor, was recently characterized as a component of the transcriptional complexes that control anthocyanin and proanthocyanidin biosynthesis during berry development (Hichri et al. 2010).

The genetic determinism of berry color and anthocyanin concentration has been studied for more than four decades. Cross offspring population studies led to the conclusion that berry color was inherited as a quality trait controlled by a few genes (Liang et al. 2009). Anthocyanin concentration is inherited as a quantitative trait controlled by many genes. Anthocyanin concentration is characterized by a high broad sense heritability (from 0.65 to 0.98), and this heritability is stable in different populations (Liang et al. 2009). The analyses of mapping populations have indeed identified a single locus on LG2 responsible for the presence or absence of skin color and total anthocyanin content in the skin (Doligez et al. 2002, Fischer et al. 2004, Fournier-Level et al. 2010, Lijavetzky et al. 2006, Salmaso et al. 2008). This locus accounts for 48 to 62% of the total variation in anthocyanin concentration in a Syrah x Grenache progeny and colocalizes with a cluster of VvMYB genes (VvMYBA1, VvMYBA2, VvMYB3, and VvMYB4) (Fournier-Level et al. 2010). Moreover, in a survey of over 200 *V. vinifera* accessions, the absence of anthocyanin in the skins of white grape varieties has been found to be strongly associated with the insertion of the *GRET1* retrotransposon in the promoter region of the *VvMYBA1* gene (This et al. 2007). Taken together, these results indicate that *VvMYBA1* is a master regulator of anthocyanin biosynthesis in berries.

Because of the specific anthocyanin composition in wild *Vitis* species, the expression of genes involved in their anthocyanin biosynthesis pathways was compared to *V. vinifera*. The global regulatory steps of the anthocyanin pathways appear to be conserved among *V. vinifera*, *V. aestivalis,* and *Muscadinia rotundifolia* (Ali et al. 2011, Samuelian et al. 2009). However a higher level of expression has been detected for the major genes involved in anthocyanin biosynthesis in the cultivar Norton derived from *Vitis aestivalis*. The expression profiles of the transcription factors MYBPA1 and MYBPA2 were also different (Ali et al. 2011). The major specificity of wild *Vitis* species is their ability to accumulate di-glucoside anthocyanins. This capacity is transmitted as a dominant trait by the wild *Vitis* species (Janvary et al. 2009, Mazza and Francis 1995). It was recently shown that a double mutation in the anthocyanin 5-*O*-glucosyltransferase gene disrupts this enzymatic activity in *V. vinifera* L. This gene is located on chromosome 9 of the Pinot noir genome, close to a putative alcohol transferase gene involved in the synthesis of the characteristic *V. labrusca* foxy aroma. Colocalization of the two genes would explain the observed correlation between the ability to form "foxy" flavor and the presence of di-glucoside anthocyanin in *Vitis* hybrids (Janvary et al. 2009).

Molecular bases of light, temperature, and water stress effects on anthocyanin biosynthesis were investigated (Castellarin and Gaspero 2007, Kappel 2010, Matus et al. 2009, Mori et al. 2007). Modifications of the expression of some structural and regulatory genes (*F3'H*, *F3'5'H*, *CHS*, *UFGT*, *OMT*, *MYBA1*, and *MYB5a*) were reported. However, it is often difficult to interpret these results because many parameters interfere during experiments (Boss and Davies 2009).

Conclusion and Perspectives

Grape berry composition is a highly complex trait. It displays a high genetic diversity, which means variability among genotypes under given growing conditions, and a large phenotypic plasticity; that is, variability for a given genotype growing under different environmental conditions and/or viticulture practices. To date, genetic and molecular studies have primarily focused on the genes underlying genetic diversity. In the future, the responses of these genes to different environments and viticulture practices, which may be responsible for phenotypic plasticity, should be further investigated. Promising results have been obtained by using transcriptomic approaches (Cramer et al. 2007, Tattersall et al. 2007). With the development of novel high-throughput phenotyping methods, such as fluorescence based noninvasive sensors (Ghozlen et al. 2010) and Fourier-transform mid-infrared spectroscopy (Versari et al. 2008), it will also be possible to extend investigations concerning the effects of environment and viticulture practices on average values and variability among berries for the various traits related to berry composition.

The next critical challenge will be to provide biological meaning to this increasing amount of data obtained by high-throughput transcriptomic, proteomic, metabolomic, and phenomic approaches. VitisNet, a tool to analyze grapevine molecular networks, has been developed and validated: 13,145 unigenes have been assigned to 219 molecular networks (Grimplet et al. 2009). The quantitative data is loaded onto molecular networks, allowing the simultaneous visualization

of changes in the transcriptome, proteome, and metabolome for a given experiment. This constitutes a first step toward an integrated approach of grapevine berry physiology. More efforts are needed, and a better understanding of berry metabolism and composition, and of their variations, will require further progress in systems biology and modeling of fruit growth and metabolism (Dai et al. 2010, Génard et al. 2010, Sadras et al. 2008).

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