Grapevine breeding under climate change: Applicability of a molecular marker linked to véraison

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Summary

Viticulture is of high economic value. Traditional grapevine cultivars (*Vitis vinifera* L.) are used in adaptation to the climatic conditions from Northern to Southern European growing areas. However, the recent trend of global warming causes quality deficits due to a shift of the plant's development to earlier times in the year. As a consequence, premature ripening happens under warm temperatures and interferes with the balanced accumulation of sugars, acids, aroma profiles and berry coloration. Modern grapevine breeding is challenged to include the ripening behavior as an important trait (besides pathogen resistance and other characteristics) into the development of novel cultivars well suited for sustainable viticulture. Breeders nowadays apply molecular markers to follow the introgression of desired traits on the genetic level. Previous work has identified a molecular tag on grapevine chromosome 16 strongly linked to the time of véraison, the start of the second phase of berry ripening, in a segregating cross population. In this study we analyzed the transferability of this marker to a set of 36 grapevine cultivars commonly used in German viticulture. Association analysis verified the predictive character of the time point of véraison for maturation time and confirmed the diagnostic potential of the véraison-linked marker in this extended set of cultivars.

K e y　w o r d s :　berry ripening; climate change; molecular marker; phenology; *Vitis vinifera* L.

Introduction

Grapevine (*Vitis vinifera* L.) is a crop of worldwide importance grown in climatically privileged regions. Its fruits are processed into products such as wine and juice or consumed as fresh table grapes or raisins. In European viticulture production of quality wine is of major significance and generates high economic value. However, viticulturists are faced with a diversity of problems related to current climatic changes (Köhler 2009). These include the spread of various pathogens but also undesired physiological consequences. Mild spring times and hot summers shift the development of grapevines by accelerating bud burst, flowering time and the process of berry ripening (Duchêne and Schneider 2005,

Jones *et al.* 2005,Vršič *et al.* 2014). In Northern viticulture areas like Germany grapevines are usually harvested in September/October, depending on the cultivar. The acceleration of the phenology (earlier bud burst and flowering) results in extended vegetation periods. So early ripening occurs under rather warm conditions and generates quality deficits of the fruits. These are caused by a reduction of berry malic acid during warm nights or water stress symptoms, deficiencies in the evolution of aroma compounds and in the decreased coloration in red-berried cultivars (Duchêne *et al.* 2010, Liang *et al.* 2011, Pastore *et al.* 2017). Breeding of new improved grapevine cultivars aims at durable pathogen resistance combined with best wine quality (Eibach *et al.* 2007). Besides resistance traits grapevine breeding has to take into account many other characteristics concerning the suitability of the new cultivars to viticulture practice and climatic adaptation (Eibach and Töpfer 2015).

Grapevine berry ripening follows a biphasic growth. In the first phase after flowering and pollination fruit set is established and little hard green berries develop until they reach a certain size. Growth then stops for a transition period and resumes for a second phase of maturation dedicated to softening of the berries, sugar accumulation, acid decline and color changes of the pericarp (Coombe 1992). Red-berried grapevines start to deposit anthocyanins in their fruit skin, white-berried grapevines lose chlorophyll and brighten. The transition point is called véraison. It is usually evaluated by checking the berries for the beginning of softening or the start of anthocyanin pigmentation. In the internationally recognized system of descriptors for grapevine traits from OIV (Organisation Internationale de la Vigne et du Vin, OIV) véraison time is characterized by five classes 1, 3, 5, 7 and 9 (OIV descriptor 303) with class 1 representing very early ripening cultivars (e.g. 'Perle von Csaba') and class 9 corresponding to very late grapevines (e.g. 'Olivette noir'). The cultivar 'Riesling' is an example of class 5. Grapevine phenology stages are classified in the BBCH code (Lorenz *et al.* 1994) where véraison corresponds to stage 81; or in the E-L System (Coombe 1995) where véraison represents stage 35.

Véraison time is an important predictor of maturity- and harvest time (Sadras and Petrie 2011). It is cultivar-dependent and thus has a significant genetic determinant which was investigated in genetic studies. A major locus was identified on chromosome 16 by QTL (quantitative trait locus) studies in segregating populations (Fischer *et al.* 2004, Costantini

et al. 2008, Duchêne *et al.* 2012, Zyprian *et al.* 2016). In previous work on a segregating population of breeding line GF.GA-47-42 x 'Villard blanc' an allele with a fragment length of 165 bp from SSR (simple sequence repeat) marker UDV-052 was found strongly linked to the early onset of ripening (Zyprian *et al.* 2016). Grapevine breeders currently start to apply marker-assisted selection, especially for traits that are difficult to score. These may be "stacked" multiple resistance loci or traits whose evaluation requires waiting for the adult stage of the plant for fruiting (in grapevine this requires to finish a juvenile phase of three to four years). A genetic indicator of the time required to reach maturity could be a very useful tool for marker-assisted breeding of new cultivars adapted to specific requirements (early/late ripening). Therefore, a marker developed from the previous mapping study was tested for transferability to other cultivars of different genetic background. A comprehensive set of cultivars was thus analyzed for key steps of phenology.

The correlation of the beginning berry ripening time with the allelic profile of marker UDV-052 in these cultivars was investigated.

Material and Methods

P l a n t   M a t e r i a l : The Institute for Grapevine Breeding Geilweilerhof (N49°21.675, E8°04.433, altitude around 170 m) harbors a collection of "national cultivars", grapevine varieties frequently grown in Germany, which were used for this study. The 36 cultivars investigated are listed in Tab. 1. All of them are grafted on rootstock SO4 and were planted in the same year 2008 with 20 to 25 vines each. The vineyard is cane pruned (to 10-12 nodes) with spacing of 1.8 by 1.1 m (row by vine) resulting in a plantation density of 5050 vines per hectare. It is managed according to local standards.

T a b l e   1

Cultivars investigated in this study and their key phenology parameters. Average values from six years of evaluation recorded in days of the year starting from January 1st. Cultivars are given with their prime name according to the *Vitis* International Variety Catalogue (www.vivc.de).

Cultivar	Berry color*	Average bud break time	Average flowering time	Average véraison time	Average harvest time
Acolon	N	101.2	162.5	208.7	269.2
Auxerrois	B	104.3	159.8	217.0	267.3
Bacchus weiss	B	102.5	159.7	211.3	265.3
Blaufränkisch	N	100.2	158.5	223.7	274.2
Cabernet Dorsa	N	100.3	159.2	212.7	273.8
Cabernet Mitos	N	106.0	162.7	219.3	274.4
Chardonnay blanc	B	100.7	157.2	223.0	275.5
Chardonnay blanc musqué	B	101.3	157.2	221.3	275.5
Chasselas blanc	B	103.2	163.3	217.7	272.8
Dakapo	N	102.5	160.3	217.0	273.0
Domina	N	101.7	158.5	219.0	273.7
Dornfelder	N	101.8	160.3	216.8	268.0
Dunkelfelder	N	100.0	160.7	207.0	272.5
Elbling weiss	B	102.8	159.3	221.5	277.4
Faberrebe	B	102.5	158.3	209.0	275.2
Gewürztraminer	B	101.3	160.7	218.3	270.2
Kerner	B	104.3	159.3	221.3	269.8
Morio Muskat	B	99.3	160.7	218.8	265.7
Müller-Thurgau	B	103.3	158.8	213.8	267.2
Muscat à petits grains blancs	B	101.2	161.7	223.8	275.8
Optima	B	102.2	159.7	209.7	269.0
Pinot blanc	B	103.2	158.2	221.7	273.7
Pinot gris	B	104.3	158.0	219.5	274.2
Pinot meunier	N	106.0	159.5	219.8	271.6
Pinot noir	N	103.5	157.5	219.2	281.0
Pinot precoce noir	N	102.0	157.3	205.3	272.6
Portugieser blau	N	102.7	159.3	218.3	269.0
Regent	N	103.7	156.0	205.8	267.0
Rieslaner	B	102.7	162.3	224.0	276.0
Riesling weiss	B	105.2	161.8	230.3	283.3
Saint Laurent	N	103.2	157.8	213.3	275.5
Scheurebe	B	107.8	161.8	222.7	274.5
Schiava grossa	N	102.3	161.2	225.7	279.6
Silvaner grün	B	102.0	159.0	222.5	274.3
Solaris	B	99.3	153.3	202.0	260.5
Traminer red	R	102.3	160.8	218.5	277.8
Minimal value		**99.3**	**153.3**	**202.0**	**260.5**
Maximal value		**107.8**	**163.3**	**230.3**	**283.3**

*Berry color N = noir, black; B = blanc, white; R = rouge, red.

P h e n o t y p i n g : The vines were evaluated for the time of bud break (swollen buds), begin of flowering (30 % cap fall), berry softening (véraison, manually checking the berries from representative bunches in the upper part, the middle and the lower part of the canopies) and harvest (sensory evaluation) for six years (2010, 2011, 2012, 2013, 2014 and 2015). These traits were observed according to the BBCH scale and recorded in counting days of the year starting from January 1st. Average values over the years were calculated (Tab. 1) and used for correlation analysis.

G e n o t y p i n g : Small leaf pieces of the cultivars were used to extract genomic DNA. The alleles of marker UDV-052 (GenBank BV097063) were amplified as described (ZYPRIAN *et al.* 2016). The marker resides at position 15756966 on chromosome 16 in the reference genome of PN 40024 12x (JAILLON *et al.* 2007) and covers a repeat of type $(CT)_n(CA)_n$.

S t a t i s t i c a l A n a l y s e s : Statistical analysis was performed using the "Pearson correlation coefficient" in the "hmsic" statistics module and ANOVA in R software version 3.0.3 Copyright 2014, The R-foundation for statistical computing. For the latter purpose the observation of the véraison-linked allele size was coded as "1", while alleles of other sizes from this marker were recorded as "0".

Results and Discussion

The Institute for Grapevine Breeding Geilweilerhof is located at the Northern border of viticulture. Records of flowering time and the time of véraison collected over 34 years at this location on the cultivar 'Riesling' and the breeding line GF.GA-47-42 clearly demonstrate a shift in phenology (Fig. 1). Assuming a linear trend, flowering became on average 16.8 days (0.5 days/year; $R^2 = 0.29$) earlier for 'Riesling' and 20.0 days (0.6 days/year; $R^2 = 0.34$) earlier for GF.GA-47-42 within this time period. This effect was even stronger for véraison with 21.2 days (0.6 days/year; $R^2 = 0.41$) for 'Riesling' and 27.4 days (0.8 days/year; $R^2 = 0.47$) for GF.GA-47-42. The observation on key parameters of phenology like bud break, flowering, berry

softening (véraison) and harvest time was thus extended and recorded for six years on 36 cultivars. The results are presented in average values in Tab. 1. Within these cultivars average budburst occurred during a short time window of 8.5 d and flowering had a time interval of 10 d on average. The diversity in development was largely extended when berry softening was recorded as indicator of véraison. On average it spread over a wide time window of 28.3 d. Harvest time stretched over a period of 22.8 d.

Correlation analysis of the phenology traits among each other (Tab. 2) indicated that the strongest relationship is detectable between véraison and harvest time (Pearson correlation coefficient 0.63; $p = 0.00$). This confirms that the time of véraison is a useful predictor for the end of berry ripening.

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Pearson correlation coefficients between the phenological traits Correlation coefficients calculated with module "hmsic" in R-software (n = 36) *p*-values of each coefficient provided in brackets

correlation	bud break	flowering	véraison	harvest
bud break	1.00	0.27 ($p = 0.1$)	0.32 ($p = 0.06$)	0.26 ($p = 0.12$)
flowering	0.27 ($p = 0.1$)	1.00	0.42 ($p = 0.01$)	0.28 ($p = 0.1$)
véraison	0.32 ($p = 0.06$)	0.42 ($p = 0.01$)	1.00	0.63 ($p = 0.0$)

The 36 cultivars were analyzed for their allelic profiles at marker UDV-052. The results are shown in Tab. 3. When the grapevine cultivars were arranged according to their véraison time it became obvious that there is a significant bias in allelic distribution and early-ripening varieties are enriched with the véraison-linked UDV-052 allele of 165 bp as originally identified in GF.GA-47-42. ANOVA analysis confirmed the correlation of this allele with the phenotype of early ripening. The groups with the véraison-linked allele and the one without are significantly separated concerning their distributions of berry softening time ($p = 0.00016$; Fig. 2). This result indicates that the linkage between early véraison and the marker allele of UDV-052 originally identified in a segregating population (ZYPRIAN *et al.* 2016)
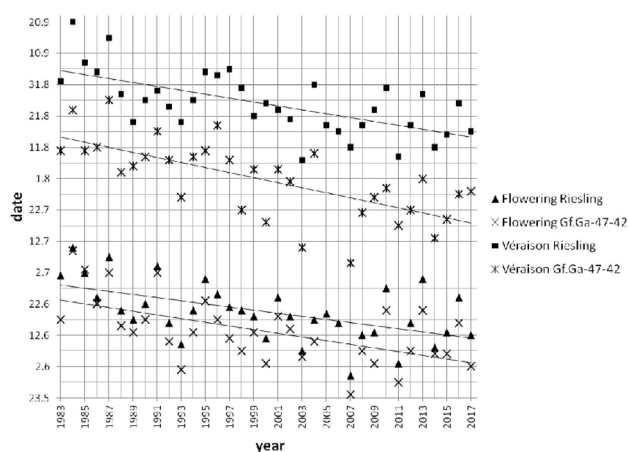

Fig. 1: Change in phenology. Date of flowering time and véraison of cultivar 'Riesling' and breeding line Gf.GA-47-42 in the last 34 years. Despite large weather depending seasonal variances a trend to earlier development is obvious.
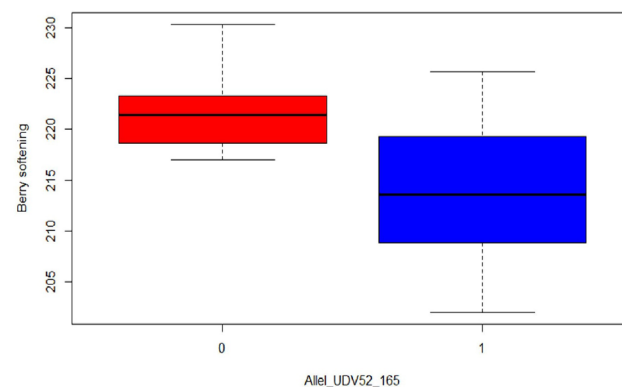

Fig. 2: Association analysis. Boxplot of the association between the average time required to reach véraison and the presence of the early véraison-linked marker allele of UDV-052 (*p*-value = 0.00016).

UDV-052 allelic profiles in the cultivars listed according to their average date of véraison. The presence of the 165 bp allele was re-coded as 1 (absence as 0) for following ANOVA analysis

Average time of véraison	Cultivar	UDV-052 alleles (bp)		UDV-052_165 recoded
202.00	Solaris	**165**	168	1
205.33	Pinot precoce noir	**165**	172	1
205.83	Regent	**165**	176	1
207.00	Dunkelfelder	**165**	156	1
208.67	Acolon	**165**	159	1
209.00	Faberrebe	**165**	172	1
209.67	Optima	**165**	172	1
211.33	Bacchus weiss	**165**	180	1
212.67	Cabernet Dorsa	**165**		1
213.33	Saint Laurent	**165**	176	1
213.83	Müller-Thurgau	**165**	180	1
216.83	Dornfelder	**165**	160	1
217.00	Auxerrois	**165**	159	1
217.00	Dakapo	172	177	0
217.67	Chasselas blanc	**165**	156	1
218.33	Portugieser blau	160	172	0
218.33	Gewürztraminer	172	180	0
218.50	Traminer red	172	180	0
218.83	Morio Muskat	152	160	0
219.00	Domina	172		0
219.17	Pinot noir	**165**	172	1
219.33	Cabernet Mitos	160	172	0
219.50	Pinot gris	**165**	172	1
219.83	Pinot meunier	**165**	172	1
221.33	Chardonnay blanc musqué	156	172	0
221.33	Kerner	**165**	180	1
221.50	Elbling weiss	156	172	0
221.67	Pinot blanc	**165**	172	1
222.50	Silvaner grün	152	172	0
222.67	Scheurebe	174	180	0
223.00	Chardonnay blanc	156	172	0
223.67	Blaufränkisch	160	162	0
223.83	Muscat à petits grains blancs	160	172	0
224.00	Rieslaner	152	180	0
225.67	Schiava grossa	**165**	174	1
230.33	Riesling weiss	159	180	0

is maintained in a set of *Vitis* cultivars adapted to Northern viticulture. Hence, this marker may be applied successfully in marker-assisted selection (or counter-selection) in grapevine breeding of improved cultivars adapted to the climatic conditions of that region.

A first practical test for the applicability of UDV-052-165 was performed by analyzing the presence of this "early" allele in seedlings with different harvest times in the year 2017 (Fig. 3). Within the seedlings harvested during the first two weeks of vintage (September 11-15 and 18-22), 50% resp. 47 % carried the early allele, while only 18% of the seedlings harvested during the third week (September 25-29) exhibited the UDV-165 allele and it was completely absent in the seedlings harvested late (October 2-6). This result confirms the usefulness of marker UDV-052-165 as indicator of early ripening.
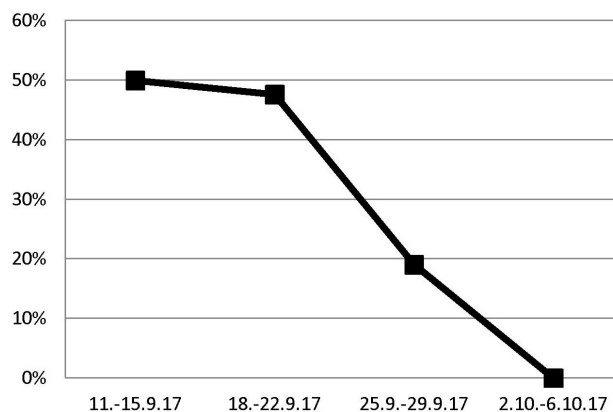

Fig. 3: Ratio of UDV-052-165 positive seedlings per week of harvest. Vintage 2017 was characterized by an exceptionally early harvest. In the breeding program at the Institute seedlings were selected for harvest and harvested over a period of four weeks, where the first grapes were harvested at September 11th and the last ones on October 6th. These seedlings were later subjected to an analysis of UDV-052 and the occurrence of the 165 allele was assessed. In the first week (for comparison: harvest time of 'Müller-Thurgau' was 07.09.2017) ten seedlings were harvested and five of them showed the UDV-052-165 allele (50 %). Of the 42 plants harvested in the second week (harvest time of 'Pinot Noir') 20 had the UDV-052-165 allele (47.62 %). However, of the 42 plants which were harvested in the third week (harvest time of 'Riesling'), only eight showed the allele linked to early véraison (19.05 %). Most interestingly, in the last week of harvest (time of 'Tempranillo') no UDV-052-165 allele was found in the 14 harvested seedlings.

Recent detailed molecular studies on the processes of berry softening and the role of ABA (abscisic acid) as key regulator of véraison revealed complex molecular regulatory networks involved (CASTELLARIN *et al.* 2016, PILATI *et al.* 2017). The marker UDV-052 amplifies an SSR motif in the first intron, just in front of the second exon, of a gene annotated as *Per1-like* or *post GPI (glycosylphosphatidylinositol) attachment to protein factor 3* (GenBank XP_002280194). This gene has five exons in total and the encoded protein is predicted to possess seven transmembrane domains (http://www.cbs.dtu.dk/services/TMHMM/). In yeast, it is involved in the biosynthesis of the GPI-anchor in the ER (Endoplasmatic reticulum) which is attached as post-translational modification to specific proteins for anchoring them to the cell membrane (IKEZAWA 2002, FUJITA and KINOSHITA 2012, CHEUNG *et al.* 2014). The grapevine genome has one other copy of the gene *Per1-like* annotated (chromosome 19; *VIT_219s0027g00810*). Although GPI anchors have been implicated in signaling in plants (SCHULTZ *et al.* 1998), it seems unlikely that the length polymorphism observed with UDV-052 alleles is affecting the functionality of *Per1-like* and may be itself a cause for the diversity in véraison time requirements. Other genes encoding potential transcription factors located nearby in the reference genome (*VIT_16s0100g00380*; *VIT_16s0100g00390*; *VIT_16s0100g00400*) may be better candidates to understand the reasons for the differences in véraison time as discussed earlier (ZYPRIAN *et al.* 2016). However, the SSR marker tested in this study could serve as valuable tool in marker-assisted selection of climate-adapted grapevine cultivars.

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Author contributions

E. Zyprian designed the genotyping, processed the data and wrote the manuscript. R. Eibach managed the plant material and its phenotypic evaluation. O. Trapp tested the marker correlation to grapevine harvest times. F. Schwander provided data on flowering and breeding over 34 years. R. Töpfer contributed the use of infrastructure and general advice. All authors critically read, revised and approved the manuscript.

Compliance with ethical standards

This work did not include any material from humans or animal sources.

Conflict of interest

The authors declare that they have no conflict of interest.

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