SZENT ISTVÁN UNIVERSITY

DIFFERENTIATION OF GRAPE COLOUR VARIANTS AND MOLECULAR EVOLUTION OF *VITIS* SPECIES

Theses of PhD dissertation

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1 HISTORICAL BACKGROUND AND OBJECTIVES

The cultivated grape (*Vitis vinifera* L. subp. *vinifera*) is one of the oldest and most important crops. Berry skin is a fundamental trait of grape varieties. Over several thousand years of viticulture as a result of mutations, natural hybridization and- from the 19th century- deliberate crosses and selection numerous colour variants of grape berries have been developed black, blue, red, pink, grey and white. The berry colour is determined by anthocyanin accumulation in the skin, which varies greatly in concentration and composition depending on the grape cultivar. The anthocyanin biosynthesis is controlled by a transcription complex including the *Myb* genes, which activates the *UFGT* gene. The white cultivars arose mostly from red-berried parents by different mutations in two adjacent *Myb* genes, *VvMybA1* and *VvMybA2*.

Anthocyanins are responsible for red and blue colours of many plant tissues, as widespread plant secondary metabolites. UDP-glucose: flavonoid 3-O-glucosyltransferase (UFGT) is critical for anthocyanin biosynthesis. UFGT is the key enzyme responsible for the accumulation of anthocyanins in grape berry skins. Its expression is transcriptionally regulated by MybA transcription factors.

An important objective of the EU project GrapeGen06 was to characterize European native varieties with morphological and microsatellite markers. The SZIU Institute of Genetics and Biotechnology carried out the characterization of a total of 259 Hungarian varieties and clones, including 97 Carpathian basin varieties, based on 12 microsatellite loci. There are several groups (color variants) of the varieties that have the same SSR allele pattern, so it cannot be characterized by a unique microsatellite fingerprint. Since these varieties varieties, so-called bud sports (*conculta*) differ in their berry color, so the genetic differences between them are to be found in the genes and regulatory regions involved in anthocyanin biosynthesis. Nowadays there is a huge interest ing the wild grapes which is due to their apotential application in breeding programs, e.g. they can have high resistance against diseases.

Vitis is phylogenetically a complex group because the traditional classification schemes of the *Vitis* and recent molecular marker-based studies do not agree with each other as for the

relationship among the *Vitis* species. In our days several works have attempted elucidate the genealogy of *Vitis* species with various DNS assays without revelant conclusions.

Based on preliminary studies with 20D18CB9 CAPS marker - which linked to *VvMybA1* transcription factor gene regulating the anthocyanin biosynthesis - we detected polymorphism between the *Vitis vinifera* and wild species. For this purpose we assumed that it can be suitable for further examinations and we can set up a new phylogenetic relationship within the *Vitaceae* family.

OBJECTIVES:

Determination of allele composition of *VvMybA1* transcription factor gene in the Carpathian Basin cultivars.

Differentiation of grape colour variants by their *VvMybA1* and *VvMybA2* allele composition.

Sequence-level comparison of the non-coding regions of the *MybA1* and *MybA2* genes of grape species of different geographical within the *Vitis* genus.

2 MATERIAL AND METHOD

2.1 Plant material

The plant material was composed of Carpathian Basin cultivars from Hungary. Young leaves were collected from University of Pécs, Research Institute of Viticulture and Enology. The *Vitis* species examined were obtained from the collection of the Institute of Viticulture and Enology, University of Pécs, Hungary, the Julius Kühn Institute, Geiweilerhof, Germany, and INRA, Montpellier, France.

2.2 DNA extraction

The young leaf samples were stored at -70°C before DNA extraction. Genomic DNA was isolated using DNeasy Plant Mini Kit (Qiagen) according to the manufacturer's instructions.

2.3 PCR conditions and markers used in this study

Presence or absence of the *Gret1* retroelement in the *VvMybA1* promoter region was detected using the primers according to KOBAYASHI et al. (2004). PCR was performed with the 20D18CB9 primer pair linked to the gene of the *VvMybA1* transcription factor which regulates anthocyanin biosynthesis (WALKER et al. 2007).

Polymerase chain reactions were performed in a Bio-Rad iCycler (Bio-Rad). The *VvMybA1* allele-specific primers were applied in touch-down PCR with WTB-Taq polymerase. For analyzing the *Vitis* species, Phusion® High-Fidelity DNA polymerase with PCR conditions recommended by by the manufacturer

2.4 SnapShot analysis and sequencing

For the loci *K980* (WALKER et al. 2007) and *C22 VvMybA2* SNP (CARRASCO et al. 2015) the SNaPshot™ assay was applied. The *VvMybA2* gene sequence was amplified using the primers and conditions reported in WALKER et al. (2007). The purified SNaPshot™ PCR products were detected on capillary electrophoresis instrument (ABI PRISM® 310 Genetic Analyzer, Life Technologies Corporation) and data analysis was performed by GeneMapper 4.0 software (Life Technologies Corporation).

The purified PCR product was ligated into a pJET1.2 cloning vector (Thermo Scientific). Samples were sequenced in an ABI PRISM 310 Genetic Analyzer (Applied Biosystems). The resulting sequences were evaluated and compared with BioEdit and MEGA6 sofwares. The phylogenetic tree was constructed based on the Clustal W algorithm with Megalign (Lasergene) software with a bootstrap value of 1000.

3 RESULTS

3.1 Determination of *VvMybA1* allele polymorphism in Carpathian Basin varieties

We started our research based on the results of a previous study, which aimed to distinguish the Carpathian basin cultivars which have the same SSR pattern by primers designed for the *VvMybA1* gene. In our work we characterized the *VvMybA1* allele composition of 118 Carpathian basin varieties

Among the 118 Carpathian Basin varieties 78 VvMybA1a/a, 33 VvMybA1a/c, 4 VvMybA1a/b and 3 VvMybA1c/c genotypes were identified. 'Gohér piros' (Rg), 'Hamuszőlő' (G), 'Rózsás leányka' (Rg) and 'Szeredi' (Rg) which have coloured berries, no functional *VvMybA1* allele could be detected, either with the *VvMybA1* allele-specific primers or with the 20D18CB9 marker, which would support their phenotypic appearance.

Out of 118 Carpathian Basin species, 78 have VvMybA1a/a genotype, so Gret-1 insertion can be detected on both alleles, which results in the formation of a white phenotype.

33 varieties a combination of the VvMybA1a/c allele was identified, meaning that one allele is non-functional due to Gret-1 insertion and the other allele is the wild-type functional allele.

For 3 varieties ('Ködös', 'Kék tihanyi', 'Tótika'), the wild type allele without the VvMybA1c Gret-1 insertion was detected in homozygous form. Finally, for 4 varieties ('Furmint piros', 'Kéknyelű piros', 'Lisztes piros', 'Muskotály piros'), the VvMybA1a/b genotype was isolated.

Most of the varieties contain the composition of the VvMybA1 allele corresponding to the berry color, but in the case of 'Gohér piros' (Rg), 'Hamuszőlő' (G), 'Rózsás leányka' (Rg) and 'Szeredi' (Rg) allele-specific fragments were not detected. This result may indicate that another gene or another functional allele of the VvMybA transcription factor produces berry coloration in the 4 varieties mentioned above.

3.2 Isolation of grape bud sports based on SNP polymorphism

In the Institute of Genetics and Biotechnology (Szent István University, Gödöllő, Hungary) in earlier studies (in the frame of GrapeGen 06 project), based on microsatellite (SSR) analysis of the Carpathian Basin cultivars the berry colour variants gave identical SSR allele patterns (SZŐKE et al. 2012).

We have tested two SNP positions (K980, C22) of the *VvMybA2* gene by SNaPshot method. During the sequencing of the samples, the mutant T (thymine) and the functional G (guanine) alleles were detected for both SNP positions, affecting anthocyanin biosynthesis. If this point mutation is present in homozygous (T) form, the allele is inactive, whereas if the genotype is heterozygous (T/G), one of the alleles is functional, the berry skin is colored.

25 cultivars were homozygous for *K980* (24 T/T and 1 G/G) and 14 samples were heterozygous (G/T), where T is the nonfunctional allele and G the functional one. Based on the other nucleotide polymorphism (*C22*), 27 cultivars were homozygous (26 T/T and 1 G/G) and 12 samples were heterozygous (G/T), with G and T, wild type and mutated allele, respectively.

Based on SNP polymorphism, we could discrinate the following varieties: 'Bajor kék' from 'Bajor szürke', and 'Bajor feketefájú', 'Gohér piros'from 'Gohér fehér'and 'Gohér változó'. In addition, the following varieties were also successfully distinguished: 'Csiljaki krasznüj'- belüj', 'Korinthusi piros- fekete', 'Piquepoul noir- gris', 'Huszajne krasznüj'- belüj'.

The 'Szeredi' (Rg), 'Hamuszőlő' (G), 'Gohér piros' (Rg), 'Rózsás leányka' varieties contain the *Gret-1* insertion (*VvMybA1a*/*VvMybA1a*) in homozygous form and this molecular background does not allow anthocyanin biosynthesis.

Examination of the SNP polymorphism of the *VvMybA2* gene, two functional alleles we were also detected in 'Gohér piros' (Rg), 'Rózsás leányka' (Rg) and 'Csiljak krasznüj' (Rg) (K980: T/G, C22: T/G).

In the case of 'Szeredi' (Rg), the SNP polymorphism revealed a homozygous mutant allele (K980: T/T, C22: T/T), so this genetic background of this variety phenotype was not confirmed by the polymorphisms of *VvMybA1* and *VvMybA2* genes.

3.3 Pylogenetic of *Vitis* species

Based on our preliminary studies, clearly detectable length polymorphism was observed on the agarose gel with the 20D18CB9 marker linked with the *VvMybA* genes among *V. vinifera* cultivars and wild *Vitis* species, and was taken to be suitable for the study of molecular evolution of the family *Vitaceae* and to establish a new phylogenetic relationship.

Based on sequencing of PCR fragments, a 34 bp deletion was revealed in 15 of the 25 North American species, so they were well separated on the dendrogram and formed a distinct cluster. Asian species do not contain this deletion, thus forming a separate group, in which 7 North American species, *V. arizonica*, *V. longii*, *V. solonis*, *V. doaniana*, *V. girdiana*, *V. tiliacea* and *V. rupestris*, are also clustered. This can be explained by the spread of grape species. It is assumed that *Vitis* species passed across the Bering Strait from Asia to the New World (DONOGHUE et al. 2001). The 34 bp deletion could also have occurred here in one of the ancient forms, and all of the new species that derived from this ancestor carry this mutation.

In *Muscadinia rotundifolia* SMALL. a 26 bp deletion was detected in a different position. In the dendrogram, this accession separated best from the others.

V. californica ENGELM, at a different site, contains a 21 bp deletion in the 20D18CB9 allele.

Interestingly, *V. doaniana* MUNSON. (which does not contain the deletion) is closest to the Eurasian species, which is possible due to the high sequence similarity, since besides the 34 bp deletion we detected, several nucleotide polymorphisms also influence the species location on the dendogram.

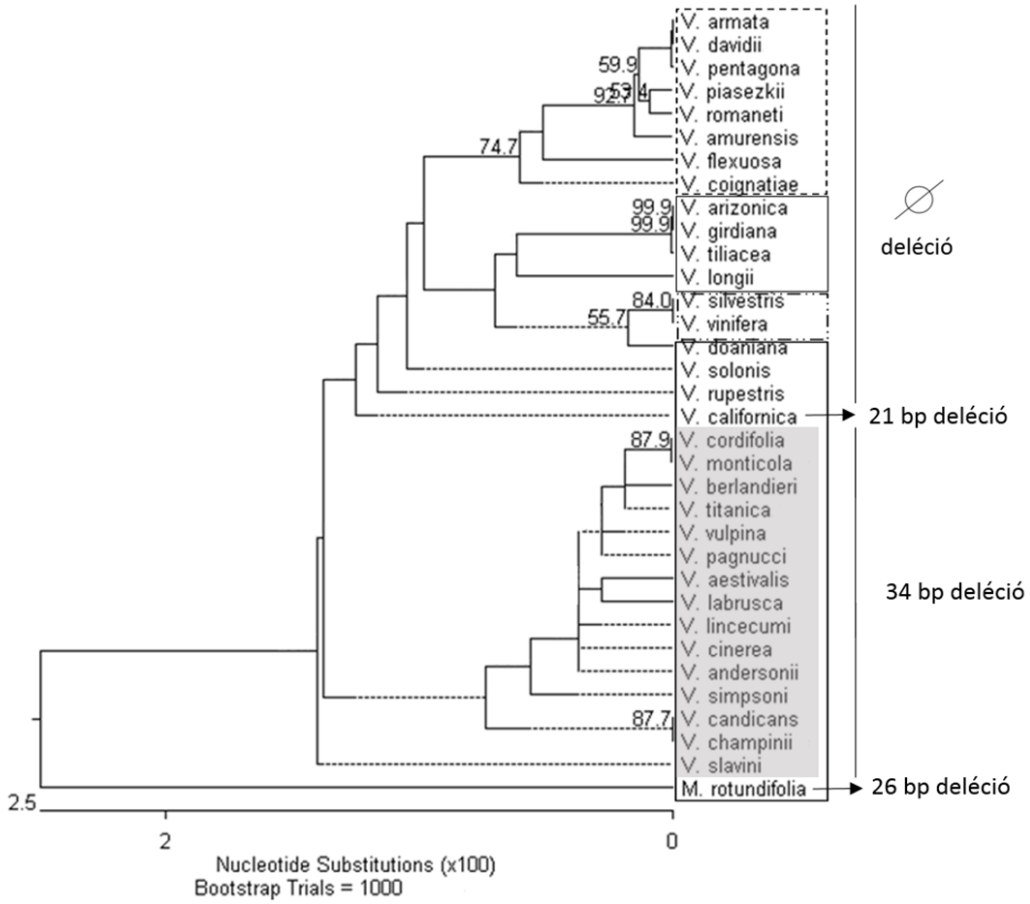

Figure 1: Dendrogram reconstructed on the basis of polymorphism of the 20D18CB9 marker sequence, based on Clustal W algorithm. Abbreviations: _ _ _ _ _ asian species, _____ north-american species, _ . . _ . . _ eurasian species, grey: north-american species containing 34 bp deletion.

3.4 New scientific results

1. Polymorphism of the *VvMybA1* gene (VvMybA1a, VvMybA1b, VvMybA1c) was detected in 118 Carpathian basin species.

2. We performed sequencing of 41 SNPs at the *VvMybA2* locus, including Carpathian basin bud sports and other European varieties.

   2/1. We discriminated cultivars based on SNP polymorphism: ‘Korinthusi piros’, ‘Piquepoul noir’, ‘Bajor kék’, ‘Gohér piros’, ‘Csiljaki krasznüj’, ‘Huszajne krasznüj’.

   2/2. Based on SNP polymorphism, we found the presence of a functional allele in the ‘Rózsás leányka’, ‘Gohér piros’ and ‘Csiljaki krasznüj’ varieties.

3. We used first the 20D18CB9 marker linked to genes encoding the berry coloring transcription factors *VvMybA1* and *VvMybA2* for phylogenetic analysis of grape species.

   3/1. Based on these, we have described a new phylogenetic relationship in *Vitis* species.

   3/2. Our sequencing results identified a higher degree of polymorphism among North American species than with Asian species. Analysis of the linked marker sequence revealed a 34 bp deletion specific only to North American species.

   3/3. In the *V. californica* ENGELM. and in the *M. rotundifolia* SMALL. we have found unique deletions which can subsequently be used as species-specific markers.

4 CONCLUSIONS AND RECOMMENDATIONS

In our previous work, we have successfully identified native bud sport that differ in the color of the berry by PCR-based markers designed for genes encoding VvMybA transcription factors (BODOR & SZŐKE et al. 2014, KEREKES et al. 2015).

From the results obtained for each group of varieties we can also conclude ancestral relationships. Because the 'Lisztes piros', 'Furmint piros' and the 'Muskotály piros' contain the *VvMybA1b* allele, they were formed from the white color variants by the deletion of the Gret-1 retrotransposon. Among the muscatelic varieties, we detected the ancient *VvMybA1c* allele without the retrotransposon in the black color variant, which is the oldest of them.

The old Carpathian basin varieties 'Ködös' (N), 'Kék tihanyi' (N) and 'Tótika' (N) carry the *VvMybA1c* allele in homozygous form. The SNP polymorphism of the *VvMybA2* gene has not yet been investigated, from which it is possible to draw a more reliable conclusion on the ancestral character of the varieties, but in any case, the presence of the VvMybA1c allele inevitably suggests its ancestral character. This evolutionary event was detected in *V. vinifera* L. after its divergence n from the other species.

A functional *VvMybA1* allele could not be detected for 'Gohér piros' (Rg), 'Hamuszőlő' (G), 'Rózsás leányka' (Rg) and 'Szeredi' (Rg). This result may also indicate that a functional allele of the *VvMybA2* transcription factor gene forms a berry color.

In the case of 'Szeredi' (Rg), the SNP polymorphism revealed a homozygous mutant allele (K980: T / T, C22: T / T), thus, examination of the *VvMybA1* and *VvMybA2* genes confirmed the molecular background of the white berry color.

In these cases, testing with additional marker systems may provide a solution to detect the genetic background of the appearance of the berry colour.

Most *Vitis* species in North America and Asia have black or dark blue berries, suggesting a high degree of conservation of the *Myb* transcription factor genes that regulate anthocyanin biosynthesis (PÉROS et al. 2015).

Despite this, polymorphism detectable on the agarose gel was already observed between the species with the marker linked with *VvMybA* genes.

Based on our sequence level analyzes, we found differences between some North American and Asian species based on a 34 bp deletion and several point mutations. North American species that do not carry this deletion show closely related with Asian species. This result is explained by the spread of *Vitis* species, which is supported by DONOGHUE et al. (2001) that the grapes have crossed the New World from Asia through the Bering Strait.

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