Tree Genetics and Molecular Breeding 2025, Vol.15, No.2, 62-69
http://genbreedpublisher.com/index.php/tgmb

Feature Review Open Access

Key Genes Regulating Fruit Size and Sugar Content in Grapevine

Wenzhong Huang
Hainan Provincial Key Laboratory of Crop Molecular Breeding, Sanya, 572025, Hainan, China
Corresponding email: wenzhong.huang@hitar.org

Tree Genetics and Molecular Breeding, 2025, Vol.15, No.2 doi: 10.5376/tgmb.2025.15.0008
Received: 25 Feb., 2025
Accepted: 28 Mar., 2025
Published: 05 Apr., 2025

Preferred citation for this article:
Huang W.Z., 2025, Key genes regulating fruit size and sugar content in grapevine, Tree Genetics and Molecular Breeding, 15(2): 62-69 (doi: 10.5376/tgmb.2025.15.0008)

Abstract This study explains the key genes that affect the size and sugar content of grape fruits and their regulatory patterns, and analyzes genes such as *VvGH9*, *VvSK1*, and *VvHB58*, which are crucial in the process of fruit enlargement and sugar increase and play an important role in fruit development and sugar accumulation. This study also mentioned the influences of epigenetics, small RNAs and environmental conditions on grape traits, as well as the application of new gene editing technologies in grape breeding. This study aims to provide new ideas and genetic targets for improving the quality of grapevines and propose useful strategies for future breeding work.

Keywords Grapevine; Gene regulation; Sugar accumulation; Fruit size; Gene editing

1 Introduction

Grapevine (*Vitis vinifera* L.) is a very important fruit crop. It can be used for winemaking, eaten as a fruit, or dried into fruits. It has high economic value and a wide range of cultivation. Vineyards can be seen in different climate zones. It is necessary to understand its genetic characteristics and physiological responses in different environments in order to grow grapevines better. The quality of grape fruits is a key factor determining whether they sell well, can be used for winemaking or eaten directly (Lecourieux et al., 2009; Li et al., 2021; Zinelabidine et al., 2021).

Genes such as *VvGH9* are related to sugar accumulation and their effects are more obvious under conditions of low sugar content. Xu et al. (2021) found that its expression is affected by sucrose, fructose and glucose, and the accumulation of sugar in grape callus tissue significantly increases when this gene is overexpressed. Huang et al.'s research in 2023 suggests that potassium content affects the accumulation of sugar and anthocyanins in fruits, and genes related to sugar metabolism such as *GST*, *AT*, *UFGT*, and *SPS* play significant roles in this process.

Lecourieux et al. demonstrated in their early research, in 2009, that the sugar-regulated protein kinase gene VvSK1 regulates hexose transport and sugar accumulation in grape cells. Its expression is influenced by sugar and abscisic acid, enabling the fruit to better absorb and accumulate glucose. *VvHB58* is a homologous box gene that can regulate fruit size and seed development through multiple hormone signaling pathways, indicating that the genetic regulation of this type of trait is very complex (Li et al., 2019).

Large-sized grapevines are more popular in the fresh food market because they are good-looking and have a good appearance, and consumers are more willing to buy them (Li et al., 2019; Rossmann et al., 2020; Zinelabidine et al., 2021). Grimplet et al. (2017) and Rossmann et al. (2020) found that the size of the fruit would affect the structure of the entire bunch of grapevines, the ability to resist pests and diseases, and the uniformity of ripening. Xu et al. (2021) demonstrated in their study that the sugar content determines the flavor of grapevines, which is crucial for both edible grapevines and those used for winemaking. High sugar content determines the alcohol content, which will affect the overall taste and aroma of wine (Castellarin et al., 2017; Zhong, 2024).

This study summarized the known key genes that regulate the size and sugar content of grape fruits and their regulatory pathways, identified which genes mainly control them, and analyzed their mechanisms of action. This study also screened out specific genes related to the size of grape fruit and sugar content, revealed their specific roles through functional research, deeply analyzed the formation mechanisms of these important traits, and understood the regulatory networks behind them.

2 Genetic Basis of Fruit Size in Grapevine

2.1 Key genes involved in fruit size regulation

The VvMYB transcription factor family plays a significant role in the two key links that determine fruit size, namely cell division and cell expansion. Bogs et al. (2007) found that VvMYBPA1 could regulate the expression of genes related to proanthocyanidin synthesis in the early stage of berry development, affecting the growth and expansion of cells as well as the size of the fruit. Rossmann et al. (2020) hold that VvMYB5b is involved in the synthetic regulation of anthocyanins and proanthocyanidins, and has an impact on the overall development process of fruits and the size of fruits.

Cell wall-modification enzymes such as xyloglucan endotransglucosylase/hydrolases (XTHs) and expansins (EXPs) are helpful for loosening the cell wall and promoting cell expansion. There are not many specific studies on *VvXTH* and *VvEXP* in grapevines, but studies on other plants have proved that these genes have a significant impact on regulating the structure of cell walls and the size of fruits. Bogs et al. (2007) and Rossmann et al. (2020) indicated that there might also be interactions between these enzymes and transcription factors such as VvMYB, which is beneficial for understanding their specific roles in grape fruit development.

2.2 Molecular pathways influencing fruit size

VvHB58 is a homologous box transcription factor. The study by Li et al. (2019) indicated that it regulates fruit size and seed quantity through multiple hormone signaling pathways such as auxin, gibberellin, and ethylene. This gene shows different expression levels at the seed development stage of seeded and seedless grape varieties, indicating that the formation of fruit size involves complex regulatory relationships among multiple hormones.

Transcription factors such as VvMYB and VvWRKY22 have regulatory effects in fruit development. Huang et al. (2021) hold that sugar is an essential energy source and material for cell growth. VvWRKY22 affects the expression of genes related to sugar, participates in sugar metabolism, and influences the size of fruits. VvMYBPA1 and VvMYB5b affect cell division and expansion as well as fruit development by regulating flavonoid related genes (Bogs et al., 2007; Deluc et al., 2008).

2.3 Recent advances in genomic studies on fruit size

Genomic research has identified many important genes related to fruit size and their regulatory networks. Rossmann et al.'s research in 2020 found that the binding site of miR396 in the gene *VvGRF4* had mutated, which would affect the inflorescence structure and fruit size. The fruit size of grapevines can be improved by modifying these specific genes.

2.4 Analysis of a key gene impacting fruit size in grapevine

The gene *VvHB58* has a regulatory effect in grapes. In tomatoes, when it is transferred into the plant body for expression, it will make the fruit smaller and the seeds fewer, indicating that its role in the development of fruit size is very prominent. Li et al. (2019) argued that its differential expression in seeded and seedless varieties indicates that it is a key gene regulating fruit size and works together through multiple hormonal pathways.

3 Genetic Basis of Sugar Content in Grapevine

3.1 Key genes involved in sugar accumulation

VvSWEET10 is expressed in large quantities at the early stage of fruit ripening and can transport hexose sugars such as glucose and fructose. The research of Zhang et al. (2019) found that when its expression increased, the sugar content in grapevines also rose significantly. Ren et al. (2020) demonstrated that *VvSWEET15* can promote the transport and hydrolysis of sugar, which is related to the higher hexose content in fruits. The expression of gene *VvSUC11* is enhanced when encountering water stress such as severe drought, indicating that it is useful for regulating sugar distribution under adverse environmental conditions (Medici et al., 2014).

Enzymes such as hexokinase (VvHXK) and fructokinase (VvFK) are crucial in the process of sugar synthesis. They add phosphoric acid to glucose and fructose. This step is a prerequisite for the utilization of sugar by plants. The expressions of VvHXK and VvFK are controlled by factors such as sugar content and hormone levels in plants, and these regulations affect the accumulation of sugar in fruits (Lecourieux et al., 2009; Xu et al., 2021).

3.2 Metabolic pathways contributing to sugar content

Grapevines produce carbohydrates through photosynthesis. These sugars are eventually transported to the fruits for storage, and the distribution of sugars among various organs is very important. Ren et al. (2020) found that the expression levels of sucrose synthase VvSS3 and some sugar transport proteins were related to the amount of sugar in the fruit. Carbohydrates can be effectively transported from the plant to the fruit, and the sugar content of the fruit can be significantly increased.

Environmental factors can also affect the sugar accumulation of fruits. When water is scarce, sugar transport genes such as *VvHT1* and *VvSUC11* will have expression changes to varying degrees, affecting the transport and distribution of sugar (Medici et al., 2014). Hormones such as abscisic acid (ABA) induced by stress can also regulate the expression of genes related to sugar and affect the sweetness of fruits (Lecourieux et al., 2009).

3.3 Transcription factors regulating sugar content

Transcription factors such as VvMYB and VvNAC are crucial in regulating sugar metabolism. They can activate or inhibit certain genes related to sugar transport and metabolism, affecting the sugar content in fruits. Météier et al. (2019) and Huang et al. (2021) found that VvMYB can regulate the expression of genes related to sugar transport, while VvNAC is more involved in plants' responses to stress and affects sugar accumulation.

There is also a synergistic effect among different sugar-related genes and transcription factors. Ren et al. (2020) demonstrated that when both VvSWEET protein and sucrose synthase VvSS3 were highly expressed simultaneously, the hexose content in the fruit would increase significantly. Huang et al. (2021) hold that the interaction between VvWRKY22 and VvSnRK1 demonstrates the complex regulatory network behind sugar metabolism.

3.4 Functional analysis of a gene regulating sugar content in grapevine

The *VvGH9* gene (glycoside hydrolase) is activated under the induction of sugars such as sucrose, fructose and glucose. Najafi et al.'s research in 2022 found that when *VvGH9* was overexpressed in grape callus, the accumulation of sugar would significantly increase (Figure 1). The function of this gene is to play a role in the process of breaking down polysaccharides into monosaccharides. Its research enables relevant researchers to better understand the genetic regulatory mechanism behind sugar accumulation in grape fruits.

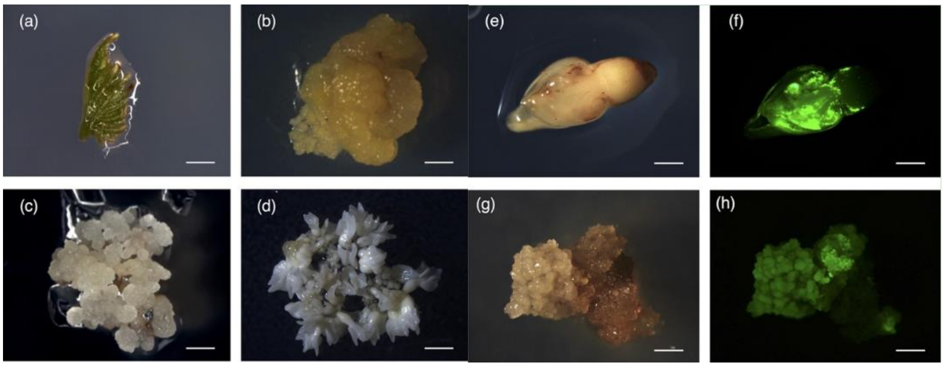

Figure 1 Grapevine embryogenic callus system (cv. Thompson Seedless) and stable transformation with the *GFP* gene (Adopted from Najafi et al., 2022)

Image caption: (a) Unopened leaves cultured on initiation medium (bar=6 mm) produced (b) sectors of embryogenic and non-embryogenic callus (bar=2 mm). (c) Embryogenic callus proliferated and (d) produced somatic embryos ready for transformation (bars=1 mm). (e) Somatic embryos after 72 h of co-cultivation with Agrobacterium tumefaciens under white light and (f) UV light (bars=0.5 mm). (g) Embryogenic callus induced from somatic embryos under white light and (h) UV light (bars=0.75 mm) (Adopted from Najafi et al., 2022)

4 Mechanistic Insights into the Co-Regulation of Fruit Size and Sugar Content

4.1 Cross-talk between pathways controlling size and sugar content

Whether the nutrition is sufficient and the changes in hormone signals will both affect the development of the grape from the time it blooms until the fruit begins to form. The signals of sugar and hormones are interrelated and work together at the early stage of fruit development. Domingos et al. (2016) found that SWEET14 sugar transporters and some hormone-related transcription factors such as MADS-box and AP2 type ethylene response factors were crucial in this process, indicating that sugar transport and hormone metabolism occur synergistically and jointly contribute to the normal development of fruits. The earlier research by Lecourieux et al. (2009) demonstrated that sugar-inducible protein kinases such as VvSK1 regulate the transport and accumulation of hexose, indicating that the sugar content and fruit size are balanced through a complex network.

4.2 Role of epigenetic modifications and small RNAs

DNA methylation, histone modification and chromatin remodeling can all affect gene expression and the development process of fruits. The research conducted by Tang et al. in 2020 indicated that when there was a problem with DNA demethylase, the fruit ripening would slow down in tomatoes, suggesting that this mechanism might be equally important in grapes. Small RNAs such as microRNAs and long non-coding RNAs also participate in regulating many metabolic processes. Wong and Matus (2017) discovered in grapes by using the method of network analysis that microRNA might regulate the metabolic pathway of phenylalanine, which is related to some important secondary metabolites and these substances have an impact on the overall quality of grapes.

4.3 Integrative omics approaches in grapevine breeding for optimized traits

The approach of integrative omics can provide a more comprehensive view of which genes, metabolites and regulatory factors are interrelated. Studies have shown that the integrated network established in this way has discovered clear synergy relationships among different types of data. Savoi et al. (2017) found that some genes and transcription factors involved in flavonoid synthesis would be jointly regulated under conditions of insufficient water, affecting the sugar accumulation and size of fruits. Wong and Matus (2017) demonstrated that the combined analysis of gene co-expression networks and promoter regulatory elements identified new transcription factors and microRNAs involved in the regulation of key metabolic pathways.

5 Case Study

5.1 Selection criteria for case study

The genes in the case study must have been confirmed to have specific functions in the physiological processes of grapes, especially in controlling fruit size and sugar accumulation. These genes need to be verified through multiple experimental methods to ensure a comprehensive and reliable understanding of their functions. Only when they have a significant impact on both fruit size and sugar content do they have practical value as key candidate genes in breeding projects.

5.2 Detailed analysis of a key gene (*VvGH9*)

VvGH9 belongs to the glycosyl hydrolase family. These enzymes can break down polysaccharides into monosaccharides and are key participants in carbohydrate metabolism. Xu et al. (2021) found that the expression level of *VvGH9* was very high at the initial stage of grape fruit development, while the sugar content of the fruit at this stage was still relatively low (Figure 2). The results of RNA sequencing and real-time quantitative PCR indicated that the expression of *VvGH9* was activated by exogenous sugars such as sucrose, fructose, and glucose, suggesting that it might be crucial in the sensing and metabolic regulation of sugars.

Najafi et al. (2022) demonstrated that when *VvGH9* was overexpressed in grape callus and tomato models, it could significantly increase sugar accumulation even in a low-glucose environment, indicating its potential to enhance the sweetness and quality of the fruit. The expression characteristics of *VvGH9* and its response to sugar stimulation also suggest that it may be useful in the process of regulating sugar input and metabolic balance during berry development. Lecourieux et al.'s research in 2014 suggested that this balance is crucial to the final size and sugar content of the fruit, which in turn are the determinants of grapevines quality and market price.

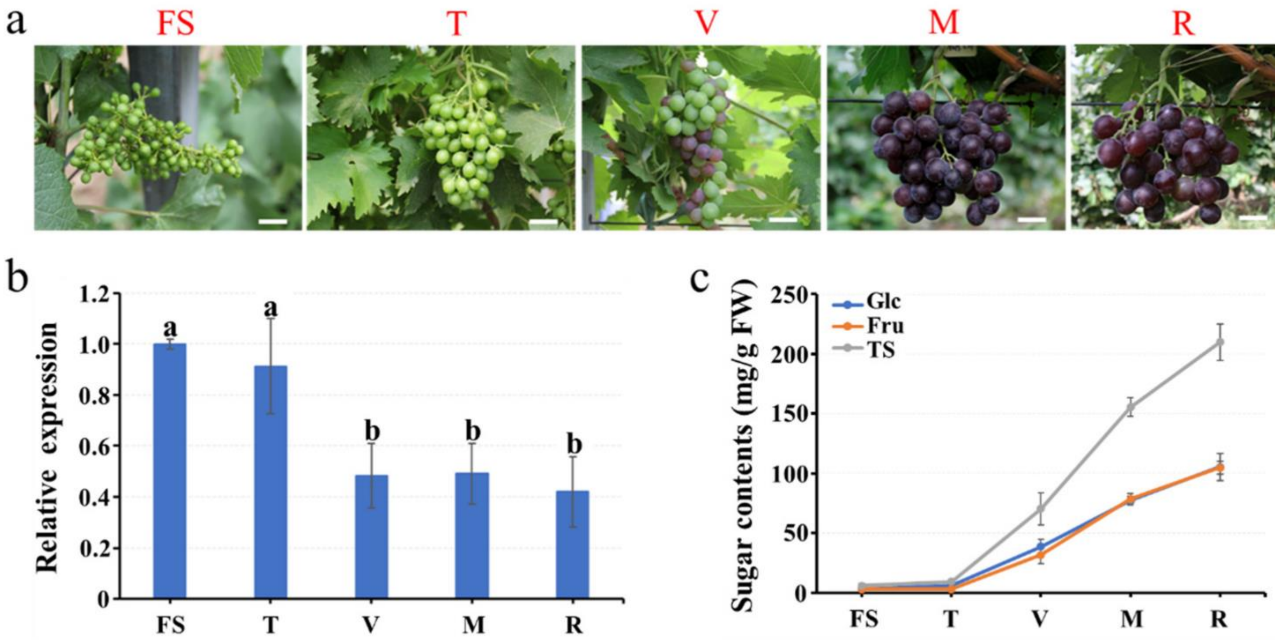

Figure 2 The relative expression level of the *VvGH9* gene and the sugar content of 'Muscat Hamburg' grape fruit at five different developmental stages (Adopted from Xu et al., 2021)

Image caption: (a) Fruit growth status in different developmental stages. Scale bars, 2 cm. (b) Relative VvGH expression in different berry developmental stages. (c) Sugar content determination results of grape berries. FS: fruit set; T: touching; V: véraison; M: mid-ripening; R: ripe. FW: fresh weight. The letters above the bars indicated the significant differences by student's t-test (P<0.05). Three biological replicates were analyzed, and the error bars represented the SD (Adopted from Xu et al., 2021)

5.3 Implications of findings for grapevine breeding programs

If breeders can clearly understand the role of the *VvGH9* gene in sugar accumulation, they can design more effective breeding strategies. The fact that *VvGH9* can help fruits accumulate sugar under conditions of low sugar content makes it a very worthy target for genetic manipulation. Lecourieux et al. (2014) and Xu et al. (2021) both hold that breeding projects can prioritize the selection of plants with stronger expression of *VvGH9* or enhance the function of this gene through genetic engineering methods to cultivate new varieties with higher sugar content, larger fruits, and better quality.

Recent studies by Zinelabidine et al. (2021) have shown that if the dominant alleles at different gene loci are used in combination with *VvGH9*, the additive effect between them may significantly enhance both the yield and quality of the fruit. This joint strategy may be helpful in breeding more high-quality grape varieties that meet the yield requirements of growers and the taste expectations of consumers.

6 Future Directions in Grapevine Research

6.1 Emerging gene editing techniques (CRISPR-Cas9)

If the appropriate promoter can be found to enhance the expression of sgRNA and Cas9, the success rate of gene editing can be improved. Ren et al. (2021) found that this method has been used to edit genes related to sugar accumulation, such as the tonoplastic monosaccharide transporter (TMT) family, and the results show that it has great prospects in regulating fruit quality. Malnoy et al. (2016) and Najafi et al. (2022) demonstrated that the gene editing method without exogenous DNA is achieved through the CRISPR/Cas9 ribonucleoprotein complex, which can avoid the regulatory issues of transgenic organisms and is also beneficial for the development of edited plants without foreign genes. Osakabe et al. (2018) and Zhou et al. (2020) both hold that CRISPR-Cas9 can improve the fruit quality of grapevines and enhance other agronomic traits such as disease resistance.

6.2 Prospects of high-throughput genomic selection

High-throughput genomic selection (HTGS) can quickly identify genes with ideal traits and conduct screening. Wan et al. (2021) believed that the combination of whole-genome sequencing data and CRISPR-Cas9 technology could directly make precise mutations on key genes and accelerate the breeding speed of superior new varieties. Zhou et al. (2020) found that this method has been tested on other fruit trees and has achieved good results in improving fruit quality, enhancing disease resistance and increasing yield. CRISPR can edit multiple genes at a time. This ability of multiple editing also enables HTGS to simultaneously improve multiple traits and accelerate the breeding process (Ren et al., 2021).

6.3 Potential for enhancing both fruit size and sugar content simultaneously

The CRISPR-Cas9 technology offers the possibility of simultaneously increasing the fruit size and sugar content of grapevines. The gene *VvGRF4*, which regulates the inflorescence structure, can be mutated site-specific. Editing it can make the fruit larger and the fruit cluster structure better. Ren et al. (2021) demonstrated that editing glucose transport genes such as *TMT1* and *TMT2* could enhance glucose accumulation. Through the precise editing of CRISPR, scientists can simultaneously target multiple key genes, increase fruit size and sugar content, and improve the overall quality of the variety. Rossmann et al. (2020) believe that the combination of CRISPR technology and marker-assisted breeding methods may lead to more ideal results and provide stronger support for the improvement of grapes.

7 Conclusion

E3 ubiquitin ligase VlPUB38 can negatively regulate fruit ripening by degrading abscisic-aldehyde oxidase. The transcription factor VvWRKY22 interacts with VvSnRK1.1/VvSnRK1.2 and affects sugar accumulation by regulating the expression of genes related to sugar and ABA. *VvGH9* can positively regulate sugar accumulation in a low-sugar environment, indicating that it may be crucial in the carbohydrate metabolism of grapes. The glucose transporter protein VvSWEET7 was upregulated after grapevines were infected with *Botrytis cinerea*, indicating that it may be important in fruit development and glucose transport. The sugar-induced protein kinase VvSK1 can regulate the transport of hexose and affect sugar accumulation in cells.

Understanding the role of VlPUB38 in the fruit ripening process is useful for better controlling the ripening time of grapes, improving fruit quality and extending the shelf life. The regulatory ability of VvWRKY22 and VvGH9 on sugar accumulation provides a new direction for improving the sweetness of grapes. The function of VvSWEET7 in pathogenic bacterial infection responses indicates that regulating it can enhance the disease resistance of grapes, reduce their reliance on pesticides, and is beneficial to sustainable agricultural development. The regulatory mechanism of VvSK1 on sugar transport provides potential technical means for increasing the sugar content and economic value of fruits.

Future research can focus on how key genes work in synergy with other regulatory factors and signaling pathways to jointly control the mechanisms of fruit development and glucose metabolism. Gene editing tools such as CRISPR-Cas9 offer great possibilities for precisely modifying these genes and breeding better new varieties. The exploration of the influence of environmental factors such as climate and soil on the expression of these genes is also beneficial for guiding grape growers to make more scientific management decisions in the context of climate change. In-depth exploration of the functions and regulatory networks of these genes can enhance the understanding of grape biology and bring new impetus to grape breeding and modern agricultural practice.

Acknowledgments

The author sincerely thanks Dr. Ge for carefully reviewing the manuscript of this study and providing detailed revision suggestions. The author also extends deep gratitude to the two anonymous peer reviewers for their valuable comments and suggestions on the manuscript of this study.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Bogs J., Jaffé F., Takos A., Walker A., and Robinson S., 2007, The grapevine transcription factor VvMYBPA1 regulates proanthocyanidin synthesis during fruit development, Plant Physiology, 143(3): 1347-1361.
https://doi.org/10.1104/pp.106.093203

Castellarin S., Pfeiffer A., Sivilotti P., Degan M., Peterlunger E., and Gaspero G., 2007, Transcriptional regulation of anthocyanin biosynthesis in ripening fruits of grapevine under seasonal water deficit, Plant, Cell and Environment, 30(11): 1381-1399.
https://doi.org/10.1111/j.1365-3040.2007.01716.x

Deluc L., Bogs J., Walker A., Ferrier T., Décendit A., Mérillon J., Robinson S., and Barrieu F., 2008, The transcription factor VvMYB5b contributes to the regulation of anthocyanin and proanthocyanidin biosynthesis in developing grape berries, Plant Physiology, 147(4): 2041-2053.
https://doi.org/10.1104/pp.108.118919

Domingos S., Fino J., Paulo O., Oliveira C., and Goulao L., 2016, Molecular candidates for early-stage flower-to-fruit transition in stenospermocarpic table grape (*Vitis vinifera* L.) inflorescences ascribed by differential transcriptome and metabolome profiles, Plant Science, 244: 40-56.
https://doi.org/10.1016/j.plantsci.2015.12.009

Grimplet J., Tello J., Laguna N., and Ibáñez J., 2017, Differences in flower transcriptome between grapevine clones are related to their cluster compactness, fruitfulness, and berry size, Frontiers in Plant Science, 8: 632.
https://doi.org/10.3389/fpls.2017.00632

Huang H., Zhao X., Xiao Q., Hu W., Wang P., Luo Y., Xia H., Lin L., Lv X., Liang D., and Wang J., 2023, Identification of key genes induced by different potassium levels provides insight into the formation of fruit quality in grapes, International Journal of Molecular Sciences, 24(2): 1218.
https://doi.org/10.3390/ijms24021218

Huang T., Yu D., and Wang X., 2021, VvWRKY22 transcription factor interacts with VvSnRK1.1/VvSnRK1.2 and regulates sugar accumulation in grape, Biochemical and Biophysical Research Communications, 554: 193-198.
https://doi.org/10.1016/j.bbrc.2021.03.092

Lecourieux F., Kappel C., Lecourieux D., Serrano A., Torres E., Arce-Johnson P., and Delrot S., 2014, An update on sugar transport and signalling in grapevine, Journal of Experimental Botany, 65(3): 821-832.
https://doi.org/10.1093/jxb/ert394

Lecourieux F., Lecourieux D., Vignault C., and Delrot S., 2009, A sugar-inducible protein kinase, VvSK1, regulates hexose transport and sugar accumulation in grapevine cells, Plant Physiology, 152(2): 1096-1106.
https://doi.org/10.1104/pp.109.149138

Li Y., Zhang S., Dong R., Wang L., Yao J., Nocker S., and Wang X., 2019, The grapevine homeobox gene *VvHB58* influences seed and fruit development through multiple hormonal signaling pathways, BMC Plant Biology, 19: 523.
https://doi.org/10.1186/s12870-019-2144-9

Malnoy M., Viola R., Jung M., Koo O., Kim S., Kim J., Velasco R., and Kanchiswamy C., 2016, DNA-free genetically edited grapevine and apple protoplast using CRISPR/Cas9 ribonucleoproteins, Frontiers in Plant Science, 7: 1904.
https://doi.org/10.3389/fpls.2016.01904

Medici A., Laloi M., and Atanassova R., 2014, Profiling of sugar transporter genes in grapevine coping with water deficit, FEBS Letters, 588(21): 3989-3997.
https://doi.org/10.1016/j.febslet.2014.09.016

Météier E., Camera S., Goddard M., Laloue H., Mestre P., and Chong J., 2019, Overexpression of the *VvSWEET4* transporter in grapevine hairy roots increases sugar transport and contents and enhances resistance to *Pythium irregulare*, a soilborne pathogen, Frontiers in Plant Science, 10: 884.
https://doi.org/10.3389/fpls.2019.00884

Najafi S., Bertini E., D'Incà E., Fasoli M., and Zenoni S., 2022, DNA-free genome editing in grapevine using CRISPR/Cas9 ribonucleoprotein complexes followed by protoplast regeneration, Horticulture Research, 10(1): uhac240.
https://doi.org/10.1093/hr/uhac240

Osakabe Y., Liang Z., Ren C., Nishitani C., Osakabe K., Wada M., Komori S., Malnoy M., Velasco R., Poli M., Jung M., Koo O., Viola R., and Kanchiswamy C., 2018, CRISPR-Cas9-mediated genome editing in apple and grapevine, Nature Protocols, 13: 2844-2863.
https://doi.org/10.1038/s41596-018-0067-9

Ren C., Liu Y., Guo Y., Duan W., Fan P., Li S., and Liang Z., 2021, Optimizing the CRISPR/Cas9 system for genome editing in grape by using grape promoters, Horticulture Research, 8: 52.
https://doi.org/10.1038/s41438-021-00489-z

Ren R., Yue X., Li J., Xie S., Guo S., and Zhang Z., 2020, Coexpression of sucrose synthase and the SWEET transporter, which are associated with sugar hydrolysis and transport, respectively, increases the hexose content in *Vitis vinifera* L. grape berries, Frontiers in Plant Science, 11: 321.
https://doi.org/10.3389/fpls.2020.00321

Rossmann S., Richter R., Sun H., Schneeberger K., Töpfer R., Zyprian E., and Theres K., 2020, Mutations in the miR396 binding site of the growth-regulating factor gene *VvGRF4* modulate inflorescence architecture in grapevine, The Plant Journal, 101(5): 1234-1248.
https://doi.org/10.1111/tpj.14588

Savoi S., Wong D., Degu A., Herrera J., Bucchetti B., Peterlunger E., Fait A., Mattivi F., and Castellarin S., 2017, Multi-omics and integrated network analyses reveal new insights into the systems relationships between metabolites, structural genes, and transcriptional regulators in developing grape berries (*Vitis vinifera* L.) exposed to water deficit, Frontiers in Plant Science, 8: 1124.
https://doi.org/10.3389/fpls.2017.01124

Tang D., Gallusci P., and Lang Z., 2020, Fruit development and epigenetic modifications, The New Phytologist, 228(3): 839-844.
https://doi.org/10.1111/nph.16724

Wan D., Guo Y., Cheng Y., Hu Y., Xiao S., Wang Y., and Wen Y., 2020, CRISPR/Cas9-mediated mutagenesis of *VvMLO3* results in enhanced resistance to powdery mildew in grapevine (*Vitis vinifera*), Horticulture Research, 7: 116.
https://doi.org/10.1038/s41438-020-0339-8

Wan L., Wang Z., Tang M., Hong D., Sun Y., Ren J., Zhang N., and Zeng H., 2021, CRISPR-Cas9 gene editing for fruit and vegetable crops: strategies and prospects, Horticulturae, 7(7): 193.
https://doi.org/10.3390/horticulturae7070193

Wong D., and Matus J., 2017, Constructing integrated networks for identifying new secondary metabolic pathway regulators in grapevine: recent applications and future opportunities, Frontiers in Plant Science, 8: 505.
https://doi.org/10.3389/fpls.2017.00505

Wong D., Schlechter R., Vannozzi A., Höll J., Hmmam I., Bogs J., Tornielli G., Castellarin S., and Matus J., 2016, A systems-oriented analysis of the grapevine R2R3-MYB transcription factor family uncovers new insights into the regulation of stilbene accumulation, DNA Research, 23(5): 451-466.
https://doi.org/10.1093/dnares/dsw028

Xu G., Wang Y., Ren C., Fan P., Kuang Y., Wang Y., and Liang Z., 2021, Genome wide analysis of *GH* gene family reveals *VvGH9* positively regulates sugar accumulation under low sugar content in grape, Horticulturae, 7(11): 453.
https://doi.org/10.3390/horticulturae7110453

Xu X., Yuan Y., Feng B., and Deng W., 2020, CRISPR/Cas9-mediated gene-editing technology in fruit quality improvement, Food Quality and Safety, 4(4): 159-166.
https://doi.org/10.1093/fqsafe/fyaa028

Zhang Z., Zou L., Ren C., Ren F., Wang Y., Fan P., Li S., and Liang Z., 2019, *VvSWEET10* mediates sugar accumulation in grapes, Genes, 10(4): 255.
https://doi.org/10.3390/genes10040255

Zhong B.J.L., 2024, The fruit revolution in the genomic era: unveiling the journey of strawberry genetic improvement, International Journal of Horticulture, 14(2): 72-83.
https://doi.org/10.5376/ijh.2024.14.0009

Zhou J., Li D., Wang G., Wang F., Kunjal M., Joldersma D., and Liu Z., 2020, Application and future perspective of CRISPR/Cas9 genome editing in fruit crops, Journal of Integrative Plant Biology, 62(3): 269-286.
https://doi.org/10.1111/jipb.12793

Zinelabidine L., Torres-Pérez R., Grimplet J., Baroja E., Ibáñez S., Carbonell-Bejerano P., Martínez-Zapater J., Ibáñez J., and Tello J., 2021, Genetic variation and association analyses identify genes linked to fruit set-related traits in grapevine, Plant Science, 306: 110875.
https://doi.org/10.1016/j.plantsci.2021.110875