AJEV Papers in Press. Published online July 26, 2011.

American Journal of Enology and Viticulture (AJEV). doi: 10.5344/ajev.2011.10116
AJEV Papers in Press are peer-reviewed, accepted articles that have not yet been published in a print issue of the journal or edited or formatted, but may be cited by DOI. The final version may contain substantive or nonsubstantive changes.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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

Zhan Wu Dai,[1] Nathalie Ollat,[1]* Eric Gomes,[1] Stéphane Decroocq,[1] Jean-Pascal Tandonnet,[1] Louis Bordenave,[1] Philippe Pieri,[1] Ghislaine Hilbert,[1] Christian Kappel,[1] Cornelius van Leeuwen,[1] Philippe Vivin,[1] and Serge Delrot[1]

[1]INRA, Université de Bordeaux, ENITAB, ISVV, UMR 1287 Ecophysiologie et Génomique Fonctionnelle de la Vigne, 210 Chemin de Leysotte, 33882 Villenave d'Ornon, France.

*Corresponding author (email: ollat@bordeaux.inra.fr; fax: +33 [0]5 5757 5903)

Acknowledgments: This review was presented in part by S. Delrot at the 2010 International Cool Climate Symposium, June 2010, Seattle, Washington.

Manuscript submitted Oct 2010, revised Apr 2011, accepted May 2011

Copyright © 2011 by the American Society for Enology and Viticulture. All rights reserved.

Abstract: Berry fresh weight and composition is under the control of complex interactions between genotype, environmental factors, and viticulture practices; 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 paper aims to bring together recent ecophysiological, genetic, and molecular knowledge to provide better understanding of the mechanisms that impact variability in berry weight and composition. We specifically reviewed i) the variation range in berry weight and composition (including sugars, organic acids, and anthocyanins) among *Vitis* genotypes, ii) the environmental and viticulture practices that cause variability for a given cultivar, iii) genetic clues underlying the genotypic variation, and iv) 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 levels. In the future, more efforts should be directed towards integration of

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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

Introduction

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 large diversity within the *Vitis* genus (This et al. 2006). Within a given genotype (cultivar or clone), variability is the result of plasticity, which is '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 etc.) and viticulture practices (*e.g.* pruning, irrigation, and cluster thinning) are known to cause variability within berries, among berries within a cluster, between 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 large 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) as well as large inter-seasonal fluctuations (Clingeleffer 2010). Moreover, wine quality and complexity not only result 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 jam-like (from over-mature berries) tastes in the final wine (Long 1986). 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 most suited cultivar in a given growing region.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

The needs to evaluate grape variability (both genetic diversity and phenotypic plasticity) are further increased by the 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 rises challenges for producing berries of optimal enological quality potential and with consistent stability in current winegrowing regions in the next decades, with the current genotypes (both scions and rootstocks) and agronomical practices.

The causes of grape variability, especially the 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 unigenes Quiagen/Operon chips (Terrier et al. 2005) to the newly developed genome-wide 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 bring together physiological, genetic, and molecular knowledge in order to provide a better understanding of the mechanisms that regulate variability in berry weight and

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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, is 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.

1. 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 as well as 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.

1.1 Genetic variability

Grape berry weight shows large genetic diversity within *Vitis* genus, ranging from less than 0.5 gram to more than 10 gram (Boursiquot et al. 1995, Houel et al. 2010, Shellie 2007). In addition to the variation between cultivars, berry weight also varies between clones of a given cultivar. For example, a reduction of 49 to 90% in berry weight has been reported between clones of smaller 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

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

enlargement (Fernandez et al. 2006c). Particularly, 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, Fernandez et al. 2006c, Fernandez et al. 2007, Houel et al. 2010).

1.2 Ecophysiological parameters underlying berry fresh weight plasticity

All published data recorded on single berries for a given cultivar, within or between clusters, displayed a large 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 around 25-30% at maturity in Merlot berries (Shellie 2010). The CV of berry weight varied between 41 to 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 intra-cluster 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 around 25 to 30% (Kasimatis et al. 1975), comparable to those in 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 intra-cluster variation in berry weight (Shellie 2010).

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Berry fresh weight within a cluster depends on berry position within the cluster. Berries at the tip (distal end of a cluster) of a cluster weigh significantly less than berries at the central 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 intra-cluster variability needs further investigation. It may be hypothesized that the berries of different positions may not equally access to 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, Jullien et al. 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 seed and seedless cultivars, in order to better explain this variability.

1.3 Genes that control genetic diversity or plasticity of berry weight

The regions of the grapevine genome that contain genes influencing berry weight have been mainly identified by two kinds of plant materials: seedless- or *flb*-related progenies. According to QTL analyses on seedless-originated progenies, berry weight would be controlled by 3 genomic regions related to seedless, 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, 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, Mejia et al. (2011) characterized the *SDI* locus precisely by integrating genetic and physical maps and adding new

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

co-dominant markers. 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 seedless 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 co-localize 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, Fernandez et al. (2007) identified several genes potentially involved in berry development by comparing gene expression between the *flb* mutant and its wild type counterpart, Ugni blanc**.** For examples, MADS-box, HDZip and BURP domain proteins are under-expressed during *flb* berry growth, as 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 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.

2. Sugar concentration

Sugar concentration in grape berry plays an important role in shaping berry organoleptic properties, determining alcohol content 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

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

grape berry is mainly determined by genotype (Liu et al. 2006, Liu et al. 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).

2.1 Genetic variability

There is a large genetic variability in both sugar composition and sugar concentration within *Vitis* genus. Total sugar concentration, usually measured as total soluble solids (TSS), varies from 18.7 to 27 °Brix at maturity among 78 *V. vinifera* cultivars including table grape, red and white wine grape cultivars (Kliewer 1967b). Among 26 species of *Vitis* including species from North America and Middle East regions, Kliewer (1967a) reported a rather larger range of variation in TSS at maturity, ranging from 13.7 (*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 level (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 always characterized by the accumulation of non-negligible levels of sucrose (range 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 wine grapes from *V. vinifera* have a glucose-fructose ratio of 1 at maturity (Kliewer 1967b).

2.2 Physiological parameters underlying berry sugar concentration plasticity

Berry sugar concentration is a relatively stable trait for a given cultivar, namely 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. Liu et al. (2006) and Shellie (2007) assessed berry sugar concentration at maturity (estimated as TSS) among 98 and 29

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

cultivars during two or four consecutive years, respectively. They did not record any statistically significant year effect on sugar concentration 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 3 years, its contribution of variance to total variance of TSS is 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 relative over- or under-cropping vines and to the timing of water limitation.

An alternative but frequently overlooked reason 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 at 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); 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

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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 interplays 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). Petrie and Clingeleffer (2006) showed that berries from thinned vines reached 16 Brix at least 9 days earlier than those from un-thinned vines, while the sugar accumulation rate is very similar for all treatments with a value of ~0.182 Brix per day. This 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 at the same period, and should be taken into account in any experiments aimed 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. Kasimatis et al. (1975) has demonstrated that the distribution of sugar concentration skews towards lower values in Thompson seedless berries at maturity. 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

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

(Wolpert and Howell 1984, Wolpert et al. 1983). Moreover, the variation in sugar concentration between-clusters was greater in immature than in mature berries in cvs. Pedro Ximines, Riesling, Semillon and Shiraz (Rankine et al. 1962). These authors also showed that variation in sugar concentration is greater for berries from vines grown under irrigation than those grown without irrigation. Recently, Petrie and Clingeleffer (2006) have shown that hand thinning increases the uniformity of sugar concentration in comparison with un-thinned and machine thinning vines. It seems mostly likely that environmental factors (such as light, temperature and humidity) and viticulture practices modify not only 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 environment conditions and viticulture practices on the level of variation of berry traits, including sugar concentration.

2.3 Genes that control genetic diversity or plasticity of berry 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 so far (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; and the third ones being sugar transporters (Agasse et al. 2009, Zhang et al. 2006). In grapevine, at least 6 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 prior the onset of veraison (Hayes et al. 2007, Zhang et

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

al. 2006) and two vacuolar invertases transcripts (*VvGIN1* and *VvGIN2)* peak at veraison in Shiraz berries (Davies and Robinson 1996). The natural reduction of vacuolar invertase activity in berries from Steuben grapevine hybrid berries led to a decrease in vacuolar hexose accumulation, and an increase in sucrose storage (Takayanagi and Yokotsuka 1997). ABA up-regulates 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. A third family of proteins involved in sugar accumulation in the berries has received considerable attention in the past 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 *12* increases simultaneously with post-veraison sugar accumulation, suggesting a role of the corresponding proteins in sucrose acquisition by berry cells, prior to 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 greater 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 named *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, albeit. VvHT1 transcript and protein levels are much higher at pre-veraison 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 remain 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*, which transcripts 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.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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 post-veraison, when the berries accumulate hexoses, and in grapevine cell suspensions, *VvSK1* transcript abundance is increased by sucrose or abscisic acid treatments. The overexpression of the *VvSK1* gene in transgenic 41b grapevine cells enhance the expression of four monosaccharide transporters (*VvHT3-6*) and leads to a 3- to 5- fold increase in glucose uptake by the cells; thus 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).

3. 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, Kliewer 1966, Ribéreau-Gayon et al. 2006).

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

3.1 Genetic diversity of berry tartaric and malic acid concentration

There is a large genetic diversity for grape berry organic acid concentration (Kliewer 1965a, b, 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). Kliewer et al. (1967) reported a range of tartrate and malate concentration at maturity from 4 to 9.4g/L of tartrate and 1.5 to 6.8 g/L for malate for 78 *V. vinifera* cultivars including table and wine ones. On a set of 98 varieties including interspecific hybrids, Liu et al. (2006) recorded a range of 1.6 to 9.1 g/L for tartrate and 0.36 to 7.06 g/L for malate. Total acid and malic acid concentrations were lower in cultivars from hybrids between *V. labrusca* and *V. vinifera*, than in *V. vinifera* cultivars. Within *V. vinifera*, wine grapes had significantly higher acid concentration than table grapes (Liu et al. 2006). Boubals et al. (1971) described a cultivar named Gora Chirine originated from Iran. This cultivar accumulates very low amount of malate and tartrate compared to other *V. vinifera* varieties, and is characterized by a much higher pH of its berry juice, but has an identical vacuolar pH at veraison (Diakou et al. 1997). Among wild *Vitis* species, the range of concentration reported at maturity by Kliewer (1967a) for tartrate is 3.1 g/L in *V. rufotomentosa* to 11.9 g/L in *V. solonis*. For malate, the range of 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 named β ratio according to Shiraishi (1995) also exhibits extensive genetic variability. Among the population studied by Kliewer (1967), the β ratio varied from 0.64 (Pinot St George) to 3.41 (Palomino). The same range of variation was reported by Shiraishi et al. (2010) within a set of varieties including interspecific hybrids. Liu et al. (2006) sorted varieties according to various criteria and showed that seedless cultivars and *V.labrusca* x *V. vinifera* hybrids were characterized by the highest β ratio (about 3.0) and *V. vinifera* table grapes by the lowest ratio (between 1.5 and 2). In wild *Vitis* species a larger range of variation is found for β ratio, ranging from 0.34 (*V. berlandieri*) to 5.85 (*V. labrusca*).

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

3.2 Physiological parameters underlying the plasticity of tartaric and malic acid concentration

Berry organic acid concentration is affected 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. Ollat and Gaudillère (1998) reported that a low leaf to fruit ratio applied shortly after fruit set on fruiting cuttings of Cabernet Sauvignon (cultivated in a growth chamber) 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). 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. Morever the onset of veraison was also delayed and there was a negative correlation between berry weight and the veraison date (Ollat and Gaudillere 1998). 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 grapevine grown in cool climates have a higher malic acid concentration in their berries (Keller et al. 2005, Kondouras et al. 2006, Pereira et al. 2006). The impact of water stress on berry malic acid concentration are less clear-cut, and both increases (Lòpez et al. 2007), decreases (Kondouras et al. 2006, Salon et al. 2005) or even no changes (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).

3.3 Genes that control genetic diversity or plasticity of tartaric and malic acid concentration

Genetic studies on berry acid concentration are rare in literature. Liu et al. (2007) reported the 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 β ratio was not affected by annual effects. As far as we

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

know, no result for QTL identification for organic acid concentration has been published yet, but some work is in progress (Duchêne and Romieu, personal communications).

Conversely, molecular data regarding the genes that control berry acid concentration have started to appear in the literature during the past decade. Tartaric acid is thought to be synthesized from L-ascorbic acid through a 5-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 databases survey and metabolic profiling led to the identification of the gene coding for the 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 3 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). In spite of this, relatively few genes involved in malate accumulation in berries have been formally identified, since there is little obvious correlation between transcript abundance and malate levels. The noticeable exceptions are two cytosolic and two mitochondrial malate dehydrogenases, whose expression levels 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 metabolomic are required to reach a more comprehensive view of molecular players involved in berry malate concentration regulation.

4. 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 1995). Anthocyanins are a class of crucial phenolic compounds, synthetized via the flavonoid pathway. In addition to control grape and wine color, they also play a major role in protection due to their

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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 cultivars and species (Mazza 1995), stage of ripening (Fournand et al. 2006, Holt et al. 2010), 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, Cortell et al. 2008, Fournand et al. 2006, Kontoudakis et al. 2011, Torchio et al. 2010).

4.1 Genetic variability

Anthocyanin profiles of numerous *V. vinifera* cultivars and *Vitis* species have been reviewed by Mazza (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, Tempranillo are characterized by a major proportion of malvidin derivatives, while Nebbiolo, an Italian variety, is typical with peonidin-3-glucoside as the most prevalent one (Guidoni et al. 2008). Pinot noir is known for not synthetizing acetylated anthocyanins (Mazza 1995). *V. 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), thirty five different anthocyanin forms were detected using LC-MS chromatography between these 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'

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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.

4.2 Physiological parameters regulating anthocyanin composition

Mineral nutrition, yield and vigour, 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). Sadras et al. (2007), while quantifying the phenotypic plasticity of both anthocyanins and sugars in berries of Cabernet Sauvignon, showed that sugar accumulation is more strictly associated to thermal time whereas anthocyanin accumulation is also affected by other sources of variations (water, yield, and climatic conditions). Consequently, under the experimental conditions tested the amount of anthocyanins displays a much larger 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, Fournand et al. (2006) observed that the 2-methoxylated forms (cyanidin and delphinidin) reach a maximum of concentration earlier than the 3-methoxylated forms (malvidin and peonidin).

The effects of mineral nutrition and vine vigour on the anthocyanin composition and concentration have also been investigated (Cortell et al. 2007a, Downey et al. 2006, Keller et al. 1998). Heavy N fertilization

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

at flowering delayed ripening and anthocyanin accumulation with malvidin-3-glucoside being enhanced in proportion to the other forms (Keller et al. 1998). The most likely mechanism that explains nitrogen effect is the excess of vigour. Cortell et al. (2007a) reported that a reduction of vine vigour increased anthocyanin accumulation, but variations of composition were not clear regarding of year and site. Kondouras et al. (2009) observed a higher concentration of malvidin-3-O-glucoside and malvidin 3-O-coumarateglucoside for Cabernet Sauvignon vines grafted onto the high vigorous rootstock 1103P than those grafted on SO4. In most cases, it is uncertain whether the vigour 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 di-hydroxylated anthocyanins in comparison to tri-hydroxylated 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 non-acetylated forms (Downey et al. 2006, Spayd et al. 2002, Tarara et al. 2008). Water deficit results in an increased in anthocyanin concentration and the proportion of trihydroxylated anthocyanins as malvidine and *p*-coumaroylated derivatives (Castellarin and Gaspero 2007, Kondouras et al. 2009, Ollé et al. 2011).

4.3 Genes involved in the 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 anthocynin 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 matches the changes in expression levels seen for several structural genes of the anthocyanin pathway (Ageorges et

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

al. 2006). Apart from *VvMBYA1*, two other MYB genes, *VvMYB5a* and *VvMYB5b* have been cloned and functionally characterized (Deluc et al. 2006, Deluc et al. 2008). Both genes are able to trans-activate 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 afterwards; 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. Recently *VvMYC1*, a gene coding for a bHLH transcription factor, was 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 4 decades. Cross offspring population studies led to the conclusion that berry color was inherited as a quality trait controlled by a small number of 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 population 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 colocalize with a cluster of VvMYB gens (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 the biosynthesis of anthocyanin in the berries.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Because of the specific anthocyanin composition in wild *Vitis* species, the expression of genes involved in anthocyanin biosynthesis pathway was compared to the *V. vinifera* one. 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 et 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 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 the chromosome 9 of the Pinot noir genome, nearby 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” flavour 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*, *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 large genetic diversity which means variability among genotypes under given growing conditions, and a large phenotypic plasticity i.e.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

variability for a given genotype growing under different environmental conditions and/or under viticulture practices. So far, genetic and molecular studies have been mostly 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 of 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 non-invasive sensors (Ghozlen et al. 2010) and Fourier-transform mid-infrared spectroscopy (Versari et al. 2008), it will be also possible to extend the investigations about 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 transcriptomics, proteomics, metabolomics, and phenomics approaches. Grimplet et al. (Grimplet et al. 2009) developed and validated a tool called VitisNet to analyze grapevine molecular networks, in which 13,145 unigenes were assigned to 219 molecular networks. 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 towards 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).

Literature Cited

Adams, D.O. 2006. Phenolics and ripening in grape berries. Am. J. Enol. Vitic. 57: 249-256.

Agasse, A., C. Vignault, C. Kappel, C. Conde, H. Geros, and S. Delrot. 2009. Sugar transport & sugar sensing in grape. *In* Grapevine Molecular Physiology & Biotechnology. K. A. Roubelakis-Angelakis (ed.), pp. 105-128. Springer, New York.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

586 Ageorges, A., L. Fernandez, S. Vialet, D. Merdinoglu, N. Terrier, and C. Romieu. 2006. Four specific
587 isogenes of the anthocyanin metabolic pathway are systematically co-expressed with the red colour of
588 grape berries. Plant Sci. 170: 372-383.

589 Ageorges, A., N. Issaly, S. Picaud, and S. Delrot. 2000. Characterization of an active sucrose transporter
590 gene expressed during the ripening of grape berry (*Vitis vinifera* L.). Plant Physiol. Biochem. 38: 177-
591 185.

592 Ali, M.B., S. Howard, S. Chen, Y. Wang, O. Yu, L.G. Kovacs, and W. Qiu. 2011. Berry skin development
593 in Norton grape: distinct patterns of transcriptional regulation and flavonoid biosynthesis. BMC Plant
594 Biol. 11: 7.

595 Bates, T. 2008. Pruning level affects growth and yield of New York Concord on two training systems. Am.
596 J. Enol. Vitic. 59: 276-286.

597 Baudry, A., M.A. Heim, B. Dubreucq, M. Caboche, B. Weisshaar, and L. Lepiniec. 2004. TT2, TT8, and
598 TTG1 synergistically specify the expression of BANYULS and proanthocyanidin biosynthesis in
599 *Arabidopsis thaliana*. Plant J. 39: 366-380.

600 Bellin, D., A. Ferrarini, A. Chimento, O. Kaiser, N. Levenkova, P. Bouffard, and M. Delledonne. 2009.
601 Combining next-generation pyrosequencing with microarray for large scale expression analysis in non-
602 model species. BMC Genomics 10: 555-564.

603 Bindi, M., L. Fibbi, B. Gozzini, S. Orlandini, and F. Miglietta. 1996. Modelling the impact of future climate
604 scenarios on yield and yield variability of grapevine. Clim. Res. 7: 213-224.

605 Boss, P.K., and C. Davies. 2009. Molecular biology of anthocyanin accumulation in grape berries. *In*
606 Grapevine Molecular Physiolgoy & Biotechnology. K. A. Roubelakis-Angelakis (ed.), pp. 263-287.
607 Springer, New York.

608 Boubals, D., M. Bourzeix, and J. Guitraud. 1971. Le Gora Chirine, variété de vigne iranienne à faible
609 teneur en acides organiques. Annal. Amelior. Plant. 21: 281-285.

610 Boursiquot, J., M. Dessup, and C. Rennes. 1995. Distribution des principaux caracteres phenologiques,
611 agronomiques et technologiques chez Vitis vinifera L. Vitis 34: 31 - 35.

612 Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13: 115-
613 155.

614 Cabezas, J.A., M.T. Cervera, L. Ruiz-Garcia, J. Carreno, and J.M. Martinez-Zapater. 2006. A genetic
615 analysis of seed and berry weight in grapevine. Genome 49: 1572-1585.

616 Cakir, B., A. Agasse, C. Gaillard, A. Saumonneau, S. Delrot, and R. Atanassova. 2003. A grape ASR
617 protein involved in sugar and abscisic acid signaling. Plant Cell 15: 2165-2180.

618 Carroll, D.E., M.W. Hoover, and W.B. Nesbitt. 1971. Sugar and organic acid concentrations in cultivars of
619 muscadine grapes. J. Am. Soc. Hortic. Sci. 96: 737-740.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Carroll, D.E., and J.E. Marcy. 1982. Chemical and physical changes during maturation of Muscadine grapes (*Vitis Rotundifolia*). Am. J. Enol. Vitic. 33: 168-172.

Castellarin, S.D., and G.D. Gaspero. 2007. Transcriptional control of anthocyanin biosynthetic genes in extreme phenotypes for berry pigmentation of naturally occurring grapevines. BMC Plant Biol. 7: 46.

Cawthon, D.L., and J.R. Morris. 1982. Relationship of seed number and maturity to berry development, fruit maturation, hormonal changes, and uneven ripening of 'concord' (*Vitis labrusca* L.) grapes. J. Am. Soc. Hortic. Sci. 107: 1097-1104.

Chorti, E., S. Guidoni, A. Ferrandino, and V. Novello. 2010. Effect of different cluster sulight exposure levels on ripening and anthocyanin accumulation in Nebbiolo grapevines. Am. J. Enol. Vitic. 61: 23-30.

Clingeleffer, P.R. 2010. Plant management research: status and what it can offer to address challenges and limitations. Aust. J. Grape Wine Res. 16: 25-32.

Conde, B.C., A. Agasse, D. Glissant, R.M. Tavares, H. Geros, and S. Delrot. 2006. Pathways of glucose regulation of monosaccharide transport in grape cells. Plant Physiol. 141: 1563-1577.

Conde, B.C., P. Silva, N. Fontes, A.C.P. Dias, R.M. Tavares, M.J. Sousa, A. Agasse, S. Delrot, and H. Geros. 2007. Biochemical changes throughout grape berry development and fruit and wine quality. Food 1: 1-22.

Coombe, B.G. 1959. Fruit set and development in seeded grape varieties as affected by defoliation, topping, girdling, and other treatments. Am. J. Enol. Vitic. 10: 85-100.

Coombe, B.G. 1976. The development of fleshy fruits. Annu. Rev. Plant Physio. 27: 207-228.

Coombe, B.G. 1992. Research on development and ripening of the grape berry. Am. J. Enol. Vitic. 43: 101-110.

Cortell, J.M., M. Halbleib, A.V. Gallagher, T.L. Righetti, and J.A. Kennedy. 2007a. Influence of vine vigor on grape (*Vitis vinifera* L. cv. Pinot noir) anthocyanins.1. Anthocyanin concentration and composition in fruit. J. Agric. Food Chem. 55: 6575-6584.

Cortell, J.M., M. Halbleib, A.V. Gallagher, T.L. Righetti, and J.A. Kennedy. 2007b. Influence of vine vigor on grape (*Vitis vinifera* L. cv. Pinot noir) anthocyanins. 2. Anthocyanins and pigmented polymers in wine. J. Agric. Food Chem. 55: 6585-6595.

Cortell, J.M., H.K. Sivertsen, J.A. Kennedy, and H. Heymann. 2008. Influence of vine vigor on Pinot noir fruit composition, wine chemical analysis, and wine sensory attributes. Am. J. Enol. Vitic. 59: 1-10.

Cramer, G., A. Ergül, J. Grimplet, R. Tillett, E. Tattersall, M. Bohlman, D. Vincent, J. Sonderegger, J. Evans, C. Osborne, D. Quilici, K. Schlauch, D. SchooleyandJ. Cushman. 2007. Water and salinity stress in grapevines: early and late changes in transcript and metabolite profiles. Funct. Integr. Genomics 7: 111-134.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Dai, Z.W., P. Vivin, F. Barrieu, N. Ollat, and S. Delrot. 2010. Physiological and modelling approaches to understand water and carbon fluxes during grape berry growth and quality development: a review. Aust. J. Grape Wine Res. 16: 70-85.

Davies, C., and S.P. Robinson. 1996. Sugar accumulation in grape berries. Plant Physiol. 111: 275-283.

Davies, C., T. Wolf, and S.P. Robinson. 1999. Three putative sucrose transporters are differentially expressed in grapevine tissues. Plant Sci. 147: 93-100.

DeBolt, S., D.R. Cook, and C.M. Ford. 2006. L-Tartaric acid synthesis from vitamin C in higher plants. Proc. Natl. Acad. Sci. 103: 5608-5613.

Deluc, L., F. Barrieu, C. Marchive, V. Lauvergeat, A. Decendit, T. Richard, J.-P. Carde, J.-M. Merillon, and S. Hamdi. 2006. Characterization of a grapevine R2R3-MYB transcription factor that regulates the phenylpropanoid pathway. Plant Physiol. 140: 499-511.

Deluc, L., J. Bogs, A.R. Walker, T. Ferrier, A. Decendit, J.-M. Merillon, S.P. Robinson, and F. Barrieu. 2008. The Transcriptionfactor VvMYB5b contributes to the regulation of anthocyanin and proanthocyanidin biosynthesis in developing grape berries. Plant Physiol. 147: 2041-2053.

Deluc, L.G., J. Grimplet, M.D. Wheatley, R.L. Tillett, D.R. Quilici, C. Osborne, D.A. Schooley, K.A. Schlauch, J.C. Cushman, and G.R. Cramer. 2007. Transcriptomic and metabolite analyses of Cabernet Sauvignon grape berry development. BMC Genomics 8: 429.

Diakou, P., A. Moing, L. Svanella, N. Ollat, D. Rolin, M. Gaudillere, and J. Gaudillere. 1997. Biochemical comparison of two grape varieties differing in juice acidity. Aust. J. Grape Wine Res. 3: 1-10.

Doligez, A., A. Bouquet, Y. Danglot, F. Lahogue, S. Riaz, P. Meredith, J. Edwards, and P. This. 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.

Downey, M.O., N.K. Dokoozlian, and M.P. krstic. 2006. Cultural practice and environmental impacts on the flavonoid composition of grapes and wine: a review of recent research. Am. J. Enol. Vitic. 57: 257-268.

Duchêne, E., F. Haurd, V. Dumas, C. Schneider, and D. Merdinoglu. 2010. The challenge of adapting grapevine varieties to climate change. Clim. Res. 41: 193-204.

Ebadi, A., P. May, and B.G. Coombe. 1996. Effect of short-term temperature and shading on fruit-set, seed and berry development in model vines of *V. vinifera*, cvs Chardonnay and Shiraz. Aust. J. Grape Wine Res. 2: 2-9.

Esteban, M.A., M.J. Villanueva, and J.R. Lissarrague. 1999. Effect of irrigation on changes in berry composition of Tempranillo during maturation. Sugars, organic acids, and mineral elements. Am. J. Enol. Vitic. 50: 418-434.

Esteban, M.A., M.J. Villanueva, and J.R. Lissarrague. 2002. Relationships between different berry components in Tempranillo (*Vitis vinifera* L) grapes from irrigated and non-irrigated vines during ripening. J. Sci. Food Agric. 82: 1136-1146.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Fanizza, G., F. Lamaj, L. Costantini, R. Chaabane, and M.S. Grando. 2005. QTL analysis for fruit yield components in table grapes (*Vitis vinifera*). Theor. Appl. Genet. 111: 658-664.

Fernandez, L., A. Doligez, G. Lopez, M. Thomas, A. Bouquet, and L. Torregrosa. 2006a. Somatic chimerism, genetic inheritance, and mapping of the fleshless berry (flb) mutation in grapevine (Vitis vinifera L.). Genome 49: 721 - 728.

Fernandez, L., M. Pradal, G. Lopez, F. Berud, C. Romieu, and L. Torregrosa. 2006b. Berry size variability in *Vitis vinifera* L. Vitis 45: 53-55.

Fernandez, L., C. Romieu, A. Moing, A. Bouquet, M. Maucourt, M.R. Thomas, and L. Torregrosa. 2006c. The grapevine fleshless berry mutation. A unique genotype to investigate differences between fleshy and nonfleshy fruit. Plant Physiol. 140: 537-547.

Fernandez, L., L. Torregrosa, N. Terrier, L. Sreekantan, J. Grimplet, C. Davies, M. Thomas, C. Romieu, and A. Ageorges. 2007. Identification of genes associated with flesh morphogenesis during grapevine fruit development. Plant Mol. Biol. 63: 307-323.

Fischer, B.M., I. Salakhutdinov, M. Akkurt, R. Eibach, K.J. Edwards, R. Töpfer, and E.M. Zyprian. 2004. Quantitative trait locus analysis of fungal disease resistance factors on a molecular map of grapevine. Theor. Appl. Genet. 108: 501-515.

Fournand, D., A. Vicens, L. Sidhoum, J.M. Souquet, M. Moutounet, and V. Cheynier. 2006. Accumulation and extractibility of grape skin tannins and anthocyanins at different advanced physiological stages. J. Agric. Food Chem. 54: 7331-7338.

Fournier-Level, A., T. Lacombe, L. Le Cunff, J.M. Boursiquot, and P. This. 2010. Evolution of the VvMybA gene family, the major determinant of berry colour in cultivated grapevine (Vitis vinifera L.). Heredity 104: 351-362.

Friend, A.P., M.C.T. Trought, and G.L. Creasy. 2009. The influence of seed weight on the development and growth of berries and live green ovaries in *Vitis vinifera* L. cvs. Pinot Noir and Cabernet Sauvignon. Aust. J. Grape Wine Res. 15: 166-174.

Garcia de Cortazar-Atauri, I., N. Brisson, N. Ollat, O. Jacquet, and J.C. Payan. 2009. Asynchronous dynamics of grapevine (*Vitis vinifera*) maturation: experimental study for a modelling approach. J. Int. Sci. Vigne Vin 43: 83-97.

Génard, M., N. Bertin, H. Gautier, F. Lescourret, and B. Quilot. 2010. Virtual profiling: a new way to analyse phenotypes. Plant J. 62: 344-355.

Ghozlen, N.B., Z.G. Cerovic, C. Germain, S. Toutain, and G. Latouche. 2010. Non-destructive optical monitoring of grape maturation by proximal sensing. Sensors 10: 10040-10068.

Giribaldi, M., L. Gény, S. Delrot, and A. Schubert. 2010. Proteomic analysis of the effects of ABA treatments on ripening *Vitis vinifera* berries. J. Exp. Bot. 61: 2447-2458.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Gray, J., and B. Coombe. 2009. Variation in Shiraz berry size originates before fruitset but harvest is a point of resynchronisation for berry development after flowering. Aust. J. Grape Wine Res. 15: 156-165.

Gray, J.D. 2002. The basis of variation in the size and composition of grape berries. Thesis, University of Adelaide, Adelaide, Australia.

Grimplet, J., G.R. Cramer, J.A. Dickerson, K. Mathiason, J. Van Hemert, and A.Y. Fennell. 2009. VitisNet: “Omics” integration through grapevine molecular networks. PLoS ONE 4: e8365.

Guidoni, S., P. Allara, and A. Schubert. 2002. Cluster thinning affects the berry skin anthocyanin composition of *Vitis vinifera* cv. Nebbiolo. Am. J. Enol. Vitic. 53: 224-226.

Guidoni, S., A. Ferrandino, and V. Novello. 2008. Effects of seasonal and agronomical practices on skin anthocyanin profile of Nebbiolo grapes. Am. J. Enol. Vitic. 59: 22-29.

Hale, C, P, and R. J. Weaver. 1962. The effect of developpemental stage on direction of translocation photosynthate in *Vitis vinifera.* Hilgardia 33: 69-131.

Hawker, J.S., H.P. Ruffner, and R.R. Walker. 1976. The sucrose content of some Australian grapes. Am. J. Enol. Vitic. 27: 125-129.

Hayes, M.A., C. Davies, and I.B. Dry. 2007. Isolation, functional characterization, and expression analysis of grapevine (*Vitis vinifera* L.) hexose transporters: differential roles in sink and source tissues. J. Exp. Bot. 58: 1985-1997.

He, F., L. Mu, G.L. Yan, N.N. Liang, Q.H. Pan, Y. Wang, M.J. Reeves, and C.Q. Duan. 2010. Biosynthesis of anthocyanins and their regulation in colored grapes. Molecules 15: 9057-9091.

Hichri, I., S.C. Heppel, J. Pillet, C. Léon, S. Czemmel, S. Delrot, V. Lauvergeat, and J. Bogs. 2010. The basic helix-loop-helix transcription factor MYC1 is involved in the regulation of the flavonoid biosynthesis pathway in grapevine. Mol. Plant 3: 509-523.

Holt, H.E., W. Birchmore, M.J. Herderich, and P.G. Iland. 2010. Berry phenolics in Cabernet Sauvignon (*Vitis vinifera* L.) during late-stage ripening. Am. J. Enol. Vitic. 61: 285-299.

Houel, C., R. Bounon, J. Chaib, C. Guichard, J.-P. Peros, R. Bacilieri, A. Dereeper, A. Canaguier, T. Lacombe, A. N'Diaye, M.-C. Le Paslier, M.-S. Vernerey, O. Coriton, D. Brunel, P. This, L. TorregrosaandA.-F. Adam-Blondon. 2010. Patterns of sequence polymorphism in the fleshless berry locus in cultivated and wild *Vitis vinifera* accessions. BMC Plant Biol. 10: 284.

Iandolino, A.B., F. Goes da Silva, H. Lim, H. Choi, L.E. Williams, and D.R. Cook. 2004. High-quality RNA, cDNA, and derived EST libraries from grapevine (*Vitis vinifera* L.). Plant Mol. Biol. Report. 22: 269-278.

Iland, P.G., and B.G. Coombe. 1988. Malate, tartrate, potassium, and sodium in flesh and skin of shiraz grapes during ripening: concentration and compartmentation. Am. J. Enol. Vitic. 39: 71-76.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

International Journal of Food Science & TechnologyLòpez, M., M. Sánchez, A. Diaz, P. Ramirez, and J. Morales. 2007. Influence of a deficit irrigation regime during ripening on berry composition in grapevines (Vitis vinifera L.) grown in semi-arid areas. Int. J. Food Sci. Nutr. 58: 491-507.

Jackson, D.I., and P.B. Lombard. 1993. Environmental and management practices affecting grape composition and wine quality - a review. Am. J. Enol. Vitic. 44: 409-430.

Jaillon, O., J.-M. Aury, B. Noel, A. Policriti, C. Clepet, A. Casagrande, N. Choisne, S. Aubourg, N. Vitulo, C. Jubin, A. Vezzi, F. Legeai, P. Hugueney, C. Dasilva, D. Horner, E. Mica, D. Jublot, J. Poulain, C. Bruyère, A. Billault, B. Segurens, M. Gouyvenoux, E. Ugarte, F. Cattonaro, V. Anthouard, V. Vico, C.D. Fabbro, M. Alaux, G. Di Gaspero, V. Dumas, N. Felice, S. Paillard, I. Juman, M. Moroldo, S. Scalabrin, A. Canaguier, I. Le Clainche, G. Malacrida, E. Durand, G. Pesole, V. Laucou, P. Chatelet, D. Merdinoglu, M. Delledonne, M. Pezzotti, A. Lecharny, C. Scarpelli, F. Artiguenave, M.E. Pè, G. Valle, M. Morgante, M. Caboche, A.F. Adam-Blondon, J. Weissenbach, F. QuétierandP. Wincker. 2007. The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla. Nature 449: 463-467.

Janvary, L., T. Hoffmann, J. Pfeiffer, L. Hausman, R. Töpfer, T. Fischer, and W. Schwab. 2009. A double mutation in the anthocyanin 5-*O*-glucosyltransferase gene disrupts enzymatic activity in *Vitis vinifera* L. J. Agric. Food Chem. 57: 3512-3518.

Jones, G. 2006. Climate change and wine: observations, impacts and future implications. Wine Industry J. 21: 21 - 26.

Jones, G.V., M.A. White, O.R. Cooper, and K. Storchmann. 2005. Climate change and global wine quality. Clim. Change 73: 319-343.

Jullien, A., E. Malézieux, N. Michaux-Ferrière, M. Chillet, and B. Ney. 2001a. Within-bunch variability in banana fruit weight: importance of developmental lag between fruits. Ann. Bot. 87: 101-108.

Jullien, A., N.G. Munier-Jolain, E. Malézieux, M. Chillet, and B. Ney. 2001b. Effect of pulp cell number and assimilate availability on dry matter accumulation rate in a banana fruit [*Musa sp.* AAA group 'Grande Naine' (Cavendish subgroup)]. Ann. Bot. 88: 321-330.

Kappel, C.D. 2010. Biologie intégrative du métabolisme de la baie de raisin. Thesis, Victor Segalen Bordeaux 2, Bordeaux, France.

Kasimatis, A.N., E.P. Vilas, F.H. Swanson, and P.P. Baranek. 1975. A study of the variability of `Thompson Seedless' berries for soluble solids and weight. Am. J. Enol. Vitic. 26: 37-42.

Keller, M. 2010. Managing grapevines to optimise fruit development in a challenging environment: a climate change primer for viticulturists. Aust. J. Grape Wine Res. 16: 56-69.

Keller, M., K.J. Arnink, and G. Hrazdina. 1998. Interaction of nitrogen availability during bloom and light intensity during veraison. I. effects on grapevine growth, fruit development, and ripening. Am. J. Enol. Vitic. 49: 333-340.

Keller, M., L.J. Mills, R.L. Wample, and S.E. Spayd. 2005. Cluster thinning effects on three deficit-irrigated *Vitis vinifera* cultivars. Am. J. Enol. Vitic. 56: 91-103.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Kennedy, J.A., C. Saucier, and Y. Glories. 2006. Grape and wine phenolics: history and perspective. Am. J. Enol. Vitic. 57: 239-248.

Kliewer, W.M. 1965a. Changes in concentration of glucose, fructose, and total soluble solids in flowers and berries of *Vitis vinifera*. Am. J. Enol. Vitic. 16: 101-110.

Kliewer, W.M. 1965b. Changes in the concentration of malates, tartrates, and total free acids in flowers and berries of *Vitis Vinifera*. Am. J. Enol. Vitic. 16: 92-100.

Kliewer, W.M. 1966. Sugars and organic acids of *Vitis vinifera*. Plant Physiol. 41: 923-931.

Kliewer, W.M. 1967a. Concentration of tartrates, malates, glucose and fructose in the fruits of the genus *Vitis*. Am. J. Enol. Vitic. 18: 87-96.

Kliewer, W.M. 1967b. The glucose-fructose ratio of *Vitis Vinifera* grapes. Am. J. Enol. Vitic. 18: 33-41.

Kliewer, W.M. 1970. Effect of time and severity of defoliation on growth and composition of 'Thompson Seedless' grapes. Am. J. Enol. Vitic. 21: 37-44.

Kliewer, W.M., and N.K. Dokoozlian. 2005. Leaf area/crop weight ratios of grapevines: influence on fruit composition and wine quality. Am. J. Enol. Vitic. 56: 170-180.

Kliewer, W.M., L. Howarth, and M. Omori. 1967. Concentrations of tartaric acid and malic acids and their salts in *Vitis Vinifera* grapes. Am. J. Enol. Vitic. 18: 42-54.

Kobayashi, Ishimaru, Hiraoka, and Honda. 2002. Myb-related genes of the Kyoho grape (*Vitis labruscana*) regulate anthocyanin biosynthesis. Planta 215: 924-933.

Kondouras, S., E. Hatzidimitriou, M. Karamolegkou, E. Dimopoulou, S. Kallithraka, J.T. Tsialtas, E. Zioziou, N. Nikolaou, and Y. Kotseridis. 2009. Irrigation and rootstock effects on the phenolic concentration and aroma potential of *Vitis vinifera* L. cv. Cabernet Sauvignon grapes. J. Agric. Food Chem. 57: 7805-7813.

Kondouras, S., V. Marinos, A. Gkoulioti , Y. Kotseridis, and C. Van Leeuween. 2006. Influence of vineyard location and vine water status on fruit maturation of nonirrigated cv. Agiogitiko (*Vitis vinifera* L.). Effect on wine phenolics and aroma component. J. Agric. Food Chem. 54: 5077-5086.

Kontoudakis, N., M. Esteruelas, F. Fort, J.M. Canals, V. De Freitas, and F. Zamora. 2011. Influence of the heterogeneity of grape phenolic maturity on wine composition and quality. Food Chem. 124: 767-774.

Lecourieux, F., D. Lecourieux, C. Vignault, and S. Delrot. 2010. A sugar-inducible protein kinase, VvSK1, regulates hexose transport and sugar accumulation in grapevine cells. Plant Physiol. 152: 1096-1106.

Liang, Z., C. Yang, J. Yang, B. Wu, L. Wang, J. Cheng, and S. Li. 2009. Inheritance of anthocyanins in berries of *Vitis vinifera* grapes. Euphytica 167: 113-125.

Lijavetzky, D., L. Ruiz-García, J. Cabezas, M. De Andrés, G. Bravo, A. Ibáñez, J. Carreño, F. Cabello, J. Ibáñez, and J. Martínez-Zapater. 2006. Molecular genetics of berry colour variation in table grape. Mol. Genet. Genomics 276: 427-435.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Liu, H.F., B.H. Wu, P.G. Fan, and S.H. Li. 2006. Sugar and acid concentrations in 98 grape cultivars analyzed by principal component analysis. J. Sci. Food Agric. 86: 1526-1536.

Liu, H.F., B.H. Wu, P.G. Fan, H.Y. Xu, and S.H. Li. 2007. Inheritance of sugars and acids in berries of grape (*Vitis vinifera* L.). Euphytica 153: 99-107.

Loewus, F.A. 1999. Biosynthesis and metabolism of ascorbic acid in plants and of analogs of ascorbic acid in fungi. Phytochemistry 52: 193-210.

Long, Z.R. 1986. Manipulation of grape flavour in the vineyard: California, North Coast region. *In* Proceedings of the Sixth Australian Wine Industry Technical Conference. T. H. Lee (ed.), pp. 82-88. Australian Industrial Publishers, Adelaide, Australia.

Lòpez, M., M. Sánchez, A. Diaz, P. Ramirez, and J. Morales. 2007. Influence of a deficit irrigation regime during ripening on berry composition in grapevines (Vitis vinifera L.) grown in semi-arid areas. Int. J. of Food Sci. Nutr. 58: 491-507.

Manning, K., C. Davies, H.C. Bowen, and P.J. White. 2001. Functional characterization of two ripening-related sucrose transporters from grape berries. Ann. Bot. 87: 125-129.

Martinez-Zapater, J., M. Carmona, J. Diaz-Riquelme, L. Fernandez, and D. Lijavetzky. 2010. Grapevine genetics after the genome sequence: Challenges and limitations. Aust. J. Grape Wine Res. 16: 33-46.

Mattivi, F., R. Guzzon, U. Vrhovsek, M. Stefanini, and R. Velasco. 2006. Metabolite profiling of grape: flavonols and anthocyanins. J. Agric. Food Chem. 54: 7692-7702.

Matus, J.T., R. Loyola, A. Vega, A. Peña-Neira, E. Bordeu, P. Arce-Johnson, and J.A. Alcalde. 2009. Post-veraison sunlight exposure induces MYB-mediated transcriptional regulation of anthocyanin and flavonol synthesis in berry skins of *Vitis vinifera* J. Exp. Bot. 60: 853-867.

May, P. 2000. From bud to berry, with special reference to inflorescence and bunch morphology in *Vitis vinifera* L. Aust. J. Grape Wine Res. 6: 82-89.

Mazza, G. 1995. Anthocyanins in grapes and grape products. Crit. Rev. Food Sci. Nutr. 35: 341-371.

Mejia, N., M. Gebauer, L. Munoz, N. Hewstone, and P. Hinrichsen. 2007. Identification of QTLs for seedlessness, berry size, and ripening date in a seedless x seedless table grape progeny. Am. J. Enol. Vitic. 58: 499 - 507.

Mejia, N., B. Soto, M. Guerrero, X. Casanueva, C. Houel, M.d.l. Angeles Miccono, R. Ramos, L. Le Cunff, J.-M. Boursiquot, P. Hinrichsen, and A.-F. Adam-Blondon. 2011. Molecular, genetic and transcriptional evidence for a role of VvAGL11 in stenospermocarpic seedlessness in grapevine. BMC Plant Biol. 11: 57-75.

Mori, K., N. Goto-Yamamoto, M. Kitayama, and K. Hashizume. 2007. Loss of anthocyanins in red-wine grape under high temperature. J. Exp. Bot. 58: 1935 - 1945.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Morita, Y., M. Saitoh, A. Hoshino, E. Nitasaka, and S. Iida. 2006. Isolation of cDNAs for R2R3-MYB, bHLH and WDR transcriptional regulators and identification of c and ca mutations conferring white flowers in the Japanese Morning Glory. Plant Cell Physiol. 47: 457-470.

Nuzzo, V., and M.A. Matthews. 2006. Response of fruit growth and ripening to crop level in dry-farmed Cabernet Sauvignon on four rootstocks. Am. J. Enol. Vitic. 57: 314-324.

Ojeda, H., A. Deloire, and A. Carbonneau. 2001. Influence of water deficits on grape berry growth. Vitis 40: 141-145.

Ollat, N., P. Diakou-Verdin, J.P. Carde, F. Barrieu, J.P. Gaudillere, and A. Moing. 2002. Grape berry development: a review. J. Int. Sci. Vigne Vin 36: 109-131.

Ollat, N., and J.P. Gaudillere. 1998. The effect of limiting leaf area during stage I of berry growth on development and composition of berries of *Vitis vinifera* L. cv. Cabernet Sauvignon. Am. J. Enol. Vitic. 49: 251-258.

Ollé, D., J.L. Guiraud, J.M. Souquet, N. Terrier, A. Ageorges, V. Cheynier, and C. Verriès. 2011. Effect of pre- and post-veraison water deficit on proanthocyanidin and anthocyanin accumulation during Shiraz berry development. Aust. J. Grape Wine Res. 17: 90-100.

Pagay, V., and L. Cheng. 2010. Variability in berry maturation of Concord and Cabernet franc in a cool climate. Am. J. Enol. Vitic. 61: 61-67.

Parra, C.S., J. Aguirreolea, M. Sánchez-Diaz, J.J. Irigoyen, and F. Morales. 2010. Effects of climate change scenarios on Tempranillo grapevine (*Vitis vinifera* L.) ripening: response to a combination of elevated CO_2 and temperature, and moderate drought. Plant Soil 337: 179-191.

Pereira, G.E., J.P. Gaudillere, P. Pieri, G. Hilbert, M. Maucourt, C. Deborde, A. Moing, and D. Rolin. 2006. Microclimate influence on mineral and metabolic profiles of grape berries. J. Agric. Food Chem. 54: 6765-6775.

Petrie, P.R., and P.R. Clingeleffer. 2006. Crop thinning (hand versus mechanical), grape maturity and anthocyanin concentrations: outcomes from irrigated Cabernet Sauvignon (Vitis vinifera L.) in a warm climate. Aust. J. Grape Wine Res. 12: 21-29.

Petrie, P.R., M.C.T. Trought, and G.S. Howell. 2000. Fruit composition and ripening of Pinot Noir (Vitis vinifera L.) in relation to leaf area. Aust. J. Grape Wine Res. 6: 46-51.

Rankine, B.C., K.M. Cellier, and E.W. Boehm. 1962. Studies on grape variability and field sampling. Am. J. Enol. Vitic. 13: 58-72.

Reynolds, A.G., S.F. Price, D.A. Wardle, and B.T. Watson. 1994. Fruit environment and crop levels effects on Pinot Noir. I. Vine performance and fruit composition in British Colombia. Am. J. Enol. Vitic. 45: 452-459.

Reynolds, A.G., and J.E. Vanden Heuvel. 2009. Influence of grapevine training systems on vine growth and fruit composition: a review. Am. J. Enol. Vitic. 60: 251-268.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Ribéreau-Gayon, P., D. Dubourdieu, B. Donèche, and A. Lonvaud 2006. Handbook of Enology The Microbiology of Wine and Vinification. John Wiley&Sons, West Sussex, England.

Roby, G., and M.A. Matthews. 2004. Relative proportions of seed, skin, and flesh, in ripe berries from Cabernet Sauvignon grapevines grown in a vineyard either well irrigated or under water deficit. Aust. J. Grape Wine Res. 10: 74-82.

Roggero, J.P., J.L. Larice, C. Rocheville-Divore, C. Archier, and S. Coen. 1988. Composition anthocyanique des cépages. II. Essai de classification sur trois ans par analyse en composntes principales et par analyse factorielle discriminante. Rev. Francaise d'Oenologie 112: 41-48.

Rüffner, H.P. 1982. Metabolism of tartaric and malic acids in *Vitis:* A review Part B. Vitis 21: 346-358.

Sadras, V.O., M. Collins, and C.J. Soar. 2008. Modelling variety-dependent dynamics of soluble solids and water in berries of *Vitis vinifera*. Aust. J. Grape Wine Res. 14: 250-259.

Sadras, V.O., and M.G. McCarthy. 2007. Quantifying the dynamics of sugar concentration in berries of *Vitis vinifera* cv.Shiraz: a novel approach based on allometric analysis. Aust. J. Grape Wine Res. 13: 66-71.

Sadras, V.O., R.M. Stevens, J.M. Pech, E.J. Taylor, P.R. Nicholas, and M.G. McCarthy. 2007. Quantifying phenotypic plasticity of berry traits using an allometric-type approach: a case study on anthocyanins and sugars in berries of Cabernet Sauvignon. Aust. J. Grape Wine Res. 13: 72-80.

Salmaso, M., G. Malacarne, M. Troggio, G. Faes, M. Stefanini, M. Grando, and R. Velasco. 2008. A grapevine (*Vitis vinifera* L.) genetic map integrating the position of 139 expressed genes. Theor. Appl. Genet. 116: 1129-1143.

Salon, J., C. Chirivella, and J. Castel. 2005. Response on cv. Bobal to timing of deficit irrigation in Requena, Spain: water relations, yield, and wine quality. Am. J. Enol. Vitic. 56: 1-8.

Samuelian, S.K., C. Camps, C. Kappel, E.P. Simova, S. Delrot, and V.M. Colova. 2009. Differential screening of overexpressed genes involves in flavonoid biosynthesis in North American native grapes: 'Noble' *muscadinia* var. and 'Cynthiana' *aestivalis* var. Plant Sci. 177: 211-221.

Santesteban, L.G., and J.B. Royo. 2006. Water status, leaf area and fruit load influence on berry weight and sugar accumulation of cv. 'Tempranillo' under semiarid conditions. Sci. Hortic. 109: 60-65.

Sato, A., M. Yamada, H. Iwanami, and N. Hirakawa. 2000. Optimal spatial and temporal measurement repetition for reducing environmental variation of berry traits in grape breeding. Sci. Hortic. 85: 75-83.

Schultz, H.R. 2000. Climate change and viticulture: A European perspective on climatology, carbon dioxide and UV-B effects. Aust. J. Grape Wine Res. 6: 2-12.

Selvaraj, Y., D.K. Pal, R. Singh, and T.K. Roy. 1995. Biochemistry of uneven ripening in gulabi grape. J. Food Biochem. 18: 325-340.

Shellie, K.C. 2007. Vitcultural performance of red and white wine grape cultivars in Southwestern Idaho. HortTechnology 17: 595-603.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Shellie, K.C. 2010. Water deficit effect on ratio of seed to berry fresh weight and berry weight uniformity in winegrape cv. Merlot. Am. J. Enol. Vitic. 61: 414-418.

Shiraishi, M. 1995. Proposed descriptors for organic acids to evaluate grape germplasm. Euphytica 81: 13-20.

Shiraishi, M. 2000. Comparison in changes in sugars, organic acids and amino acids during berry ripening of sucrose- and hexose-accumulating grape cultivars. J. Jpn. Soc. Hortic. Sci. 69: 141-148.

Shiraishi, M., H. Fujishima, and H. Chijiwa. 2010. Evaluation of table grape genetic resources for sugar, organic acid, and amino acid composition of berries. Euphytica 174: 1-13.

Singleton, V.L., C.S. Ough, and K.E. Nelson. 1966. Density separations of wine grape berries and ripeness distribution. Am. J. Enol. Vitic. 17: 95-105.

Sivilotti, P., C. Bonetto, M. Paladin, and E. Peterlunger. 2005. Effect of soil moisture availability on Merlot: from leaf water potential to grape composition. Am. J. Enol. Vitic. 56: 9-18.

Spayd, S.E., J.M. Tarara, and J.C. Ferguson. 2002. Separation of sunlight and temperature effects on the composition of *Vitis vinifera* cv. Merlot berries. Am. J. Enol. Vitic. 53: 171-182.

Swansom, C.A., and E.D.H. Elshishiny. 1958. Translocation of sugars in the Concord grape. Plant Physiol. 33: 33-37.

Sweetman, C., L.G. Deluc, G.R. Cramer, C.M. Ford, and K.L. Soole. 2009. Regulation of malate metabolism in grape berry and other developing fruits. Phytochemistry 70: 1329-1344.

Takayanagi, T., and K. Yokotsuka. 1997. Relationship between sucrose accumulation and sucrose-metabolizing enzymes in developing grapes. Am. J. Enol. Vitic. 48: 403-407.

Tarara, J.M., J. Lee, S.E. Spayd, and C.F. Scagel. 2008. Berry temperature and solar radiation alter acylation, proportion, and concentration of anthocyanin in Merlot grapes. Am. J. Enol. Vitic. 59: 235-247.

Tardaguila, J., F.M. de Toda, S. Poni, and M.P. Diago. 2010. Impact of early leaf removal on yield and fruit and wine composition of *Vitis vinifera* L. Graciano and Carignan. Am. J. Enol. Vitic. 61: 372-381.

Tarter, M.E., and S.E. Keuter. 2005. Effect of rachis position on size and maturity of Cabernet Sauvignon berries. Am. J. Enol. Vitic. 56: 86-89.

Tattersall, E., J. Grimplet, L. DeLuc, M. Wheatley, D. Vincent, C. Osborne, A. Ergul, E. Lomen, R. Blank, K. Schlauch, J. Cushman, and G. Cramer. 2007. Transcript abundance profiles reveal larger and more complex responses of grapevine to chilling compared to osmotic and salinity stress. Funct. Integr. Genomics 7: 317 - 333.

Terrier, N., D. Glissant, J. Grimplet, F. Barrieu, P. Abbal, C. Couture, A. Ageorges, R. Atanassova, C. Leon, J.-P. Renaudin, F. Dedaldechamp, C. Romieu, S. DelrotandS. Hamdi. 2005. Isogene specific oligo arrays reveal multifaceted changes in gene expression during grape berry (*Vitis vinifera* L.) development. Planta 222: 832-847.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

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

This, P., T. Lacombe, and M. Thomas. 2006. Historical origins and genetic diversity of wine grapes. Trends Genet. 22: 511 - 519.

Tijskens, L.M.M., P. Konopacki, and M. Simcic. 2003. Biological variance, burden or benefit? Postharvest Biol. Technol. 27: 15-25.

Torchio, F., E. Cagnasso, V. Gerbi, and L. Rolle. 2010. Mechanical properties, phenolic composition and extractibility indices of Berbera grapes of different soluble solids contents from several growing areas. Anal. Chim. Acta 660: 183-189.

Van Leeuwen, C., and G. Seguin. 1994. Incidences de l'alimentation en eau de la vigne, appreciée par l'état hydrique du feuillage, sur le développement de l'appareil végétatif et la maturation du raisin (*Vitis vinifera* var. 'Cabernet Franc'). J. Int. Sci. Vigne Vin 28: 81-110.

Van Leeuwen, C., O. Trégoat, X. Choné, B. Bois, D. Pernet, and J.P. Gaudillere. 2009. Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. How can it be assessed for vineyard management purposes? J. Int. Sci. Vigne Vin 43: 121-134.

Versari, A., G.P. Parpinello, A.U. Mattioli, and S. Galassi. 2008. Determination of grape quality at harvest using fourier-transform mid-infrared spectroscopy and multivariate analysis. Am. J. Enol. Vitic. 59: 317-322.

Vignault, C., M. Vachaud, B. Cakir, D. Glissant, F. Dedaldechamp, M. Buttner, R. Atanassova, P. Fleurat-Lessard, R. Lemoine, and S. Delrot. 2005. VvHT1 encodes a monosaccharide transporter expressed in the conducting complex of the grape berry phloem. J. Exp. Bot. 56: 1409-1418.

Walker, R.R., D.H. Blackmore, P.R. Clingeleffer, G.H. Kerridge, E.H. Rühl, and P.R. Nicholas. 2005. Shiraz berry size in relation to seed number and implications for juice and wine composition. Aust. J. Grape Wine Res. 11: 2-8.

Webb, L.B., P.H. Whetton, and E.W.R. Barlow. 2007. Modelled impact of future climate change on the phenology of winegrapes in Australia. Aust. J. Grape Wine Res. 13: 165-175.

Wei, X., S.R. Sykes, and P.R. Clingeleffer. 2002. An investigation to estimate genetic parameters in CSIRO's table grape breeding program. 2. Quality characteristics. Euphytica 128: 343-351.

Wolpert, J.A., and G.S. Howell. 1984. Sampling Vidal Blanc grapes. II. sampling for precise estimates of soluble solids and titratable acidity of juice. Am. J. Enol. Vitic. 35: 242-246.

Wolpert, J.A., G.S. Howell, and T.K. Mansfield. 1983. Sampling Vidal Blanc grapes. I. Effect of training system, pruning severity, shoot exposure, shoot origin and cluster thinning on cluster weight and fruit quality. Am. J. Enol. Vitic. 32: 72-76.

Zenoni, S., A. Ferrarini, E. Giacomelli, L. Xumerle, M. Fasoli, G. Malerba, D. Bellin, M. Pezzotti, and M. Delledonne. 2010. Characterization of transcriptional complexity during berry development in *Vitis vinifera* using RNA-Seq. Plant Physiol. 152: 1787-1795.

AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS • AJEV PAPERS IN PRESS

Zhang, X.Y., X.L. Wang, X.F. Wang, G.H. Xia, Q.H. Pan, R.C. Fan, F.Q. Wu, X.C. Wu, and D.P. Zhang. 2006. A shift of phloem unloading from symplasmic to apoplasmic pathway is involved in developmental onset of ripening in grape berry. Plant Physiol. 142: 220-232.

Zhang, Y.L., Q.Y. Meng, H.L. Zhu, Y. Guo, H.Y. Gao, Y.B. Luo, and J. Lu. 2008. Functional characterization of a LAHC sucrose transporter isolated from grape berries in yeast. Plant Growth Regul. 54: 71-79.