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Molecular genetic map construction and QTL analysis of fruit maturation period in grapevine

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ABSTRACT. In this study, we aimed at finding the genetic regularity of grape maturation period. Early-maturing grapevine, "87-1", was used as the female parent and late-maturing, "9-22", as the male parent, to create an F1 hybrid population. A total of 149 individual plants and their parents were selected as the mapping population. Sequence-related amplified polymorphism and simple-sequence repeat analyses were performed. We performed a linkage analysis and constructed a molecular genetic map. In the obtained map, the female and male parents each covered 19 linkage groups containing 188 and 175 maker loci, respectively. The total map distances for the female and male parents were 1074.5 and 1100.2 cM, respectively, whereas the average genetic distances between each two loci were 5.7 and 7.8 cM, respectively. The interval-mapping method was used in a quantitative trait locus (QTL) analysis for fruit maturation period. A total of 12 QTLs associated with fruit maturation period were detected. These included four QTLs in the male parent genetic map that were located in linkage groups M5, M11, M14-1, and M16, with a 62.6-75.7% rate of contribution of each QTL. Another three QTLs were found in the female parent genetic map, located in linkage groups F6, F14-1, and F18, with a 72.7-77.7%

rate of contribution of each QTL. Five more QTLs were detected in the consensus map, located in linkage groups LG11, LG14-1, LG16, LG17, and LG18, with 8.9-75.7% phenotypic variance explained by each QTL.

Key words: Grape; Fruit maturation period; QTL

INTRODUCTION

Grapevine is an important fruit species that is cultivated all over the world. Until 2013, the worldwide cultivated area was about 7.15 million hectares with a total production of about 77.18 million tons (http://http://faostat3.fao.org/download/Q/QC/E). As a perennial woody fruit tree, grapevine shows high genetic heterozygosity, and a long generation cycle. This has, in part, limited the progress of research on grapevine genetic characters. Due to the valuable guidance that molecular genetic maps provide in plant breeding and genetic engineering, these types of maps have become a research hotspot in life sciences. High-density genetic maps can facilitate the analysis of important agronomic traits at the molecular level. These maps may also lay the foundation for marker-assisted breeding and improvement of the breeding efficiency.

With the technology development of molecular biology and molecular markers, the molecular genetic maps for many kinds of plants, such as rice (Cai et al., 2015), maize (Zheng and Liu, 2013), pumpkin (Ge et al., 2015), and pepper (Moulin et al., 2015), have been constructed. In addition, finished quantitative trait locus (QTL) mapping for a variety of traits, greatly explained the genetic mechanisms of these traits. Molecular marker technology has also been widely used and significant progress has been made in grapes, including species identification (Agar et al., 2012; Fan et al., 2014), hybrid identification (Kayesh et al., 2014), screening of disease-resistance markers (Zhang et al., 2014), molecular genetic map construction, and so on. Since Lodhi et al. (1995) reported the first grapevine molecular genetic map, researchers worldwide have constructed many high-quality genetic maps, based on different mapping populations (Grando et al., 2003; Riaz et al., 2004; Wang et al., 2012; Guo et al., 2015). Meanwhile, many QTL analyses have also been conducted, for example, there are reports on QTL analysis of some important quality characters and disease resistance of grapevine. These studies include analyses of grain weight (Doligez et al., 2002; Fanizza et al., 2005), fruit aroma (Doligez et al., 2006b; Battilana et al., 2009), Pierce's disease resistance (Krivanek et al., 2006; Riaz et al., 2006), anti-nematode traits (Xu et al., 2008), berry firmness (Carreño et al., 2015), anti-powdery mildew traits (Fischer et al., 2004; Akkurt et al., 2007; Zyprian et al., 2009; Van Heerden et al., 2014), anti-phylloxera traits (Zhang et al., 2009), and so on.

The maturation period is an important trait for grapevine cultivation and breeding. Existing reports suggest that the maturation period in grapevine is a typical quantitative trait that is controlled by multiple genes (Xu, 1997; Guo et al., 2003; Song et al., 2005). Most of the studies on the stage preceding grape maturation have adopted conventional quantitative genetic analyses that do not provide deep insights into the genetic mechanisms. There are few QTL analyses of the grape maturation period. Mejía et al. (2007) and Costantini et al. (2008) found correlated QTLs for the grape maturation period. Therefore, there is still a great need to continue the research of the molecular genetic mechanisms of grape maturation.

In this study, a large mapping population was generated by cross-fertilization of an early-maturing female parent and a late-maturing male parent. Subsequently, a molecular genetic

map was built, using sequence-related amplified polymorphism (SRAP) and simple-sequence repeat (SSR) analysis. The QTL analysis of the fruit maturation phase in grapevine could provide a basis for molecular breeding of grapevine focused on the fruit maturation phase, it can also provide references for the regulatory mechanism and gene clones of grape maturation.

MATERIAL AND METHODS

Plant material

A hybrid (F1) population was constructed in 2007 by crossing an early-maturing female parent "87-1" and a late-maturing male parent "9-22". Cultivar "87-1", the early-maturing female parent displays high yield, high quality, high disease resistance, strong rose fragrance, etc. Cultivar "9-22", the late-maturing male parent, has a late-fruit maturation, large grain size, crisp flesh, high-soluble solid content, etc. The F1 generation showed great variation in fruit size, skin color, maturation period, fruit fragrance, etc. For the mapping population, we selected 149 individual F1 plants. The F1 plants and their parents, i.e., 151 individuals in total, were used to conduct the molecular marker analysis and construct a genetic map. The mapping population and parents were all grown in the grape-breeding nursery at the Shenyang Agricultural University.

Extraction of genomic DNA

Young leaves were collected from the field at the germination stage. The leaves were quickly frozen in liquid nitrogen and then kept at -80°C until further analysis. Genomic DNA was extracted from the young leaves, using the modified CTAB method (Hanania et al., 2004). Following the detection of genomic DNA concentration, the samples were diluted to 20 ng/μL for subsequent use.

SSR primers and polymerase chain reaction (PCR)

A total of 468 pairs of primers were used, based on grapevine genome sequence information. These included primers from the following primer series: VMC (Thomas and Scott, 1993), VVMD (Bowers et al., 1996, 1999), VrZAG (Sefc et al., 1999), VVI (Merdinoglu et al., 2005), UDV (Di Gaspero et al., 2005), and Chr (Blasi et al., 2011). A PCR was performed in 16-μL total reaction mix, containing 10 ng genomic DNA, 2.0 mM Mg^{2+}, 100 μM deoxyribonucleoside triphosphates (dNTPs), 0.3 μM random primer, 1X PCR buffer, and 0.8 U Taq polymerase (New England Biolabs, Beijing, China). The following PCR program was used: 25 cycles at 94°C for 4 min, 94°C for 1 min, 50°-63°C annealing for 1 min, 72°C extension for 1 min, and a final extension step at 72°C for 7 min. The PCR products were separated by 5% polyacrylamide gel electrophoresis (PAGE) and visualized by silver staining.

SRAP primers and PCR amplification

We selected 30 pairs of SRAP primers from Li and Quiros (2001) that gave stable, clear, and highly polymorphic bands. The PCR mix (20 μL) contained 10 ng genomic DNA, 2.0 mM Mg^{2+}, 100 μM dNTPs, 0.5 μM primer, 1X PCR buffer and 1.5 U Taq polymerase

(NEB). The SRAP-PCR procedure included the following cycles: 94°C for 5 min; 5 cycles consisting of 94°C for 1 min, 35°C annealing for 1 min, 72°C extension for 1.5 min; 35 cycles consisting of 94°C for 1 min, 50°C annealing for 1 min, 72°C extension for 1.5 min; followed by a final extension step at 72°C for 10 min. The PCR products were separated by 7% PAGE and detected by silver staining.

Investigation of fruit maturation period

We investigated the fruit development time, from the flowering to the fruit maturation period, for every plant. After the observations made early in the year, the full-bloom stage of grape in the Shenyang region of China occurred in early June; the full-bloom stage of the mapping population in this study occurred mostly between June 1 and June 5. In reference to previous studies, the full-bloom stage of most grapevines occurs on June 1 (Guo et al., 2003; Zhao et al., 2011). Therefore, in this study, we assumed June 1 as the starting point and then calculated the number of days until the grapes were completely ripe as the fruit maturation period. The standard time of grape maturation was assumed to be the time when the soluble solid content reached 15% together with a change in the grape flavor, the soluble solid contents were released using a hand-held refractometer (Model WZ-103, Zhongyou Optical Instrument Corp., China), the grape flavors were tasted by the professional people.

Genetic map construction and QTL analysis

Molecular genetic maps for the parents were constructed using the JoinMap 3.0 software (Van Ooijen and Voorrips, 2001). The following parameters were set: the cross-pollinating mapping function, LOD = 3.0 to 5.0, and a maximum recombination rate of 0.4. The recombination rate was transformed into map distance (cM), using the Kosambi function. MapChart 2.2 (Voorrips, 2002) was used to construct the molecular genetic map of the parents. The order of the linkage groups was coded according to the international reference map (Doligez et al., 2006a; Di Gaspero et al., 2007). Interval mapping was carried out with MapQTL 5.0 (Van Ooijen, 2004), and QTLs were detected using the conditional permutation test.

RESULTS

Molecular genetic map construction

Of the 468 SSR primer pairs, we screened out 200 pairs to construct the genetic map. In total, 44 female-specific markers, 54 male-specific markers, and 102 consensus markers were identified. Using the 30 pairs of SRAP primers, we obtained 53 female-specific, 27 male-specific, and 39 consensus markers.

The 97 female-specific markers and the 141 consensus markers were used to construct the genetic map of the female parent “87-1”. Finally, 188 markers were added to the genetic map, which had a total length of 1074.5 cM (Figure 1). These markers constituted 19 linkage groups. The average length of the groups was 56.6 cM and the average distance between each two markers was 5.7 cM. The longest linkage group, LG19, which contained nine SSR markers and five SRAP markers, had a length of 111 cM.

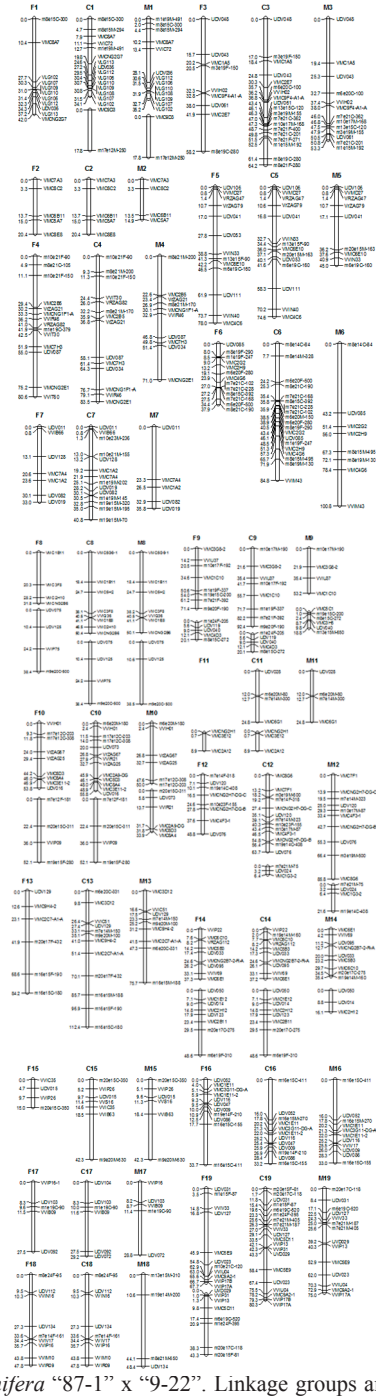

Figure 1. Linkage map of *Vitis vinifera* "87-1" x "9-22". Linkage groups are numbered according to Doligez et al. (2006a). For each linkage group, the parental maps are shown on the left ("87-1") and right ("9-22") and the consensus map is in the center. The distances of the markers from the top are indicated on the left in cM.

Based on the 81 male-specific markers and the 141 consensus markers, a genetic map of the male parent '9-22' was constructed, followed by the addition of 175 markers to the genetic map. Its total length amounted to 1100.2 cM (Figure 1). The markers formed 19 linkage groups, the average length of the groups was 57.9 cM, and the average distance between each two markers was 7.8 cM. The longest group, LG12, included nine SSR markers and five SRAP markers and was 107.4 cM in length. The order of the most co-dominant markers in the obtained map was the same as that found in the international reference map, except for several marker inversions and absences.

Location of QTLs for the fruit maturation period traits

The distribution of the progeny plants within the mapping population, based on the grape maturation period, is shown in Figure 2. In terms of the grape maturation period, the results showed a large variation in the hybrid progeny, between 68 and 111 days, with an average of 87.2 days. The maturation period for the female parent, "87-1", was 73 days and 106 days for the male parent, "9-22".

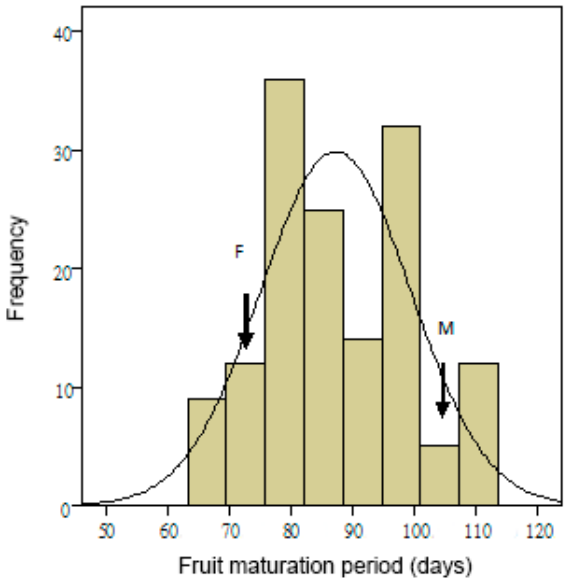

Figure 2. Frequency distribution of fruit maturation in progeny plants. The parental phenotypes are indicated by arrows. M (male, "9-22"), F (female, "87-1").

The results from the QTL analysis revealed 12 QTLs associated with the fruit maturation period trait. Four QTLs (MMa1-MMa4) that function in the control of the maturation period trait were found in the male parent. These QTLs were shown to be located in linkage groups M5, M11, M14-1, and M16, respectively. The rate of contribution of each QTL to the phenotypic value was 62.6-75.7%. Three QTLs associated with fruit maturation period (FMa1, FMa2, and Ma3) were found in the female parent. These were located in linkage groups F6, F14-1, and F18, respectively. The rate of contribution of each of these

QTLs to the phenotypic value was 77.7, 75.7, and 72.7%, respectively. Furthermore, five QTLs (CMa1-CMa5) related to the grape maturation period were detected in the consensus map. These QTLs were located in linkage groups LG11, LG14-1, LG16, LG17, and LG18. The phenotypic variance explained by each of these QTLs ranged from 8.9 to 75.7% (Table 1).

Table 1. Distribution of QTLs for fruit maturation period traits in the genetic linkage map.

	Linkage group[a]	QTL	LOD	Permutation test[b]	Nearest marker	Peak (cM)	R^2 (%)
Male parent	M5	*MMa1*	6.64	5.9	UDV041, m20e15M-163	26.1	75.1
	M11	*MMa2*	4.56	3.4	M7e14M-300, VMC6G1	22.7	74.1
	M14-1	*MMa3*	8.85	8.2	UDV014, VMC2H12	11.8	75.7
	M16	*MMa4*	18.5	17.7	M16e15C-411, UDV052	13	62.6
Female parent	F6	*FMa1*	7.7	7.6	VMC2H9, m6e20F-280	16.2	77.7
	F14-1	*FMa2*	8.7	8.6	UDV014, VMC2H12	12	75.7
	F18	*FMa3*	4.9	4.2	M8e24F-95	0	72.7
Consensus map	LG11	*CMa1*	4.56	3.8	M7e14M-300, VMC6G1	22.7	74.1
	LG14-1	*CMa2*	8.66	8.6	UDV014, VMC2H12	12	75.7
	LG16	*CMa3*	18.46	17.5	M16e15C-411, UDV052	13	62.7
	LG17	*CMa4*	2.51	2.4	VVIB09	11.6	8.9
	LG18	*CMa5*	4.87	4.4	M8e24F-95	0	72.7

[a]Linkage group following the International Grape Genome Program (IGGP). [b]Determined by a permutation test at $P \leq 0.05$. R^2 indicates the phenotypic variance explained by the QTL.

DISCUSSION

Most of the early research on grape maturation period traits was conducted using traditional genetic analyses and showed that the maturation period traits were quantitative traits (Guo et al., 2003). In the present study, the mapping population stemmed from the hybridization of an early-maturing and a late-maturing grape variety. Subsequently, a combination of SSR and SRAP markers were used to construct a molecular genetic map, followed by an analysis of QTL mapping for fruit maturation period. Some QTLs were identified as associated with fruit maturation period.

Reports of QTL mapping for grape maturation period are rare. Mejía et al. (2007) reported QTLs associated with maturation period in linkage groups 17 and 18. Costantini et al. (2008) also detected areas that control the maturation period traits, but in linkage groups 2, 6, and 16. These QTLs have been detected in the maps of both parents and have been found repeatedly in different years. The fact that in our study, most of the determined QTLs could be detected in the female parent, the male parent, as well as the consensus map, suggests that these QTLs could be considered reliable. Some of the QTLs found in this study confirm earlier reports; for example, FMa1 in linkage group 6 and MMa4 and CMa3 in linkage group 16 were located near the area of linkage groups 6 and 16 reported by Costantini et al. (2008). The QTLs FMa3 and CMa5 in linkage group 18 were located near the area of the QTL RAD, also in linkage group 18, in the report of Mejía et al. (2007). It would be interesting to further explore the identified QTLs. In addition, in LG14, we have detected QTLs associated with the grape maturation period in adjacent regions in the female, male, and consensus maps with high LOD score. QTLs were found to be located between the molecular markers UDV014 and VMC2H12 with a length of 2.26 Mb. There are 71 genes located in this region (http://www.genoscope.cns.fr/externe/GenomeBrowser/Vitis/). We aim to study these genes further, using bioinformatic methods, and expect to get the candidate gene response for the fruit maturation period in the future.

Our study, however, has some limitations. To increase the genetic map density and improve the accuracy, we will conduct more research on the QTLs reported here. As the reported results are only based on one year's worth of data, they should only be considered a preliminary guidance. For greater reliability, we will conduct the QTL analysis for the grape maturation period traits across different years, to test the stability of the QTLs in different years. Thus, we hope to lay the grounds for refined QTL mapping location and marker-assisted selection in the next step.

Conflicts of interest

The authors declare no conflict of interest.

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