Zeballos, JL.; Adibi, W.; Giménez Millán, R.; Monforte Gilabert, AJ.; Moreno, MA.; Gogorcena, Y. (2016). Mapping QTLs associated with fruit quality traits in peach Prunus persica (L.) Batsch using SNP maps. Tree Genetics and Genomes. 12(3):1-17. doi:10.1007/s11295-016-0996-9.

Mapping QTLs associated with fruit quality traits in peach [*Prunus persica* (L.) Batsch] using SNP maps

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Abstract

Fruit quality is an essential criterion used to select new cultivars in peach breeding programs and is determined based on a combination of organoleptic and nutritional traits. The aim of this study was to identify quantitative trait loci (QTLs) for fruit quality traits in an F_1 nectarine population derived from 'Venus' and 'Big Top' cultivars. The progeny were evaluated over 4 years for agronomical and biochemical characteristics, and genotyped using SSR markers and 'IPSC 9K peach SNP array v1'. Two genetic maps were constructed using 411 markers. The 'Venus' map spanned 259 cM on nine linkage groups (LGs) with 104 markers. The 'Big Top' map spanned 464 cM on ten LGs with 122 markers. Single or Multiple QTL models mapping was applied separately for each year and all years combined. A total of 54 QTLs mapped over 12 LGs belonged to seven peach chromosomes. Most of the QTLs were consistent over the 4 years of study and were validated with the Multi-year analysis. QTLs for total phenolic, flavonoid, and anthocyanin contents were reported for the first time in peach. LG4 in 'Venus' and LG5 in 'Big Top' showed the highest numbers of QTLs. This work represents the first study in an F_1 nectarine family to identify peach genomic regions that control fruit quality traits using 'IPSC 9K SNP array v1' and provides useful information for marker-assisted breeding to produce peaches with better antioxidant content and healthy attributes.

Key words: peach physical map, vitamin C, total phenolics, flavonoids, anthocyanins, sugars

Introduction

Peach [*Prunus persica* (L.) Batsch] is the third most important fruit crop worldwide in terms of production (FAOSTAT 2015). In Spain, the first peach exporter to Europe, peach is an economically important crop; it covers a large area (84,400 ha in 2013), being the second in peach production in the European Union and third worldwide (FAOSTAT 2015).

Fruit quality is important for the peach industry because it can modify consumer preference. Traits such as flesh texture, color, sweetness, acidity, and other organoleptic attributes may affect consumption of specific varieties (Crisosto 2002). In recent years, consumers have attached greater importance to functional foods, which have health-promoting properties, such as antioxidant, antimutagenic, and anticarcinogenic effects (Orazem et al. 2011; Vizzotto et al. 2014). In conjunction these traits represent food quality, which has become a primary goal in many international peach breeding programs in recent decades (Infante et al. 2008; Cantín et al. 2009a; Byrne et al. 2012). Unfortunately, most traits related to fruit quality are quantitatively inherited and the genetic control of many of these traits is still unknown (Eduardo et al. 2011). Determining the genetic basis of these traits is necessary to understand their genetic control and will provide necessary information to develop specific approaches to enhance breeding programs (Peace and Norelli 2009).

Peach is one of the best characterized fruit tree species which, due to its short juvenility period and the simplicity of its genome, serves as a model for genetic studies in Rosaceae (Zeballos 2012 and references therein). Moreover, the availability of the T × E *Prunus* reference map (Dirlewanger et al. 2004), the release of the peach genome v1.0 and v2.0 (Arús et al. 2012; Verde et al. 2013), and the recent development of single nucleotide polymorphism (SNP) genotyping platforms offer the opportunity to determine the inheritance of many qualitative and quantitative traits at the molecular level (Frett et al. 2014). Likewise, alignment of the updated physical map to the *Prunus* reference map would provide the *Prunus* research community with a basis for comparing the positions of the major genes and quantitative trait loci (QTLs) identified in several previous studies across different mapping populations.

However, as mentioned above, many agricultural traits are quantitative in nature, and determining their genetic basis is complicated because the majority of genes have little

effect and few have substantial effects (Brem and Kruglyak 2005). Many studies have been carried out for QTL identification in *Prunus* (Zeballos 2012). Nevertheless, many important agronomic traits of *Prunus* species have not yet been mapped, and only a few are currently being used for marker-assisted selection (including major genes for disease and pest resistance, self-incompatibility, slow ripening, and fruit quality traits such as flesh color, endocarp staining, flesh adherence to stone, non-acid fruit, skin pubescence, skin color, and fruit shape) (Dirlewanger et al. 2004; Eduardo et al. 2015; Ru et al. 2015 and references therein). Important QTLs that control fruit quality traits have been found for total sugar content, organic acid content, fruit weight, acidity, blooming and harvest dates (Dirlewanger et al. 1999; Etienne et al. 2002; Quilot et al. 2004), blooming and ripening dates (Eduardo et al. 2011; Dirlewanger et al. 2012), chilling injury susceptibility (Cantín et al. 2010a), and other traits anchored in the T × E *Prunus* reference map that have been widely described by Arús et al. (2012).

Most previous studies have been limited because of the low marker density in the maps (Eduardo et al. 2013). However, the availability of SNP genotyping resources has assisted in fine mapping of peach (Martínez-García et al. 2013a,b; Zhebentyayeva et al. 2014). More recently, attempts have been made to map QTLs in peach using the newly developed SNP genotyping array v1 (Verde et al. 2012). Several QTLs that control traits such as chilling and heat requirements (Romeu et al. 2014), blush (Frett et al. 2014), maturity date (Pirona et al. 2013; Fresnedo-Ramírez et al. 2015; Nuñez-Lillo et al. 2015) or other pomological traits such as fruit weight, soluble solids content or pH (Fresnedo-Ramírez et al. 2015) have been mapped. Moreover, the current analytical techniques are more powerful for large-scale phenotyping than older methods, and new traits related to fruit quality are being incorporated in QTL analysis. For example, aroma and other volatile compounds were partially mapped onto the *Prunus* reference map (Illa et al. 2011; Eduardo et al. 2013) and were analyzed using a high-throughput gas chromatography-mass spectrometry (GC-MS)-based metabolomics approach (Sánchez et al. 2012). Some phenolic compounds (pigments) were mapped on the T × E reference map (Ogundiwin et al. 2009), and other phenolic compounds (Chagné et al. 2012; Verdu et al. 2014) and vitamin C (Davey et al. 2006) were identified in apple, but to our knowledge no QTLs that control phenolic compounds (including total phenolic, flavonoid, or anthocyanin contents) or vitamin C have been mapped in peach. These antioxidant compounds are important and potentially beneficial to human health

because they are involved in the prevention of degenerative diseases such as hypertension, coronary heart diseases, Alzheimer's disease, stroke, and cancer (Boeing et al. 2012; Martin et al. 2013; Vizzotto et al. 2014).

To our knowledge, there is no peach breeding program that enhances antioxidant contents, despite the importance of healthy nutraceutical compounds from peach and other fruits (Wargovich et al. 2012). The peach breeding program at the Experimental Station of Aula Dei-CSIC has studied, over a period of 10 years, a nectarine population derived from a cross between 'Venus' and 'Big Top' cultivars. This progeny have been phenotyped for agronomic and fruit quality attributes over a period of 4 years. Moreover, this population has been genotyped with simple-sequence repeats (SSRs) and 'IPSC 9K peach SNP array v1' markers.

The main objective of this study was to identify genetic regions associated with the most important peach pomological traits using the 'Venus' × 'Big Top' mapping population. To achieve this goal, two genetic maps were constructed with IPSC 9K peach SNP array v1 and six SSR markers, and the obtained maps were previously compared with the peach physical map and anchored to the *Prunus* reference map T × E. A QTL analysis was performed using the maps and the phenotypic data obtained during the 4 years of evaluation (2007–2010). In this paper, we describe the identification of genomic regions that regulate the main fruit quality traits in peach using IPSC 9K peach SNP array v1. Quantitative trait loci for total phenolic, flavonoid, and anthocyanin contents are reported for the first time in this species.

Material and Methods

Plant material

The mapping population included 75 offspring of F_1 progeny from a cross between two diploid outbreed nectarine cultivars, with 'Venus' as the female parent and 'Big Top' as the male parent. Both cultivars are nectarines with red skin and yellow flesh. 'Venus' is freestone and acidic, whereas 'Big Top' is clingstone and sub-acidic. The progeny were established in the Aula Dei Experimental Station orchards in 2002 as described by Cantín et al. (2009b). One tree per genotype was grafted on GF 677 and grown under standard irrigation, fertilization, and pest control conditions. Winter pruning and spring thinning were conducted as in commercial orchards.

Agronomical and pomological evaluation

Over a period of 4 years (2007–2010), agronomic and pomological traits were measured in each seedling tree. Production (yield), fruit weight, flesh firmness, soluble solids concentration (SSC), pH, titratable acidity (TA) were evaluated for 3 years (2007, 2009 and 2010); relative antioxidant capacity (RAC), and contents of vitamin C, total phenolic, flavonoids, anthocyanins, and individual sugars were evaluated for 4 years as previously reported (Cantín et al. 2009b; 2010b; Abidi et al. 2011; 2015). For production, all fruits from each tree were harvested and weighed (Kg/tree). Then, a sub-sample of 20 fruits/tree was weighed to calculate the average fruit weight, which was used for subsequent analysis. Flesh firmness was measured in 10 fruits with a hand penetrometer. Five fruits were homogenized in a blender to determine SSC of juice with a temperature-compensated refractometer (model ATC-1, Atago Co., Tokyo, Japan), and pH and TA were measured with an automatic titration system (862 Compact Titrosampler, Metrohm, Herisau, Switzerland). Ripening index (RI) was calculated as the ratio of SSC to TA. For biochemical analyses, five arbitrarily selected fruits were peeled and cut in small cubes (~1 cm^3) to pool homogeneous sub-samples of 5 g-flesh, immediately frozen in liquid nitrogen and then stored at −20 °C until analysis. To preserve ascorbic acid, sub-samples were frozen with 5 mL of meta-phosphoric acid (5%) in liquid nitrogen and then stored at −20 °C. Then, samples were homogenized in a polytron for 2 min with 10 mL of extraction solution of 0.5 mol L^{-1} HCl in 800 mL L^{-1} methanol for phenolic content, 800 mL L^{-1} ethanol for sugar content, and 50 mL L^{-1} metaphosphoric for vitamin C and processed as previously described (Cantín et al. 2009b; Abidi et al. 2011). Vitamin C, total phenolic, flavonoid, and anthocyanin contents, and RAC were evaluated with colorimetric methods and measured using a spectrophotometer (Beckman Coulter DU 800, Beckman Coulter, Brea, CA, USA) as previously described (Abidi et al. 2011; 2015). For the sugar profile, sugar composition and quantification were analyzed by high-performance liquid chromatography as described by Cantín et al. (2009a) with some modifications as described in Abidi et al. (2011).

Statistical analysis

Descriptive statistics of all phenotypic data were calculated using SPSS® 22.0 (IBM®). Data were averaged and minimum and maximum values were identified. To evaluate

whether the data followed a normal distribution, a normality analysis by Kolmogorov-Smirnov and Shapiro-Wilk test was performed separately each year/trait. Histograms for each trait were constructed with all data set. Pearson's correlation coefficients among years were calculated for 2007, 2008, 2009 and 2010. The number of records, varied from year to year. Correlations among variables were performed with the mean value for all years. Since correlations between years for most of the traits were low or moderate, QTL analysis was carried out separately for each year. The Box-Cox transformation method was used for non-normally distributed traits to perform multiple QTL model (MQM)-QTL analysis.

Population genotyping and marker selection

For genotyping, total DNA was extracted from the young leaves of both parents, 'Venus' and 'Big Top', and each progeny using the DNeasy® Plant Mini Kit (QIAGEN Inc., Valencia, CA, USA) following the manufacturer's instructions. DNA concentration and quality was checked using PicoGreen® dye and measured in a fluorospectrometer. Then, all samples were genotyped using IPSC 9K peach SNP array v1, which includes 8,144 SNP markers (Verde et al. 2012), using the single-base extension assay (Steemers et al. 2006) and Illumina® Infinium® HD Assay Ultra protocol (Illumina, San Diego, CA, USA). The analysis was conducted by the Endocrinology Laboratory Service at "Hospital Clínico Universitario de Valencia".

For mapping, we also selected genotypic data of six SSR markers previously evaluated in the same progeny (BPPCT025, BPPCT033, BINEPPCU6377, pchcms5, UCDCH15, and UDP98-024) (Cantín et al. 2010a; Abidi et al. 2012).

Self-pollinated seedlings were identified using homozygous SNP markers with different alleles in both parents. Seedlings with the same genotype as the female parent were excluded from further analysis.

Markers with missing data (in one or both parents), non-polymorphic, redundant, or deviated from the expected segregation proportion were excluded. When markers had the same segregation pattern, only one marker was included to improve computational algorithm efficiency (Van Ooijen 1992).

For the segregation deviation test, a Chi-square test was performed with $p = 0.05$ as the threshold (Zeballos et al. 2015). In a second round, the markers were adjusted to a 1:1 segregation ratio with a $p = 0.005$ threshold.

Map construction

JoinMap®4 software (Van Ooijen 2006) was used to construct the linkage maps as a cross-pollinated population, following the software manual instructions. To use the double pseudo-test cross strategy (Grattapaglia and Sederoff 1994), the option "Create maternal and paternal population nodes*"* command in JoinMap was used. Two mapping rounds were performed.

A preliminary number of groups and linkage groups (LGs) were established using the recombination fraction criterion (see details in Zeballos et al. 2015). A second mapping round was performed with the selected SNPs by including the SSR markers, the order of markers in each LG was established using the maximum likelihood mapping option, and map distances were calculated using Kosambi's mapping function. Further details regarding genetic map construction can be found in Zeballos (2012).

QTL analysis

QTL analysis was carried out using R/qtl (v1.22-21) software with the Single-QTL-Model (SQM) or Multiple-QTL-Model (MQM) procedures using the R platform (Broman et al. 2003). Single regression (Haley-Knott) was conducted for non-normalized (non-transformed) traits (pH, TA, RI, Firmness 2007 and Glucose 2009). QTL analyses were performed for each trait separately for each year and with the overall mean (2007–2010). The likelihood of the presence of a QTL was expressed as a log of odds (LOD) score. LOD significance thresholds were determined with the permutation test procedure; option settings included 1,000 permutations, and significance was set to $p = 0.05$. When the LOD score exceeded the significance threshold somewhere along an LG, a segregating QTL was declared. For the confidence interval, we used the "bayesint command" in R/qtl with $p = 0.90$ and $p = 0.95$ for outer and inner interval bounds, respectively (Broman and Saunak 2009). Graphical representation of QTLs on maps was generated with MapChart® v2.2 software (Voorrips 2002).

A multiyear QTL analysis was carried out using QTLNetwork-2.1 software (http://ibi.zju.edu.cn/software/qtlnetwork/) to explore environmental effects and increase accuracy for QTL detection (Yang et al 2008).

Results

Phenotyping

Six out of the 75 initial seedlings of the 'Venus' × 'Big Top' progeny were identified as self-pollinating. With the SNP markers, a new genotype was identified in addition to the five previously reported as self-pollinated in the same population (Cantín et al. 2010a). Results for the pomological traits evaluated over 4 years (2007–2010) in the remaining seedlings are summarized in Table 1. Wide phenotypic variation was found for most of the traits studied in this progeny (Abidi et al. 2011; Zeballos et al. 2015), which supports the quantitative nature of these traits. Distribution of the traits has been reported as Supplementary Fig. 1. Pearson's correlations between years and traits are summarized in Supplementary Tables 1 and 2. Significant correlations were found in years 2007, 2009 and 2010, high for yield, fruit weight, pH, TA, and RI, and moderate for firmness and SSC. Pearson's coefficients were significant in 2007, 2008 and 2009 for glucose, sorbitol and fructose. The lower correlation values were found for antioxidants in 2007 and sugars (except sorbitol) in 2010, respectively. The evaluated traits showed significant and high correlations for SSC and sugars (total sugars, sucrose, glucose, sorbitol and fructose). Titratable acidity and pH were highly negatively correlated (r=-0.804). The higher Pearson's correlations were between total sugars and sucrose (r=0.910) and total phenolics and flavonoids (r=0.828).

Marker screening and linkage mapping

Out of the 8,144 SNPs, 5,323 were non-polymorphic (43 had missing data for either parent and 5,280 were homozygous in both parents), 1,808 showed the same segregation pattern, and 338 presented a distorted segregation. Finally, a total of 675 SNPs were informative, with GenTrain scores that ranged from 0.35 to 0.92; of these, 270 SNPs were heterozygous in both parents and therefore discarded from analysis because they were not suitable for this mapping strategy. The final number of selected markers was 405; 223 used for the 'Venus' map and 182 for the 'Big Top' map. Two preliminary dense genetic maps were constructed for 'Venus' and 'Big Top' with 160 and 208 markers, respectively, found on 11 LGs (Zeballos et al. 2015). Final LG assignment was performed after comparison with the peach genome v1.0 physical map

(GDR, 2015), and markers with identical segregation patterns that were previously excluded were included for the next step (Zeballos 2012). This information was updated with the peach genome v2.0 physical map (Phytozome v11.0, https://phytozome.jgi.doe.gov/pz/portal.html), see Supplementary Table 3).

Genetic linkage map of the 'Venus' parent

The second mapping round included 102 SNPs and five SSRs (BPPCT025, BINEPPCU6377, pchcms5, UCDCH15, and UDP98-024). The resulting map grouped 99 SNPs (the remaining three markers were not linked) and five SSRs in nine LGs that spanned 259.9 cM (Fig. 1).The length of the LGs ranged from 1.47 cM to 85.7 cM, with an average distance between adjacent markers of 2.49 cM. Seven scaffolds were represented in this map (1, 2, 3, 4, 6, 7, and 8). Scaffolds 1 and 2 were split into two LGs, and scaffold 5 was not represented in the female parent map. The marker SNP_IGA_536394 was correctly mapped on LG V6 (Fig. 1) as it was assigned in Peach v2.0 (Pp06, in bold in Supplementary Table 3).

Genetic linkage map of the 'Big Top' parent

After establishing the most suitable order of markers, the second mapping round placed 122 SNPs and one SSR (BPPCT033) on 10 LGs (Fig. 2). The map spanned 464.3 cM, the length of LGs ranged from 1.47 cM to 85.4 cM, and the average distance between adjacent markers was 3.8 cM. Nine scaffolds were represented in this map (1, 2, 3, 4, 5, 6, 7, 8, and 13). Scaffolds 1 and 6 were split into two LGs. The marker SNP_IGA_430365 was mapped on LG B7 in contrast with the position assigned on the physical map (scaffold 4 and Pp03, in bold in Supplementary Table 3). The other marker apparently mapped in different scaffold, SNP_IGA_913769 on LG B3 was positioned in chromosome Pp03 in the Peach physical genome v2.0 (in bold in Supplementary Table 3).

QTL analysis

Using the SQM and MQM methods, at least one QTL was found for 16 out of 17 traits evaluated. No significant QTL was found for vitamin C, although on LG V4, two QTLs that did not overcome the threshold explained more than 10% of the phenotypic variance (11.5 and 12.8%, respectively). The list of QTLs with their magnitude of impact across years is presented in Table 2. Analyzing the data by year, 54 QTLs were

detected and mapped over 12 LGs that represented seven scaffolds (Fig. 3 and Fig. 4). The portion of phenotypic variance explained by each significant QTL ranged between 7.7 and 85.3% of the total variance (Table 2). When using the multi-year approach QTLs were detected for all traits except for flavonoids (Table 2). For the multi-year analysis, the explained variation was between 0.9 and 71.1%. The fraction of the variation explained for the environmental interaction (VGE) ranged from 0.1 to 12.0% . VGE were below 6% except for Firmness (12%) and Anthocyanin content (8%).

In both parental maps, QTLs were found for fruit weight; firmness; SSC; total sugar, sucrose, sorbitol, fructose, total phenolic and flavonoid contents; and RAC (Table 2). Production (yield, Kg/tree), and glucose content were mapped only onto the 'Venus' map (Table 2 and Fig. 3), whereas QTLs for pH, TA, RI, and anthocyanin content were only mapped onto the 'Big Top' map (Table 2 and Fig. 4). QTLs detected for fruit weight, pH, TA, RI, and sorbitol content explained more than 50% of the variance, and had LOD scores values up to 18.0, 28.0, 27.6, 21.6, and 22.2, respectively (Table 2). The number of QTLs found over each LG in the different years of evaluation varied between one and 20. In the 'Venus' map (Table 2 and Fig. 3), LGs V1_1, V2_1, V3, V7, and V8 had only one QTL, LG V2_2 had four, and LG V4 had 19 QTLs. In the 'Big Top' map (Table 2 and Fig. 4), LGs B1_2 and B4 had only one QTL, LGs B2 and B8 had two, and LG B5 had 20 QTLs that controlled different traits.

With regard to the QTLs identified based on mean value (not shown in Fig. 3 and Fig. 4), most of the traits were consistently significant over time (Table 2, Supplementary Table 4). For example, for fruit weight, QTLs identified on LG V4 in the yearly analysis were in the same region as QTLs detected with the mean or multi-year analysis. Similar situations were observed in QTLs for firmness, SSC, and for sorbitol content, which were mapped in the same position on LG V4 (Table 2, Supplementary Table 4). On LG B5, QTLs for the traits pH; TA; RI; and sucrose, and anthocyanin contents were mapped at the same position as the mean and the multi-year analysis (Table 2). Some QTLs, such as those for glucose and flavonoid contents, did not appear when using mean value, even though they were identified in analysis across multiple years. However, some QTLs were mapped based only on the mean value such as for production, and total phenolic content (qPDR.V-Ch3-Mean and qPHE.V-Ch4-Mean, respectively), or only detected by the multi-year analysis (qPDR.V-Ch1_2- MYear, qPDR.V-Ch4- MYear, qGLU.BT-Ch3-MYear, and qFRU.BT-Ch8- MYear).

We identified a region on LG V8 with two QTLs that are potentially involved in production; the LOD score, additive effect, and proportion of phenotypic variance explained by qPDR.V-Ch8-2010 and qPDR.V-Ch8-Mean confirm the genetic control of this region on yield. Furthermore, three QTLs for fruit weight on LG V4 (qFW.V-Ch4-2007, 2009 and 2010) identified across 3 years (Table 2, Fig. 3, and Supplementary Table 4) were found in the same region as the mean, also confirmed with the multiyear analysis, which supports the presence of QTLs influencing fruit weight in both regions (at 46 cM and 60 cM). In addition, on LG B8, one QTL for fruit weight (qFW.BT-Ch8-2010) was also identified in 2010, and another QTL was observed using the mean value (qFW.BT-Ch8-Mean), also identified with the multi-year analysis (qFW.BT-Ch8-MYear).

For firmness, we identified two QTLs on LG V4 and two other QTLs on LG B5. The first region (qFF.V-Ch4-2007 and 2009) was on LG V4 had QTLs within an 8-cM interval (Table 2). The QTLs mapped on LG B5 (qFF.BT-Ch5-2009 and 2010) were 9 cM apart, but the position was confirmed with the QTLs detected using the mean value (qFF.BT-Ch5-Mean, 12 cM) and with the multiyear analysis (qFF.BT-Ch5-MYear, 10.9 cM). Furthermore, eight QTLs were detected and mapped for SSC across different years; five (qSSC.V-Ch4-2007a, 2007b, 2009a, 2009b, and 2010) were on LG V4, one (qSSC.V-Ch2_2-2009) on LG V2_2, and two (qSSC.BT-Ch5-2009 and 2010) on LG B5 (Table 2 and Fig. 3). On LG V4, two different regions (at 29–32 and 44 cM) were simultaneously repeated in 2007 and 2009, which indicates the presence of two different QTLs. Only the second position was confirmed with the mean value and the multi-year analysis (Table 2). On LG B5, two QTLs (qSSC.BT-Ch5-2009 and 2010) were detected, and the QTL with the mean value (qSSC.BT-Ch5-Mean) and the multi-year analysis (qSSC.BT-Ch5-MYear) were in the middle.

QTLs for pH, TA, and RI (SSC/TA) were exclusively mapped over LG B5 and around the same region. The proportions of phenotypic variances explained by these QTLs varied from 42.4 to 85.3%. QTLs for pH (qpH.BT-Ch5-2007, 2009, 2010) were located at the same genomic region across 3 years, and the same position was detected with the mean pH value (Table 2, Supplementary 4) and the multi-year analysis. TA was mapped on LG B5 at 2-3 cM across 3 years and with the mean (qTA.BT-Ch5-2007, 2009, 2010, and Mean). However, two positions were detected with the multiyear analysis (qTA.BT-Ch5-MYear-a and b at 2.9 and 53.7 cM). RI was not previously mapped on any peach

map, and because this trait is a function of SSC and TA, it is correlated with both traits. Three QTLs were found on LG B5 during 3 years (2007, 2009, and 2010), and the QTL in 2009 (qTA.BT-Ch5-2009) was repeatedly observed using the mean value (qTA.BT-Ch5-Mean) and with the multi-year analysis (qTA.BT-Ch5-MYear).

QTLs for total sugar, sucrose, glucose, sorbitol, and fructose contents were mainly found in LGs V4 and B5 (Table 2, Fig. 3 and Fig. 4). These QTLs were mapped at short distance intervals for each trait. In addition, some QTLs detected with the mean value were placed at the same or very close positions as other QTLs detected across years and with the multi-year analysis (Table 2). Remarkably, high LOD scores were obtained for qSOR.V-Ch4-2007, and 2009 (12.9 and 18.6, respectively), and the high values of phenotypic variances were explained by the nearest markers (51.2, and 57.7, respectively).

The QTLs identified for phenolic compounds were mainly on LGs B2, V2_2, V4, and B5. QTLs for total phenolic and flavonoid contents were found in both parents and distributed on different LGs, and none of them were repeated over the years studied (Table 2). Alternatively, QTLs for anthocyanin content were identified at the same position on LG B5 for 2 years with the mean value also validated with the multi-year analysis (Table 2 and Fig. 4). The QTLs detected for RAC on LGs V4, were validated with the multi-year analysis.

Discussion

Genetic maps

This work presents the first genetic map of the nectarine population ‘Venus’ × ‘Big Top’ with ‘IPSC 9K peach SNP array v1’. Two preliminary studies carried out in the same population mapped 17 SSR markers on LG4 (Cantín et al. 2010a) and six on LG6 (Abidi et al. 2012). In the present map, LG4 includes a total of 36 markers, with 26 and 10 markers in the ‘Venus’ and ‘Big Top’ maps, respectively. LG6 included a total of 39 markers, with 21 markers in the ‘Venus’ map and 18 markers distributed in two LGs in the ‘Big Top’ map. SNPs allow increased saturation and genome coverage and therefore provide higher precision and accuracy for QTL dissection in this population, as was found in other *Prunus* progenies (Eduardo et al. 2013; Martínez-García et al. 2013b; Da Silva-Linge et al. 2015).

Both genetic maps had more than eight LGs, which is the expected number of chromosomes in *Prunus persica*. Scaffolds 1 and 2 in the 'Venus' map and scaffolds 1 and 6 in the 'Big Top' map were split into two LGs. The absence of linkage between markers that belong to the same chromosome is common in genetic mapping (Chaparro et al. 1994; Dirlewanger et al. 1998; Zhebentyayeva et al. 2008; Eduardo et al. 2013). To our knowledge, this is the sixth full map produced with the 'IPSC 9K peach SNP array v1' in peach, although others have been constructed with this array technology in other *Prunus*-derived progenies (Eduardo et al. 2013; Yang et al. 2013; Martínez-García et al. 2013a; Frett et al. 2014; Pacheco et al. 2014; Romeu et al. 2014; Da Silva-Linge et al. 2015; Nuñez-Lillo et al. 2015). The length of genetic linkage maps mostly based on SNP markers were more saturated compared with the previously published maps, with the exception of the T × E *Prunus* reference map (Dirlewanger et al. 2006). In our population, 104 SNPs were mapped in 'Venus' and 122 in 'Big Top', which spanned 259 cM in the 'Venus' map and 464 cM in the 'Big Top' map. Other maps have been developed using 'IPSC 9K peach SNP array v1' in different F1 populations. Eduardo et al. (2013) analyzed 'Bolero' × 'OroA' progeny and obtained two maps with 231 and 87 markers in nine and five LGs, which span 405 and 228.5 cM, for the 'Bolero' and 'OroA' maps, respectively. Romeu et al. (2014) found less saturation on 'V6' and 'Granada' maps (178 SNPs and 76 SNPs that span 480 and 276 cM, representing 2.94 and 3.87 cM/marker, respectively). Furthermore, two dense maps constructed with other SNP markers in peach- and peach-almond-derived progenies spanned 422 and 369 cM, respectively (Martínez-García et al. 2013b). The average marker density in the previously mentioned maps was similar and comparable to our results, although in some cases the genome was not entirely covered (Romeu et al. 2014; Sánchez et al. 2014). Scaffolds 1, 2, and 6 with unsaturated regions explain the absence of linkage (Fig, 1) and why two LGs were found on one chromosome. Scaffold 1 split into two LGs in both parents, scaffold 2 was in the 'Venus' map, and scaffold 6 was in the 'Big Top' map. Different authors revealed unsaturated regions in scaffolds 1, 2, 4, and 5 (Frett et al. 2014), and 4, 5, 7, and 8 (Sánchez et al. 2015). Moreover, Sánchez et al. (2014) found that chromosomes 2, 1, and 3 were missing in a pseudo-test cross population between the cultivars 'MxR_01' and 'Granada'. The lack of polymorphic SNPs in certain chromosomes is caused by homozygosis in the peach genome and is probably due to germplasm background (Romeu et al. 2014; Sánchez et al. 2014; Nuñez-Lillo et

al. 2015). Verde et al. (2012) evaluated and validated the SNP array and reported common gaps in chromosomes 1, 2, and 5. These unsaturated sections may represent putative centromeric regions that would explain these events. Anchoring to the reference genome sequence (Verde et al. 2013), the putative order of the SNPs in our map was initially established in Mbp by comparison with the physical map v1.0. Although assembly and orientation mistakes have been somehow accumulated in the sequence genome, in general marker order in our maps was in agreement with peach genome sequence v1.0 (Supplementary Table 3). In this work, three markers unexpectedly occurred on different LGs compared with the putative order established in the array: SNP_IGA_536394 on LG V6, SNP_IGA_430365 on LG B7, and SNP_IGA_913769 on LG B3. Nevertheless by comparison with the physical map v2.0, all markers were reassigned to their correct chromosome except SNP_IGA_430365 that was positioned on chromosome Pp03 (Supplementary Table 3). The new position on LG B3 for SNP_IGA_913769, which was physically located in scaffold 13 on peach genome v1.0, was confirmed with genome assembly v2.0. As a conclusion, the refinements included in the updated peach genome version v2.0 have confirmed chromosome positions determined in our genetic maps.

Other changes related to the putative order of the SNPs were corrected by comparison with the peach physical map v2.0 (one inversion on LG B1_1 and order for B7 and B8) (see Supplementary Table 3). Moreover, we confirmed a new orientation for chromosomes 2 and 7 by comparing mapped markers on B2 and B7 chromosomes with their positions in the peach physical map v2.0. It is expected to correct the changes described in peach populations mapped with the same SNP array and methodology (Eduardo et al. 2013; Romeu et al. 2014; Sánchez et al. 2014; Da Silva-Linge et al. 2015). As it was previously mentioned pseudomolecule 2 was wrongly mapped in T × E (Verde et al. 2013), and inversions and translocations have been commonly described on chromosomes, LG1, LG2, LG4, LG7, and LG8 (Eduardo et a. 2013; Martínez-García et al. 2013b; Da Silva-Linge et al. 2015). Finally, lack of markers on V5 may be due to identity by descent or ascertainment biases in the SNP markers represented in the array (Nielsen et al. 2004; Albrechtsen et al. 2010), as discussed by Eduardo et al. (2013). However, other specific characteristic of the population, such as size, genetic background, or any other unknown particularity may be affected.

QTL analysis

Based on the results in our population, even though the progeny size is limited, we identified important regions in the peach genome that control fruit quality traits. Many of the QTLs detected in our progeny were previously found in other peach mapping populations. However, we described 16 QTLs that control peach fruit quality traits for the first time (one for production, fruit weight, firmness and total sugar and sucrose contents; two for total phenolic anthocyanin contents, and RAC; and five for flavonoid content). Five of them were validated with the multi-year approach.

The precision of phenotypic evaluation is very important for accurate QTL mapping. A reliable QTL map can only be produced from reliable phenotypic data. Replicated phenotypic evaluations during different years improve the accuracy of QTL mapping by reducing experimental error and background noise (Salazar et al. 2013). Most of the QTLs found in our study were consistent for at least 2 years and were detected also with the multi-year analysis, although others were not repeated across all 4 years of study. The multi-year approach allowed the detection of QTLs that were not considered significant by doing single-year analysis (Dirlewanger et al. 2012). The characteristics of these QTLs are included in Table 2 and Supplementary Table 4. Variation in QTL position over time is commonly found in QTL analysis, and similar performance, including non-repetitiveness of QTLs across different years, different locations found in yearly analyses, and detection with the mean value, as reported by other authors for peach and other *Prunus* species (Dirlewanger et al. 1999; Etienne et al. 2002; Verde et al. 2002; Quilot et al. 2004; Eduardo et al. 2011; Dirlewanger et al. 2012; Salazar et al. 2013).

The QTL that controls peach production found on LG V8 is reported for the first time. No other authors have evaluated this trait as yield in terms of Kg/tree, although Dirlewanger et al. (1999) reported a QTL on LG6 for productivity (number of fruits per tree), which is a somewhat related trait in terms of overall productivity. However, from an agronomical point of view, these are separate traits. A remote possibility exists that these QTLs could be related to a translocation between LG6 and LG8, as was reported in the F_2 'Garfi' × 'Nemared' population (Jáuregui et al. 2001). For fruit weight, as we found in the 'Venus' × 'Big Top' population, some authors have identified QTLs on LG1, LG2, LG4, and LG6 in other mapping populations in peach (Quilot et al. 2004;

Eduardo et al. 2011; Fresnedo-Ramírez et al. 2015). However, newly discovered QTLs that control peach fruit weight were reported for the first time on LG7 (Da Silva-Linge et al. 2015), LG5 (Fresnedo-Ramírez et al. 2015) and LG8 (qFW.BT-Ch8-2010). The QTLs qFW.V-Ch4-2009 and 2010 for fruit weight found on LG V4 were located on the same genomic region across multiple years, with the nearest marker at 45 cM. This indicates the presence of a single QTL on LG V4 for this trait also confirmed with the mean and the multi-year analysis. The QTL qFW.V-Ch4-2007 (60 cM) was also confirmed with the multi-year analysis (62.1 cM). The other QTL, located on B8, had a high LOD score and explained an important part of the variation, which was only detected in 2010 (25 cM) but partially confirmed with the mean (9 cM) and the multiyear analysis (16 cM). The low saturation in this region of the chromosome is one possible explanation for these results.

The QTLs for firmness on LG V4 (qFF.V-Ch4-2007 and 2009) and LG B5 (qFF.BT-Ch5-2009 and 2010) potentially represent two single QTLs that were validated with the mean (qFF.V-Ch4-Mean) and multi-year analysis (qFF.V-Ch4-MYear; qFF.BT-Ch5-MYear). The QTLs found for firmness on LG V4 (qFF.V-Ch4-2009 and mean) were previously reported by Cantín et al. (2010a) in the same population. Furthermore, for SSC, we found different genomic regions on LG4, as other authors have previously identified in peach (Abbott et al. 1998; Dirlewanger et al. 1999; Quarta et al. 2000; Etienne et al. 2002; Quilot et al. 2004; Cantín et al. 2010a; Eduardo et al. 2011; Sánchez et al. 2014). Cantín et al. (2010a) found a QTL for SSC on LG4 that explained more than 80% of the total variation using SSR markers and composite interval mapping for QTL mapping in this population. Two QTLs on LG4 could explain the variation in total SSC. The first region (qSSC.V-Ch4-2007a, 2009a) explained less than 19% of phenotypic variance, and the second (qSSC.V-Ch4-2007b, 2009b, and 2010) explained 28.0, 27.6, and 21.4% of the total variance, respectively. The second region was confirmed with the mean value at 44 cM and validated at the same position with the multi-year analysis. Other genomic regions that control SSC on LG V2_2 (qSSC.V-Ch2_2-2009) and LG B5 (qSSC.BT-Ch5-2009 and 2010) were also reported in other populations and were found on LG2 in peach (Verde et al. 2002; Quilot et al. 2004; Eduardo et al. 2011) and LG5 in peach (Quilot et al. 2004) and apricot (Salazar et al. 2013) and both LGs in peach and *Prunus* related progenies (Fresnedo-Ramírez et al. 2015). Many QTLs have been previously described for SSC because it is one of the

most widely studied traits; SSC is used as a standard universal method to define quality in fruits and it is a quick and simple evaluation method.

Other major QTLs that control pH and TA were found only on in the 'Big Top' map on LG5. The additive effect and proportion of total variance explained by these QTLs (up to 85%) revealed which regions control these traits. Moreover, these QTLs had a consistent position relative to the *D* gene, which controls lack of acidity in fruit (Abbott et al. 1998; Dirlewanger et al. 1998; 2004). For TA, other authors mapped QTLs in the proximal part of LG5 (Dirlewanger et al. 1999; Etienne et al. 2002), as was found on the 'Big Top' map (qTA.BT-Ch5-2007, 2009 and 2010). Another position at 53.7 cM was also detected in our population with the multi-year analysis (qTA.BT-Ch5-MYear). Quilot et al. (2004) identified a QTL associated with TA at 52 cM on LG5 when mapping two interspecific populations. These positions are also consistent with markers developed for sub-acidic traits in peach (Eduardo et al. 2014) and with the co-localization of QTLs for TA and pH on LG5 (Fresnedo-Ramírez et al. 2015). On the contrary, any equivalent QTL on LG5 was found in apricot for malic acid (which is synonymous with TA) and pH (Salazar et al. 2013), even in peach (Eduardo et al. 2011). The position of the QTLs found for RI (SSC/TA) indicates that TA has more influence than SSC in the genetic control of this trait, because the QTLs were in the same position as acidity (TA) (Table 2). This fact was also confirmed with the significant correlations found between these traits (Supplementary Table 2).

Some of the QTLs that control total sugar content, which explain more than 15% of phenotypic variance, were detected across 2009 and 2010 and were mapped on LG2, LG4 and LG5. QTLs for this trait were previously described on LG2 (Quarta et al. 2000; Quilot et al. 2004) and LG5 (Quilot et al 2004) but never on LG4. However, in this study only the region that controls total sugar content on LG5 was repeated with the mean and validated with the multi-year approach.

For sucrose content, the QTL detected on LG B5 (qSUC.BT-Ch5-2007) was consistent with the QTLs found with the mean and the multi-year analysis (Table 2, Supplementary Table 4, and Fig. 4), which indicates the presence of a major QTL that controls this trait. QTLs for sucrose were previously described on LG3, LG5, LG6, and LG7 (Dirlewanger et al. 1999; Etienne et al. 2002; Quilot et al. 2004). LG4 was not previously reported to control sucrose content in peach. In addition, the QTLs that control glucose and fructose contents found on LG V4 at 48 cM were consistent with

the QTLs found at the same position with the multi-year analysis. The LOD scores and percent of total variance found also indicate the existence of a major QTL that controls glucose and fructose contents on LG4 as previously detected in other peach mapping populations (Abbott et al. 1998; Dirlewanger et al. 1999; Etienne et al. 2002; Quilot et al. 2004). The QTLs found for fructose content were also previously reported by various authors on LG5 (Abbott et al. 1998; Dirlewanger et al. 1999), and on LG1 and LG2 (Quilot et al. 2004).

The four QTLs that control sorbitol content were in a cluster located on LG 4 between 45 and 54 cM in the map. The high LOD scores and total phenotypic variance explained by these QTLs across the 4 years indicates the presence of a major QTL on LG4 that controls sorbitol content also consistent with the mean and the multi-year approach. QTLs for sorbitol were previously described on LG2, LG4, and LG5 (Dirlewanger et al. 1999; Quilot et al. 2004), however, any QTL on LG2 was found in this study.

Finally, QTLs for total phenolic and flavonoid contents were mapped on LG2 in both parental maps. The proximity of the nearest assigned markers indicates that a single QTL on LG2 controls phenolic content. It is very well known that flavonoids are highly correlated with phenolic content (r=0.828; Supplementary Table 2) because flavonoids belong to this family (Cantín et al. 2009b; Abidi et al. 2011; Font i Forcada et al. 2013). The observation that QTLs of RAC, total phenolics, and flavonoid contents reside at the same position on LG4 indicates that most RAC activity is related to flavonoid content (r=0.761; Supplementary Table 2), as was previously reported (Cantín et al. 2009b; Abidi et al. 2011; Font i Forcada et al. 2013). Other QTLs for antioxidant compounds were found on other LGs (V3, V7, B5 and B8). Only QTLs that control anthocyanin content were consistent over 2 years on LG B5, and confirmed with the mean and validated with the multi-year approach.

Considering the synteny between *Prunus* and *Malus* (Dirlewanger et al. 2004; Arús et al. 2012), in our progeny, the QTLs detected that control phenolic content were not located in the same genomic regions as in apple (Chagné et al. 2012, Verdu et al. 2014). Chagné et al. (2012) found QTLs for flavonoid and anthocyanin contents on LG16 (syntenic with LG6 and part of LG1 in *Prunus*), anthocyanin content on LG9, and phenolic content on LG17 (both syntenic with LG3) and LG15 (syntenic with part of LG1). Other positions have been found in cider apples for anthocyanin content on LG5 (syntenic with LG4) and flavonoid content on LG15 and LG17 (part of LG1 and LG3 in

Prunus, respectively). All of these data indicate that the genomic regions that control polyphenols in the Rosaceae family are not entirely conserved.
Our results provide the first insights into the genetic control of total phenolic content in peach. Mapping of QTLs for polyphenolic content provides important knowledge for future studies to develop new cultivars with increased antioxidant properties.

Conclusions

We report, for the first time, the identification of QTLs for fruit quality traits in 'Venus' × 'Big Top' progeny using 'IPSC 9K peach SNP array v1', which was developed by Illumina. We detected 54 QTLs that represent 34 genomic regions across 4 years of evaluation using the SQM and MQM mapping strategies. We found new and stable QTLs for fruit weight, firmness, total phenolic and anthocyanin contents, and relative antioxidant capacity in peach. LGs V4 in 'Venus' and B5 in 'Big Top' contained the most important genomic regions that control fruit quality traits in peach. The co-localization and clustering of the majority of the detected QTLs might indicate that these genes are tightly linked. In some cases, pleiotropic effects may occur. Furthermore, the multi-year approach helped to confirm and detect minor QTLs or QTLs from traits potentially affected by climatic conditions.
The results presented in this work enhance the existing maps developed with the same SNP array and open the possibility of using marker-assisted selection to improve fruit quality in peach. Further studies must be carried out to validate the QTLs revealed here to identify new candidate genes in peach. Moreover, these data will facilitate the development of new peach cultivars that bear fruit with increased concentrations of polyphenolic compounds that benefit human health.

Acknowledgments

We are grateful to C.H. Crisosto (University of California, Davis) for providing SSR markers (UCDCH15 and BINEPPCU6377). We thank E. Sierra and S. Segura for technical assistance and plant management in the field and N. Ksouri for bioinformatic assistance. We are grateful to A. Casas and E. Igartua for assistance and support with the statistical analysis using JoinMap®4 software. This study was funded by the Spanish Ministry of Economy and Competitiveness (MINECO) grants AGL-2008-00283, AGL2011-24576, and AGL2014-52063-R and co-funded by FEDER and the Regional Government of Aragón (A44) with European Social Fund. W. Abidi was supported by a JAE-Pre fellowship from Consejo Superior de

Investigaciones Científicas (CSIC), which enabled him to visit the University of California, Davis, and IBMCP-Valencia Spain. J.L. Zeballos received a Master fellow funded by the Spanish Agency for International Cooperation and Development (AECID).

Data archiving statement

V × BT linkage maps and QTL positions are available on Genome Database for Rosaceae at tfGDR1025 accession number.

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Tables and figures

Table 1 Units, minimum, maximum and mean values for the pomological traits evaluated in the 'Venus' × 'Big Top' progeny during four years (2007-2010) (partially presented in Zeballos et al. 2015). Data are mean ± SE (n=198-257)

Trait	Units	Min	Max	Mean	S.E.
Production/yield	kg/tree	0.83	19.70	7.09	± 0.29
Fruit weight (FW)	g	69.44	375.87	185.22	± 3.30
Firmness	Newton	6.23	60.76	40.78	± 0.68
Soluble Solids Concentration (SSC)	ºBrix (g SS/100 g FW)	9.20	20.20	13.36	± 0.13
pH	pH units	3.00	4.40	3.68	± 0.02
Titratable Acidity (TA)	g malic acid /100 g FW	0.24	1.52	0.64	± 0.02
Ripening Index (RI: SSC/TA)	g SS/g malic acid	7.55	66.98	25.60	± 0.84
Total sugars	g/kg FW	45.35	160.34	86.85	± 1.14
Sucrose	g/kg FW	23.16	109.79	57.18	± 0.90
Glucose	g/kg FW	6.58	24.00	11.58	± 0.20
Sorbitol	g/kg FW	1.00	18.79	5.83	± 0.25
Fructose	g/kg FW	7.43	21.53	12.07	± 0.17
Vitamin C	mg AsA/100 g FW	1.17	12.11	4.10	± 0.13
Total phenolics	mg GAE/100 g FW	12.10	58.85	32.32	± 0.87
Flavonoids	mg CE/100 g FW	1.58	60.13	12.69	± 0.61
Anthocyanins	mg C3GE/kg FW	0.32	25.72	3.14	± 0.21
Relative Antioxidant Capacity (RAC)	mg TE/kg FW	125.31	1099.59	447.87	± 11.26

Abbreviations: AsA ascorbic acid, *GAE* gallic acid equivalents, *CE* catechin equivalents, *C3GE* cyanidin-3-glucoside equivalents, *TE* trolox equivalents, *Min* minimum value, *Max* maximum value, *S.E.* standard error.

Table 2 QTLs found for agronomic and fruit quality traits detected in the 'Venus' x 'Big Top' progeny.

Trait, QTL name and QTL code, position, LOD score, Threshold, Genetic variance and effects of the QTLs detected, and position of the nearest SNP marker. Genetic Variance (VG)= Fraction of the total variation explained by the QTL, a= Additive effect. Dist= marker position on the genetic linkage map. Abbreviations: RAC=Relative Antioxidant Capacity, RI=Ripening Index, SSC=Soluble Solids Concentration, TA=Titratable Acidity. See Table 1 for units. QTLs from multi-year analysis colored in gray: Genetic environmental interaction (VGE)= Fraction of the total variation explained by the genetic environmental interaction and marker ranges.

Trait	QTL name	QTL code	cM	LOD score	Threshold	VG (%)	VGE (%)	Additive effect (a)	Flanking Markers	Dist cM
Production	qPRD.V-Ch1_2-MYear		11.6			8.0	0.6	1.03	SNP_IGA_22603-SNP_IGA_24260	
	qPRD.V-Ch3-Mean	PRD X-b	9	3.34	2.13	16.3		2.46	SNP_IGA_308290	8.87
	qPRD.V-Ch3-MYear		14.3			8.6	0.3	-1.00	SNP_IGA_317404-SNP_IGA_319280	
	qPRD.V-Ch4-MYear		24,4			10.1	0.4	-1.06	SNP_IGA_389984-Pp17Cl	
	qPRD.V-Ch8-2010	PRD 10	13	2.90	2.14	17.0		2.62	SNP_IGA_841298	13.19
	qPRD.V-Ch8-Mean	PRD X-a	24	3.74	2.13	18.1		2.62	SNP_IGA_862321	23.96
Fruit weight	qFW.V-Ch1_1-2010	FW 10-c	20	2.66	2.00	7.7		30.28	SNP_IGA_121534	19.64
	qFW.V-Ch4-2007	FW 07	60	3.97	2.10	22.1		39.21	SNP_IGA_525520	59.11
	qFW.V-Ch4-2009	FW 09	46	7.54	2.08	34.9		42.53	SNP_IGA_408981	45.50
	qFW.V-Ch4-2010	FW 10-a	47	17.97	2.00	50.1		68.15	SNP_IGA_408981	45.50
	qFW.V-Ch4-Mean	FW X-a	46	17.38	2.13	54.7		49.50	SNP_IGA_408981	45.50
	qFW.V-Ch4-MYear		46.5			33.6	3.2	-16.36	SNP_IGA_408981-SNP_IGA_437516	
	qFW.V-Ch4-MYear		62.1			29.9	1.5	-10.67	SNP_IGA_5558633-SNP_IGA_467302	
	qFW.BT-Ch8-2010	FW 10-b	25	3.45	2.19	19.9		40.81	SNP_IGA_835981	31.76
	qFW.BT-Ch8-Mean	FW X-b	9	3.07	2.21	15.3		28.90	BPPCT033	0.00
	qFW.BT-Ch8-MYear		16.0			11.6	2.0	16.80	BPPCT033-SNP_IGA_835981	
Firmness	qFF.V-Ch4-2007	FIR 07	48	8.37	2.33	43.2		12.95	SNP_IGA_408981	45.50
	qFF.V-Ch4-2009	FIR 09-a	55	3.37	2.12	19.5		5.89	SNP_IGA_440110	54.65
	qFF.V-Ch4-Mean	FIR X-a	54	8.70	2.15	37.2		6.59	SNP_IGA_440110	54.65
	qFF.V-Ch4-MYear		48.5			18.3	12.0	-3.28	SNP_IGA_408981-SNP_IGA_437516	
	qFF.BT-Ch5-2009	FIR 09-b	12	4.74	2.21	24.9		6.56	SNP_IGA_555093	11.90
	qFF.BT-Ch5-2010	FIR 10	3	3.42	2.17	19.9		4.47	SNP_IGA_544961	2.94
	qFF.BT-Ch5-Mean	FIR X-b	12	2.27	2.23	14.6		4.01	SNP_IGA_585182	35.73
	qFF.BT-Ch5-MYear		10.9			7.0	2.3	1.90	SNP_IGA_553456-SNP_IGA_555093	
SSC	qSSC.V-Ch2_2-2009	SSC 09-d	0	2.52	2.15	10.7		1.34	SNP_IGA_140938	0.00
	qSSC.V-Ch4-2007a	SSC 07-a	29	3.45	2.06	18.5		-0.29	SNP_IGA_399337	29.19
	qSSC.V-Ch4-2007b	SSC 07-b	44	5.29	2.06	28.0		0.99	SNP_IGA_407115	44.03
	qSSC.V-Ch4-2009a	SSC 09-a	32	2.61	2.15	11.3		0.30	SNP_IGA_400572	32.13
	qSSC.V-Ch4-2009b	SSC 09-b	44	6.49	2.15	27.6		1.57	SNP_IGA_407115	44.03
	qSSC.V-Ch4-2010	SSC 10-a	54	3.85	2.10	21.4		1.78	SNP_IGA_440110	54.65
	qSSC.V-Ch4-Mean	SSC X-a	44	4.02	2.20	22.0		1.37	SNP_IGA_407115	44.03
	qSSC.V-Ch4-MYear		44.0			16.3	0.8	-071	SNP_IGA_407115-SNP_IGA_408981	

Trait	QTL name	QTL code	cM	LOD score	Threshold	VG (%)	VGE (%)	Additive effect (a)	Flanking Markers	Dist cM
SSC	qSSC.BT-Ch5-2009	SSC 09-c	21	3.02	2.23	17.1		1.48	SNP_IGA_572589	24.39
	qSSC.BT-Ch5-2010	SSC 10-b	33	2.60	2.14	15.2		1.18	SNP_IGA_585182	35.73
	qSSC.BT-Ch5-Mean	SSC X-b	29	2.32	2.18	13.5		1.04	SNP_IGA_572589	24.39
	qSSC.BT-Ch5-MYear		28.4			7.5	1.7	0.51	SNP_IGA_572589-SNP_IGA_585182	
pH	qpH.BT-Ch5-2007	pH 07	4	15.17	2.36	52.2		0.40	SNP_IGA_544961	2.94
	qpH.BT-Ch5-2009	pH 09	3	27.96	2.48	85.3		0.58	SNP_IGA_544961	2.94
	qpH.BT-Ch5-2010	pH 10	4	21.42	2.55	75.7		0.53	SNP_IGA_544961	2.94
	qpH.BT-Ch5-Mean	pH X	3	26.66	2.62	84.0		0.51	SNP_IGA_544961	2.94
	qpH.BT-Ch5-MYear		3.9			71.1	1.5	0.25	SNP_IGA_544961-SNP_IGA_548597	
TA	qTA.BT-Ch5-2007	TA 07-a	3	12.67	2.63	60.4		0.43	SNP_IGA_544961	2.94
	qTA.BT-Ch5-2009	TA 09	3	25.4	2.56	82.5		-0.37	SNP_IGA_544961	2.94
	qTA.BT-Ch5-2010	TA 10	2	14.8	2.54	62.6		-0.59	SNP_IGA_544961	2.94
	qTA.BT-Ch5-Mean	TA X	3	27.63	2.53	84.6		-0.46	SNP_IGA_544961	2.94
	qTA.BT-Ch5MYear-a		2.9			62.9	0.2	-0.23	SNP_IGA_544961-SNP_IGA_548597	
	qTA.BT-Ch5MYear-b		53.7			0.9	2.7	0.01	SNP_IGA_595212-SNP_IGA_597937	
RI (SSC/TA)	qRI.BT-Ch5-2007	RI 07	0	7.55	2.45	42.4		14.57	SNP_IGA_543368	0.00
	qRI.BT-Ch5-2009	RI 09	3	17.41	2.56	69.8		17.06	SNP_IGA_544961	2.94
	qRI.BT-Ch5-2010	RI 10	4	11.38	2.54	53.1		19.58	SNP_IGA_548597	5.93
	qRI.BT-Ch5-Mean	RI X	3	21.55	2.51	76.8		17.52	SNP_IGA_544961	2.94
	qRI.BT-Ch5-MYear		3.9			53.0	1.1	8.71	SNP_IGA_544961-SNP_IGA_548597	
Total sugars	qTSU.V-Ch2_2-2009	TSU 09-b	0	2.52	2.14	15.5		11.66	SNP_IGA_140938	0.00
	qTSU.BT-Ch4-2010	TSU 10	34	2.20	2.05	14.9		15.20	SNP_IGA_477941	33.97
	qTSU.BT-Ch5-2009	TSU 09-c	19	3.15	2.23	16.6		12.01	SNP_IGA_559057	14.84
	qTSU.BT-Ch5-Mean	TSU X-c	23	2.43	2.01	15.1		10.10	SNP_IGA_572589	24.39
	qTSU.BT-Ch5-MYear		20.8			12.2	0.1	6.08	SNP_IGA_559057-SNP_IGA_572589	
Sucrose	qSUC.V-Ch4-2010	SUC 10	11	2.37	2.13	18.9		-11.73	SNP_IGA_378159	11.02
	qSUC.BT-Ch5-2007	SUC 07	5	2.87	2.16	18.6		-12.86	SNP_IGA_548597	5.93
	qSUC.BT-Ch5-2009	SUC 09	17	4.21	2.19	22.0		10.89	SNP_IGA_559057	14.84
	qSUC.BT-Ch5-Mean	SUC X	3	6.14	2.13	30.4		10.61	SNP_IGA_544961	2.94
	qSUC.BT-Ch5-MYear		4.9			16.8	0.5	5.70	SNP_IGA_544961-SNP_IGA_548597	
Glucose	qGLU.V-Ch4-2007	GLU 07	48	4.07	2.06	23.8		2.33	SNP_IGA_408981	45.50
	qGLU.V-Ch4-MYear		47.5			9.0	6.0	-0-67	SNP_IGA_408981-SNP_IGA_437516	
	qGLU.BT-Ch3-MYear		26.5			5.4	2.0	0.50	SNP_IGA_913739-SNP_IGA_346608	

Trait	QTL name	QTL code	cM	LOD score	Threshold	VG (%)	VGE (%)	Additive effect (a)	Flanking Markers	Dist cM
Sorbitol	qSOR.V-Ch4-2007	SOR 07	46	12.88	2.14	51.2		4.50	SNP_IGA_408981	45.50
	qSOR.V-Ch4-2008	SOR 08	49	5.75	2.02	27.3		4.35	SNP_IGA_437516	51.66
	qSOR.V-Ch4-2009	SOR 09	46	18.59	2.27	57.7		6.48	SNP_IGA_408981	45.50
	qSOR.V-Ch4-2010	SOR 10a	54	5.62	2.16	36.8		3.82	SNP_IGA_440110	54.65
	qSOR.V-Ch4- Mean	SOR X	47	22.22	2.12	60.5		4.71	SNP_IGA_408981	45.50
	qSOR.V-Ch4- MYear		45.5			48.6	2.1	-2.42	SNP_IGA_408981-SNP_IGA_437516	
	qSOR.BT-Ch5-2010	SOR 10b	40	2.56	2.16	20.5		2.72	SNP_IGA586202	40.28
	qSOR.BT-Ch5-MYear		32.4			8.6	0.2	1.07	SNP_IGA_572589-SNP_IGA_585182	
Fructose	qFRU.V-Ch2_1-2008	FRU 08-a	3	2.90	2.00	13.2		-2.13	SNP_IGA_249781	0.00
	qFRU.V-Ch4-2007	FRU 07-a	48	2.73	2.14	17.6		1.80	SNP_IGA_408981	45.50
	qFRU.V-Ch4-MYear		47.5			6.0	2.8	-0.56	SNP_IGA_408981-SNP_IGA_437516	
	qFRU.BT-Ch1_2-2008	FRU 08-b	23	2.62	2.21	16.5		2.27	SNP_IGA_25403	23.04
	qFRU.BT-Ch1_2-Mean	FRU X-b	23	2.48	2.26	15.9		1.41	SNP_IGA_25403	23.04
	qFRU.BT-Ch5-2007	FRU 07-b	54	3.57	2.28	22.7		2.03	SNP_IGA_595212	53.74
	qFRU.BT-Ch5-MYear		53.7			9.9	2.7	0.61	SNP_IGA_595212-SNP_IGA_597937	
	qFRU.BT-Ch8-MYear		34.8			6.7	4.0	0.44	SNP_IGA_835981-SNP_IGA_864110	
Total Phenolics	qPHE.V-Ch2_2-2009	PHE 09-a	0	2.32	2.16	14.3		4.18	SNP_IGA_140938	0.00
	qPHE.V-Ch4-Mean	PHE X	45	2.67	2.18	15.8		4.71	SNP_IGA_408981	45.50
	qPHE.BT-Ch2-2009	PHE 09-b	1	2.50	2.21	15.0		-4.18	SNP_IGA_141612	1.47
	qPHE.BT-Ch2-MYear		8.6			9.2	1.4	-2.63	SNP_IGA_230389-SNP_IGA_231766	
Flavonoids	qFLV.V-Ch2_2-2010	FLV 10-a	1.5	2.76	1.82	17.0		4.59	SNP_IGA_185060	1.47
	qFLV.V-Ch3-2008	FLV 08-c	3	2.18	2.02	10.1		-4.97	SNP_IGA_298154	2.98
	qFLV.V-Ch4-2008	FLV 08-a	53	4.40	2.02	17.8		7.22	SNP_IGA_437516	51.66
	qFLV.V-Ch7-2008	FLV 08-b	0	4.04	2.02	18.6		-7.45	SNP_IGA_787282	0.00
	qFLV.BT-Ch2-2010	FLV 10-b	0	2.86	1.93	17.1		-4.59	SNP_IGA_161939	0.00
Anthocyanins	qANT.BT-Ch5-2009	ANT 09	3	3.24	1.93	18.7		-3.84	SNP_IGA_544961	2.94
	qANT.BT-Ch5-2010	ANT 10	3	5.28	2.19	27.6		-4.15	SNP_IGA_544961	2.94
	qANT.BT-Ch5-Mean	ANT X	3	6.02	2.14	30.0		1.98	SNP_IGA_544961	2.94
	qANT.BT-Ch5-MYear		2.9			13.2	8.0	-1.07	SNP_IGA_544961-SNP_IGA_548597	
RAC	qRAC.V-Ch4-2009	RAC 09-a	46	7.47	2.14	34.9		117.17	SNP_IGA_408981	45.50
	qRAC.V-Ch4-Mean	RAC X	54	3.58	2.03	20.2		82.55	SNP_IGA_440110	54.65
	qRAC.V-Ch4-MYear		45.0			11.6	6.0	-26.80	SNP_IGA_407115-SNP_IGA_408981	
	qRAC.BT-Ch8-2009	RAC 09-b	82	2.72	2.28	9.3		-59.61	SNP_IGA_884538	81.39

Figures captions

Fig. 1 Genetic linkage map of 'Venus'

Nine linkage groups of 'Venus'. In each linkage group names, 'V' refers to the 'Venus' parental, the first number to the scaffold that it represents and the second one to the sub-group when scaffold is represented by more than one linkage group. See the absence of scaffold 5 and the separation in two groups of scaffolds 1 and 2. SSR markers are in bold (UDP98-024 and UCDCH15 in V4; pchcms5 and BPPCT025 in V6; and BINEPPCU6377 in V8), and the SNP_IGA_536394 in V6 is underlined

Fig. 2 Genetic linkage map of 'Big Top'

Ten linkage groups of 'Big Top'. In each linkage group, 'B' refers to the 'Big Top' parental, the first number to the scaffold that it represents and the second one to the sub-group when scaffold is represented by more than one linkage group. See the separation of scaffolds 1 and 6 in two linkage groups. SSR marker (BPPCT033) in B8 is in bold and markers (SNP_IGA_913769 in B3 and SNP_IGA_430365 in B7) are underlined

Fig. 3 QTL map of 'Venus'

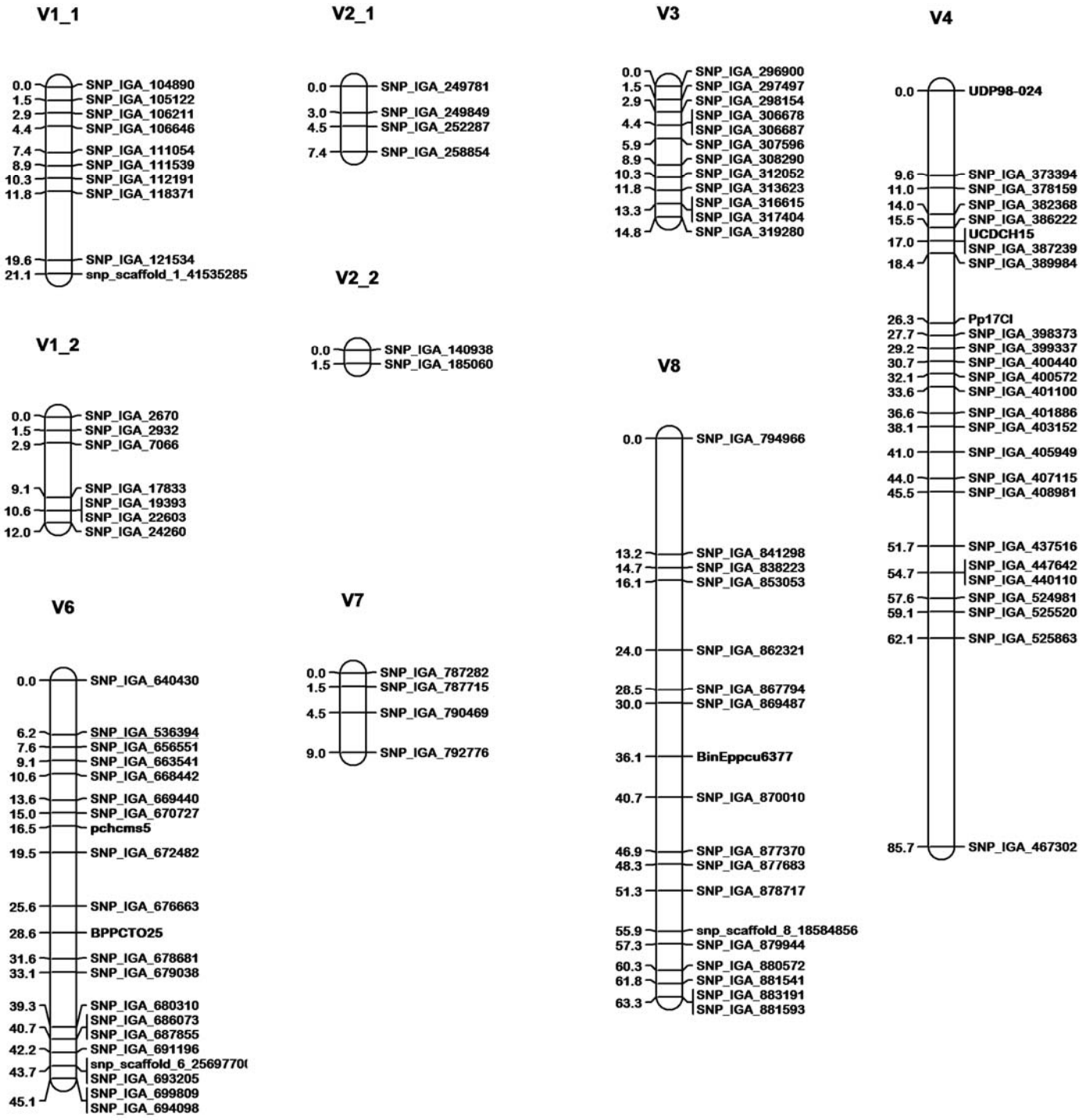
Location of putative QTLs controlling fruit quality traits analyzed by year in 'Venus' map and determined by Single Regresion or MQM mapping. 'V' refers to the 'Venus' parental, the first number to the scaffold that it represents and second to the sub-group when scaffold is represented by more than one linkage group. Markers are listed at the right side of each LG and the genetic distances are listed at the left side. QTLs are drawn at the left of each corresponding LG and were represented in such a way that the thick line represents the inner confidence interval bound and the thin line represents the whole significance interval of the QTL. QTLs detected with the mean were not represented. The QTLs codes are described in Table 2 and Supplementary Table 4.

Fig. 4 QTL map of 'Big Top'

Location of putative QTLs controlling fruit quality traits analyzed by year in 'Big Top' map and determined by Single Regresion or MQM mapping. B' refers to the 'Big Top' parental, the first number to the scaffold that it represents and second to the sub-group when scaffold is represented by more than one linkage group. Markers are listed at the right side of each LG and the genetic distances are listed at the left side. QTLs are

drawn at the left of each corresponding LG and were represented in such a way that the thick line represents the inner confidence interval bound and the thin line represents the whole significance interval of the QTL. QTLs detected with the mean were not represented. The QTLs codes are described in Table 2 and Supplementary Table 4.

Figure 1.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V3
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Figure 2.

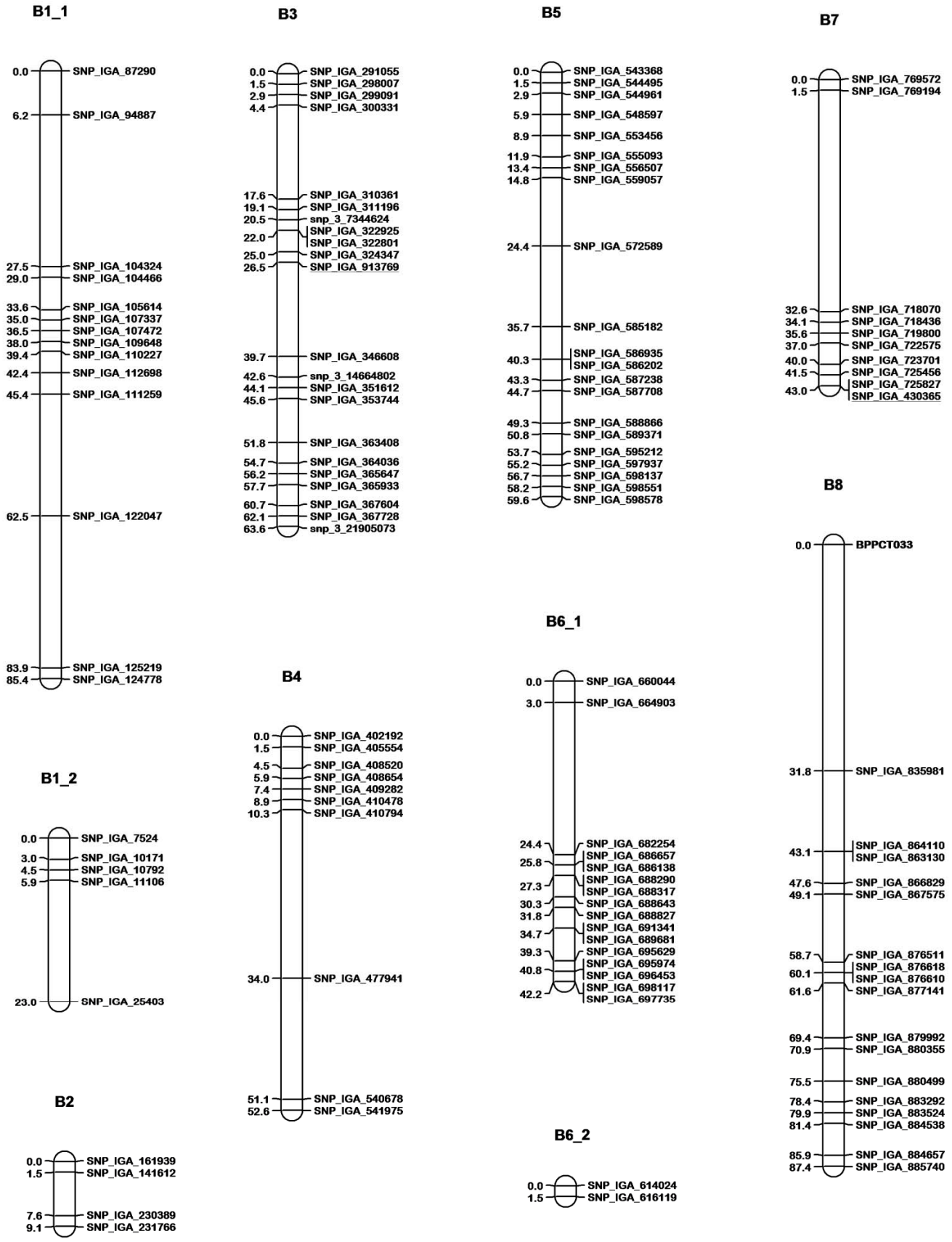
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Figure 3.

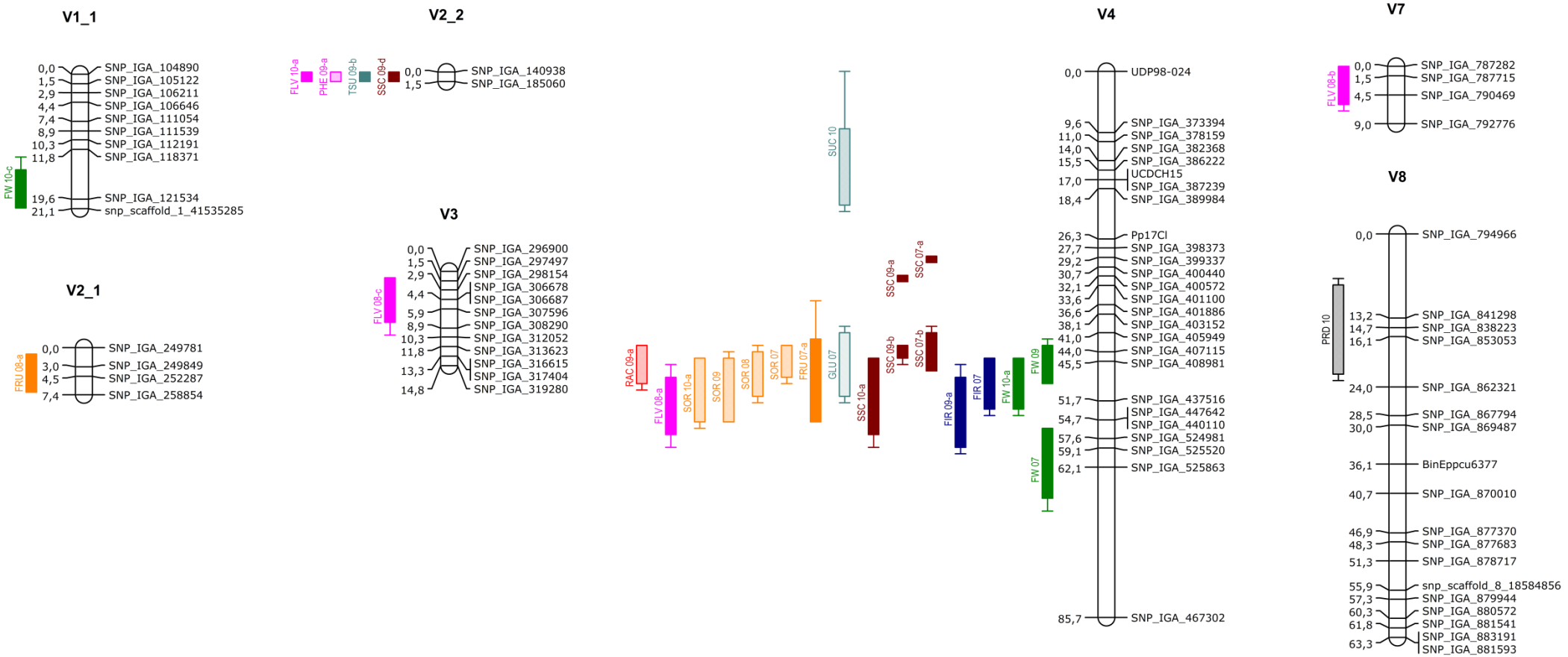
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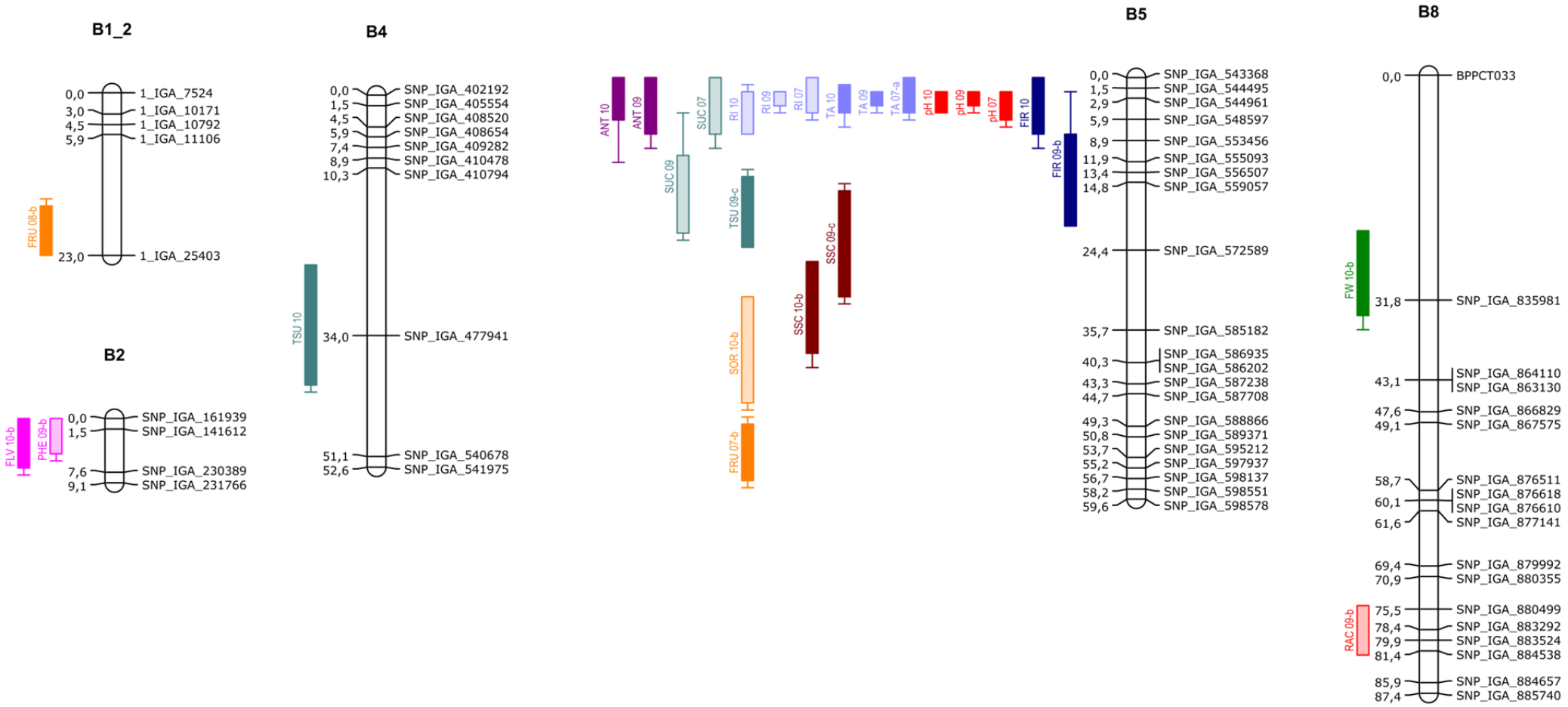
Figure 4.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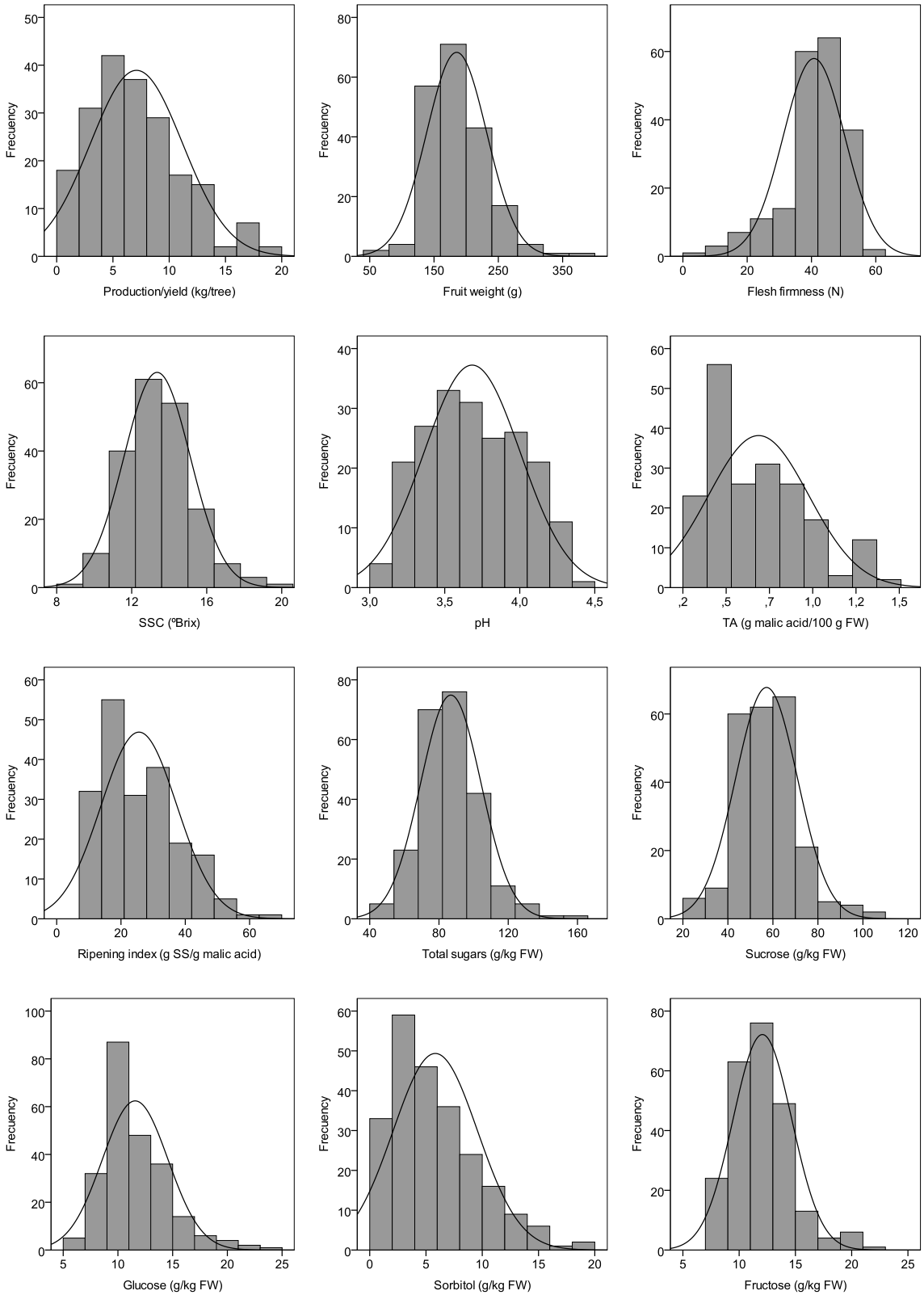
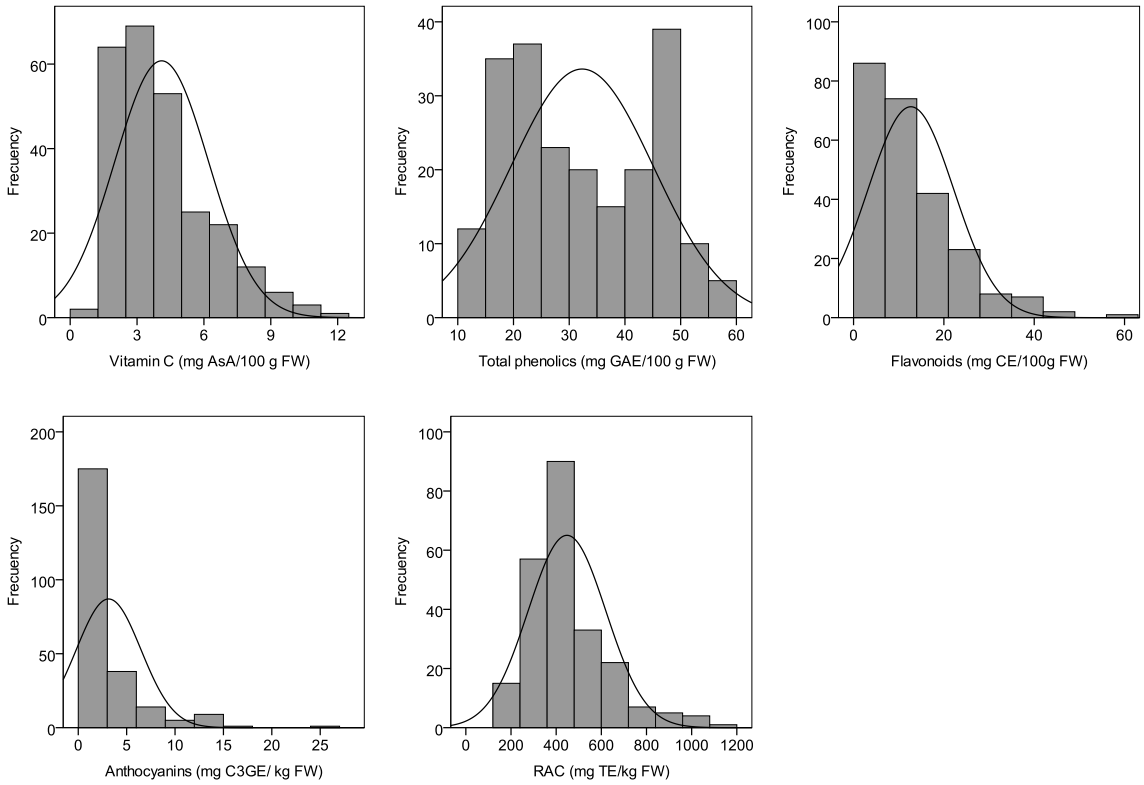
Supplementary Fig. 1. Distribution of phenotypic data in the population during four seasons (2007-2010).



Supplementary Fig. 1 (continued)



Supplementary Table 1. Pearson's correlation coefficients for pomological traits 2007, 2008, 2009 and 2010 using all individuals evaluated each year.

Traits	Year	2008	2009	2010
Production /yield	**2007**		0.593**	0.674**
	2009			0.484**
Fruit weight	**2007**		0.443**	0.276*
	2009			0.85**
Firmness	**2007**		0.287*	0.189
	2009			0.392**
SSC	**2007**		0.236	0.321**
	2009			0.476**
pH	**2007**		0.742**	0.680**
	2009			0.862**
TA	**2007**		0.740**	0.513**
	2009			0.776**
RI	**2007**		0.566**	0.435**
	2009			0.642**
Total sugars	**2007**	0.191	0.248	0.127
	2008		0.041	0.362*
	2009			0.170
Sucrose	**2007**	0.078	0.223	0.117
	2008		0.016	0.173
	2009			0.047
Glucose	**2007**	0.383**	0.330*	0.191
	2008		0.311*	0.213
	2009			0.129
Sorbitol	**2007**	0.506**	0.649**	0.456**
	2008		0.411**	0.346*
	2009			0.484**
Fructose	**2007**	0.472**	0.342**	0.277
	2008		0.397**	0.301*
	2009			0.130
Vitamin C	**2007**	0.082	0.065	-0.064
	2008		0.049	0.182
	2009			0.073
Total phenolics	**2007**	0.073	0.138	0.116
	2008		0.185	0.299
	2009			0.467**
Flavonoids	**2007**	-0.145	0.128	-0.016
	2008		0.246	0.549**
	2009			0.417**
Anthocyanins	**2007**	0.083	-0.110	0.079
	2008		-0.119	0.004
	2009			0.430**
RAC	**2007**	0.100	0.063	0.072
	2008		0.211	0.620**
	2009			0.354**

*P <0.05; **P <0.01; Others not significant.

Supplementary Table 2. Pearson's correlation coefficients between the pomological traits evaluated in the 'Venus' × 'Big Top' progeny during four years (2007-2010).

	Fruit weight	Firmness	SSC	pH	TA	RI	Total sugars	Sucrose	Glucose	Sorbitol	Fructose	Vitamin C	Total phenolics	Flavonoids	Anthocyanins	RAC
Production/yield	0.019	- 0.110	- 0.242	0.002	0.043	- 0.188**	- 0.282**	- 0.246**	- 0.112	- 0.143	- 0.161*	- 0.001	- 0.081	- 0.152*	- 0.157*	- 0.200**
Fruit weight	1.00	0.310**	0.197**	0.023	- 0.030	0.095	0.091	0.049	- 0.116	0.351**	- 0.090	- 0.095	- 0.176*	- 0.146	0.082	0.391**
Firmness		1.00	0.181*	0.268**	- 0.134	0.202**	0.285**	0.139	0.280**	0.414**	0.330**	0.219**	- 0.502**	- 0.407**	- 0.003	0.134
SSC			1.00	0.163*	- 0.121	0.368**	0.670**	0.523**	0.315**	0.633**	0.338**	0.405**	0.231*	0.266**	- 0.080	0.371**
pH				1.00	- 0.804**	0.799**	0.304**	0.404**	- 0.172*	0.140	- 0.088	0.243**	- 0.195*	- 0.177*	- 0.260**	- 0.199*
TA					1.00	- 0.869**	- 0.260**	- 0.360**	0.198**	- 0.110	0.125	- 0.054	- 0.025	- 0.012	0.307**	0.060
RI						1.00	0.379**	0.461**	- 0.141	0.205**	- 0.088	0.065	0.010	0.009	- 0.235**	0.052
Total sugars							1.00	0.910**	0.356**	0.658**	0.658**	0.463**	0.129	0.156*	- 0.051	0.151*
Sucrose								1.00	0.013	0.453**	0.026	0.384**	0.022	- 0.020	- 0.020	- 0.057
Glucose									1.00	0.190**	0.799**	0.122	0.366**	0.493**	- 0.161*	0.515**
Sorbitol										1.00	0.179**	0.388**	0.044	0.041	- 0.031	0.097
Fructose											1.00	0.165**	0.256**	0.415**	- 0.136*	0.443**
Vitamin C												1.00	- 0.204**	- 0.003	0.189**	- 0.022
Total phenolics													1.00	0.828**	- 0.329**	0.632**
Flavonoids														1.00	- 0.186**	0.761**
Anthocyanins															1.00	- 0.184**
RAC																1.00

*P <0.05; **P <0.01; Others not significant.

Supplementary Table 3. List of the SNPs mapped in the 'Venus' × 'Big Top' population and its physical position in Peach genome v1.0 and v2.0.

Scaffold 1	Peach v1	Peach v2
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SNP_IGA_10171	scaffold_1:3,319,106	Pp01:3318869
SNP_IGA_10792	scaffold_1:3,563,709	Pp01:3563475
SNP_IGA_11106	scaffold_1:3,660,651	Pp01:3660418
SNP_IGA_17833	scaffold_1:5,803,431	Pp01:6252790
SNP_IGA_19393	scaffold_1:6,411,736	Pp01:6861098
SNP_IGA_22603	scaffold_1:7,500,056	Pp01:7949418
SNP_IGA_24260	scaffold_1:8,357,315	Pp01:8806675
SNP_IGA_25403	scaffold_1:8,812,754	Pp01:9262114
SNP_IGA_87290	scaffold_1:25,762,314	Pp01:26736917
SNP_IGA_94887	scaffold_1:28,142,364	Pp01:29116355
SNP_IGA_104324	scaffold_1:33,105,631	Pp01:34079472
SNP_IGA_104466	scaffold_1:33,154,340	Pp01:34128181
SNP_IGA_104890	scaffold_1:33,430,259	Pp01:34404100
SNP_IGA_105122	scaffold_1:33,489,785	Pp01:34463626
SNP_IGA_105614	scaffold_1:33,659,804	Pp01:34633645
SNP_IGA_106211	scaffold_1:33,935,933	Pp01:34909774
SNP_IGA_106646	scaffold_1:34,095,609	Pp01:35069450
SNP_IGA_107337	scaffold_1:34,358,459	Pp01:35332300
SNP_IGA_107472	scaffold_1:34,496,362	Pp01:35469583
SNP_IGA_109648	scaffold_1:35,351,837	Pp01:36325047
SNP_IGA_110227	scaffold_1:35,577,807	Pp01:36551019
SNP_IGA_111054	scaffold_1:35,832,121	Pp01:36805333
SNP_IGA_111259	scaffold_1:36,067,680	Pp01:37040892
SNP_IGA_111539	scaffold_1:36,269,360	Pp01:37242573
SNP_IGA_112191	scaffold_1:36,617,840	Pp01:37591210
SNP_IGA_112698	scaffold_1:36,761,277	Pp01:37734647
SNP_IGA_118371	scaffold_1:39,205,411	Pp01:40178780
SNP_IGA_121534	scaffold_1:40,713,626	Pp01:41686892
SNP_IGA_122047	scaffold_1:41,007,523	Pp01:41980790
snp_scaffold_1_41535285	scaffold_1:41,535,285	Pp01:42508498
SNP_IGA_124778	scaffold_1:42,628,464	Pp01:47187541
SNP_IGA_125219	scaffold_1:42,831,911	Pp01:46984218

Scaffold 2	Peach v1	Peach v2
SNP_IGA_140938	scaffold_2:778744	Pp02:2524809
SNP_IGA_141612	scaffold_2:881016	Pp02:2627082
SNP_IGA_161939	scaffold_2:2478864	Pp02:4224893
SNP_IGA_185060	scaffold_2:4006746	Pp02:5751793
SNP_IGA_230389	scaffold_2:9280916	Pp02:1338721
SNP_IGA_231766	scaffold_2:9415276	Pp02:1204461
SNP_IGA_249781	scaffold_2:12440279	Pp02:15218516
SNP_IGA_249849	scaffold_2:12464202	Pp02:15242439
SNP_IGA_252287	scaffold_2:13006417	Pp02:15784654
SNP_IGA_258854	scaffold_2:14440907	Pp02:17219077

Scaffold 3	Peach v1	Peach v2
SNP_IGA_291055	scaffold_3:67897	Pp03:929735
SNP_IGA_296900	scaffold_3:2528714	Pp03:3390662
SNP_IGA_297497	scaffold_3:2774393	Pp03:3635392
SNP_IGA_298007	scaffold_3:2988044	Pp03:3849042
SNP_IGA_298154	scaffold_3:3034975	Pp03:3895956.
SNP_IGA_299091	scaffold_3:3163382	Pp03:4024362
SNP_IGA_300331	scaffold_3:3477694	Pp03:4338580
SNP_IGA_306678	scaffold_3:4819681	Pp03:5680211
SNP_IGA_306687	scaffold_3:4821129	Pp03:5681659
SNP_IGA_307596	scaffold_3:5061446	Pp03:5921975
SNP_IGA_308290	scaffold_3:5396389	Pp03:6256189
SNP_IGA_310361	scaffold_3:5894946	Pp03:6754745
SNP_IGA_311196	scaffold_3:6030258	Pp03:6890057
SNP_IGA_312052	scaffold_3:6228215	Pp03:7088012
SNP_IGA_313623	scaffold_3:6546629	Pp03:7406427
SNP_IGA_316615	scaffold_3:7285845	Pp03:8145641
snp_3_7344624	scaffold_3:7344624	Pp03:8204420
SNP_IGA_317404	scaffold_3:7421669	Pp03:8281465
SNP_IGA_319280	scaffold_3:7855057	Pp03:8714889
SNP_IGA_322801	scaffold_3:9057222	Pp03:9916964
SNP_IGA_322925	scaffold_3:9071075	Pp03:9930816
SNP_IGA_324347	scaffold_3:9363762	Pp03:10223404
SNP_IGA_346608	scaffold_3:14226902	Pp03:19570000
snp_3_14664802	scaffold_3:14664802	Pp03:20007900
SNP_IGA_351612	scaffold_3:15617364	Pp03:20960378
SNP_IGA_353744	scaffold_3:16355753	Pp03:21698237
SNP_IGA_363408	scaffold_3:19666648	Pp03:25009525
SNP_IGA_364036	scaffold_3:19916263	Pp03:25258726
SNP_IGA_365647	scaffold_3:20537330	Pp03:25879794
SNP_IGA_365933	scaffold_3:20719430	Pp03:26061895
SNP_IGA_367604	scaffold_3:21686505	Pp03:27028967
SNP_IGA_367728	scaffold_3:21798019	Pp03:27140481
snp_3_21905073	scaffold_3:21905073	Pp03:27247536
SNP_IGA_913769	**scaffold_13:560511**	Pp03:12526639

Scaffold 4	Peach v1	Peach v2
SNP_IGA_373394	scaffold_4:865720	Pp04:865823..
SNP_IGA_378159	scaffold_4:1320979	Pp04:1321081
SNP_IGA_382368	scaffold_4:2689227	Pp04:2689336
SNP_IGA_386222	scaffold_4:4045369	Pp04:4045426
SNP_IGA_387239	scaffold_4:4533189	Pp04:4533174
SNP_IGA_389984	scaffold_4:5021007	Pp04:5020995
Pp17Cl	scaffold_4:6739336	Pp04:6739305
SNP_IGA_398373	scaffold_4:6934721	Pp04:6934689
SNP_IGA_399337	scaffold_4:7090751	Pp04:7090720
SNP_IGA_400440	scaffold_4:7275570	Pp04:7275539
SNP_IGA_400572	scaffold_4:7323880	Pp04:7323849
SNP_IGA_401100	scaffold_4:7541219	Pp04:7541276
SNP_IGA_401886	scaffold_4:8222657	Pp04:8233517
SNP_IGA_402192	scaffold_4:8341151	Pp04:8352011
SNP_IGA_403152	scaffold_4:8966988	Pp04:8977975
SNP_IGA_405554	scaffold_4:9606600	Pp04:9617585
SNP_IGA_405949	scaffold_4:9690588	Pp04:9701574
SNP_IGA_407115	scaffold_4:9936483	Pp04:9947470
SNP_IGA_408520	scaffold_4:1018305	Pp04:10194038
SNP_IGA_408654	scaffold_4:10203034	Pp04:10214022
SNP_IGA_408981	scaffold_4:10269107	Pp04:10280095
SNP_IGA_409282	scaffold_4:10373637	Pp04:10384625
SNP_IGA_410478	scaffold_4:10749097	Pp04:10760086
SNP_IGA_410794	scaffold_4:10879662	Pp04:10890653
SNP_IGA_430365	scaffold_4:15542419	**Pp03:11413283**
SNP_IGA_437516	scaffold_4:17094116	Pp04:15182577
SNP_IGA_440110	scaffold_4:17988261	Pp04:16076720
SNP_IGA_447642	scaffold_4:19688796	Pp04:17777038
SNP_IGA_467302	scaffold_4:22631600	Pp04:19028425
SNP_IGA_477941	scaffold_4:23497381	Pp04:19894211
SNP_IGA_524981	scaffold_4:27077999	Pp04:23475348
SNP_IGA_525520	scaffold_4:27189300	Pp04:23586650
SNP_IGA_525863	scaffold_4:27240864	Pp04:23638214
SNP_IGA_536394	scaffold_4:29309528	**Pp06:15357613**
SNP_IGA_540678	scaffold_4:29861447	Pp04:25176043
SNP_IGA_541975	scaffold_4:30100038	Pp04:25414548

Supplementary Table 3 (continued)

Scaffold 5	Peach v1	Peach v2
SNP_IGA_543368	scaffold_5:302944	Pp05:302946
SNP_IGA_544495	scaffold_5:610568	Pp05:610569
SNP_IGA_544961	scaffold_5:698214	Pp05:698215
SNP_IGA_548597	scaffold_5:1518380	Pp05:1518366
SNP_IGA_553456	scaffold_5:2477325	Pp05:2477309
SNP_IGA_555093	scaffold_5:2962847	Pp05:2962831
SNP_IGA_556507	scaffold_5:3280480	Pp05:3280731
SNP_IGA_559057	scaffold_5:3731230	Pp05:3731800
SNP_IGA_572589	scaffold_5:5811983	Pp05:5813029
SNP_IGA_585182	scaffold_5:9212543	Pp05:9213434
SNP_IGA_586202	scaffold_5:9505270	Pp05:9506161
SNP_IGA_586935	scaffold_5:9743759	Pp05:9742162
SNP_IGA_587238	scaffold_5:9843120	Pp05:9841523
SNP_IGA_587708	scaffold_5:9984769	Pp05:9983173
SNP_IGA_588866	scaffold_5:10385263	Pp05:10383553
SNP_IGA_589371	scaffold_5:10559273	Pp05:10557562
SNP_IGA_595212	scaffold_5:12814968	Pp05:12809737
SNP_IGA_597937	scaffold_5:13898935	Pp05:13893708
SNP_IGA_598137	scaffold_5:13971069	Pp05:13965842
SNP_IGA_598551	scaffold_5:14088605	Pp05:14083378
SNP_IGA_598578	scaffold_5:14100903	Pp05:14095676

Scaffold 6	Peach v1	Peach v2
SNP_IGA_614024	scaffold_6:3207977	Pp06:2000736
SNP_IGA_616119	scaffold_6:3792224	Pp06:1417402
SNP_IGA_640430	scaffold_6:11288052	Pp06:11302830
SNP_IGA_656551	scaffold_6:14806613	Pp06:16672871
SNP_IGA_660044	scaffold_6:15385770	Pp06:17252030
SNP_IGA_663541	scaffold_6:16185826	Pp06:18052094
SNP_IGA_664903	scaffold_6:16618275	Pp06:18484543
SNP_IGA_668442	scaffold_6:18064690	Pp06:19930779
SNP_IGA_669440	scaffold_6:18064690	Pp06:20179491
SNP_IGA_670727	scaffold_6:18664554	Pp06:20528913
SNP_IGA_672482	scaffold_6:19231727	Pp06:21096087
SNP_IGA_676663	scaffold_6:20667470	Pp06:22531824
SNP_IGA_678681	scaffold_6:21455421	Pp06:23319779
SNP_IGA_679038	scaffold_6:21583109	Pp06:23447467
SNP_IGA_680310	scaffold_6:22132364	Pp06:23996532
SNP_IGA_682254	scaffold_6:22647696	Pp06:24511760
SNP_IGA_686073	scaffold_6:23719823	Pp06:25584106
SNP_IGA_686138	scaffold_6:23734168	Pp06:25598451
SNP_IGA_686657	scaffold_6:23922965	Pp06:25787248
SNP_IGA_687855	scaffold_6:24177743	Pp06:26042026
SNP_IGA_688290	scaffold_6:24361336	Pp06:26225619
SNP_IGA_688317	scaffold_6:24366460	Pp06:26230743
SNP_IGA_688643	scaffold_6:24495830	Pp06:26360114
SNP_IGA_688827	scaffold_6:24629506	Pp06:26493790
SNP_IGA_689681	scaffold_6:24847752	Pp06:26712037
SNP_IGA_691196	scaffold_6:25176727	Pp06:27041352
SNP_IGA_691341	scaffold_6:25224983	Pp06:27089604
snp_scaffold_6_25697700	scaffold_6:25697700	Pp06:27562320
SNP_IGA_693205	scaffold_6:25725352	Pp06:27589956
SNP_IGA_694098	scaffold_6:26090466	Pp06:27955072
SNP_IGA_695629	scaffold_6:26491953	Pp06:28356561
SNP_IGA_695974	scaffold_6:26549830	Pp06:28414438
SNP_IGA_696453	scaffold_6:26660505	Pp06:28525113
SNP_IGA_697735	scaffold_6:27016342	Pp06:28880950
SNP_IGA_698117	scaffold_6:27083444	Pp06:28948052
SNP_IGA_699809	scaffold_6:27830167	Pp06:29694774

Scaffold 7	Peach v1	Peach v2
SNP_IGA_718070	scaffold_7:2531116	Pp07:2304002
SNP_IGA_718436	scaffold_7:2605985	Pp07:2229107
SNP_IGA_719800	scaffold_7:2867252	Pp07:1967839
SNP_IGA_722575	scaffold_7:3449144	Pp07:1386205
SNP_IGA_723701	scaffold_7:3679697	Pp07:1156552
SNP_IGA_725456	scaffold_7:4319294	Pp07:515531
SNP_IGA_725827	scaffold_7:4431425	Pp07:403402
SNP_IGA_769194	scaffold_7:12557752	Pp07:12156489
SNP_IGA_769572	scaffold_7:12650182	Pp07:12248919
SNP_IGA_787282	scaffold_7:19662720	Pp07:19261236
SNP_IGA_787715	scaffold_7:19780789	Pp07:19379306
SNP_IGA_790469	scaffold_7:20920976	Pp07:20519494
SNP_IGA_792776	scaffold_7:22589975	Pp07:22188387

Scaffold 8	Peach v1	Peach v2
SNP_IGA_794966	scaffold_8:642747	Pp08:642666
SNP_IGA_835981	scaffold_8:7614568	Pp08:10502545
SNP_IGA_838223	scaffold_8:8196773	Pp08:9920158
SNP_IGA_841298	scaffold_8:8555314	Pp08:9561732
SNP_IGA_853053	scaffold_8:1040172	Pp08:11146221
SNP_IGA_862321	scaffold_8:13204775	Pp08:13949281
SNP_IGA_863130	scaffold_8:13401103	Pp08:14145609
SNP_IGA_864110	scaffold_8:13728163	Pp08:14472670
SNP_IGA_866829	scaffold_8:14559613	Pp08:15304115
SNP_IGA_867575	scaffold_8:14856769	Pp08:15601270
SNP_IGA_867794	scaffold_8:14928943	Pp08:15673444
SNP_IGA_869487	scaffold_8:15387696	Pp08:16132196
SNP_IGA_870010	scaffold_8:15538262	Pp08:16282763
SNP_IGA_876511	scaffold_8:17429074	Pp08:18173532
SNP_IGA_876610	scaffold_8:17467662	Pp08:18212120
SNP_IGA_876618	scaffold_8:17469436	Pp08:18213894
SNP_IGA_877141	scaffold_8:17587403	Pp08:18331861
SNP_IGA_877370	scaffold_8:17727387	Pp08:18471843
SNP_IGA_877683	scaffold_8:17823461	Pp08:18567917
SNP_IGA_878717	scaffold_8:18085149	Pp08:18829606
snp_scaffold_8_18584856	scaffold_8:18584856	Pp08:19329311
SNP_IGA_879944	scaffold_8:18626022	Pp08:19370477
SNP_IGA_879992	scaffold_8:18640954	Pp08:19385409
SNP_IGA_880355	scaffold_8:18762779	Pp08:19507234
SNP_IGA_880499	scaffold_8:18802717	Pp08:19547172
SNP_IGA_880572	scaffold_8:18851122	Pp08:19595577
SNP_IGA_881541	scaffold_8:19095898	Pp08:19840354
SNP_IGA_881593	scaffold_8:19108751	Pp08:19853207
SNP_IGA_883191	scaffold_8:19733954	Pp08:20478408
SNP_IGA_883292	scaffold_8:19926659	Pp08:20671113
SNP_IGA_883524	scaffold_8:20088710	Pp08:20833164
SNP_IGA_884538	scaffold_8:20597072	Pp08:21341296
SNP_IGA_884657	scaffold_8:20661785	Pp08:21406010
SNP_IGA_885740	scaffold_8:21203991	Pp08:21948219

Supplementary Table 4. QTLs found for agronomic and fruit quality traits detected in the 'Venus' x 'Big Top' progeny.

Trait, QTL name and QTL code, position, LOD score, Treshold, Genetic variance and effects of the QTLs detected, and position of the nearest SNP marker. Genetic Variance (VG)= Fraction of the total variation explained by the QTL, a= Additive effect. expressed as the effect of substituting an A allele by B in the AA genotype. Dist= marker position on the genetic linkage map. Abbreviations: RAC=Relative Antioxidant Capacity, RI=Ripening Index, SSC=Soluble Solids Concentration, TA=Titratable Acidity. See Table 1 for units.

Trait	QTL name	QTL code	Pos cM	LOD score	Threshold	Genetic Variance VG %	Geno. means AA	AB	Allele_effect a	Nearest Marker	Dist cM
Production	qPRD.V-Ch3-Mean	PRD X-b	9	3.34	2.13	16.3	5.69	8.01	2.46	SNP_IGA_308290	8.87
	qPRD.V-Ch8-2010	PRD 10	13	2.90	2.14	17.0	0.50	0.75	0.25	SNP_IGA_841298	13.19
	qPRD.V-Ch8-Mean	PRD X-a	24	3.74	2.13	18.1	5.80	8.42	2.62	SNP_IGA_862321	23.96
Fruit weight	qFW.V-Ch1_1-2010	FW 10-c	20	2.66	2.00	7.7	202.60	232.88	30.28	SNP_IGA_121534	19.64
	qFW.V-Ch4-2007	FW 07	60	3.97	2.10	22.1	149.50	188.71	39.21	SNP_IGA_525520	59.11
	qFW.V-Ch4-2009	FW 09	46	7.54	2.08	34.9	155.92	198.45	42.53	SNP_IGA_408981	45.50
	qFW.V-Ch4-2010	FW 10-a	47	17.97	2.00	50.1	186.05	254.20	68.15	SNP_IGA_408981	45.50
	qFW.V-Ch4-Mean	FW X-a	46	17.38	2.13	54.7	165.41	214.91	49.50	SNP_IGA_408981	45.50
	qFW.BT-Ch8-2010	FW 10-b	25	3.45	2.19	19.9	192.91	233.72	40.81	SNP_IGA_835981	31.76
	qFW.BT-Ch8-Mean	FW X-b	9	3.07	2.21	15.3	177.97	206.87	28.90	BPPCT033	0.00
Firmness	qFF.V-Ch4-2007	FIR 07	48	8.37	2.33	43.2	26.59	39.54	12.95	SNP_IGA_408981	45.50
	qFF.V-Ch4-2009	FIR 09-a	55	3.37	2.12	19.5	41.62	47.51	5.89	SNP_IGA_440110	54.65
	qFF.V-Ch4-Mean	FIR X-a	54	8.70	2.15	37.2	38.13	44.72	6.59	SNP_IGA_440110	54.65
	qFF.BT-Ch5-2009	FIR 09-b	12	4.74	2.21	24.9	40.45	47.01	6.56	SNP_IGA_555093	11.90
	qFF.BT-Ch5-2010	FIR 10	3	3.42	2.17	19.9	43.15	47.61	4.47	SNP_IGA_544961	2.94
	qFF.BT-Ch5-Mean	FIR X-b	12	2.27	2.23	14.6	38.64	42.65	4.01	SNP_IGA_585182	35.73
SSC	qSSC.V-Ch2_2-2009	SSC 09-d	0	2.52	2.15	10.7	12.94	14.28	1.34	SNP_IGA_140938	0.00
	qSSC.V-Ch4-2007a	SSC 07-a	29	3.45	2.06	18.5	13.14	12.85	-0.29	SNP_IGA_399337	29.19
	qSSC.V-Ch4-2007b	SSC 07-b	44	5.29	2.06	28.0	12.63	13.62	0.99	SNP_IGA_407115	44.03
	qSSC.V-Ch4-2009a	SSC 09-a	32	2.61	2.15	11.3	13.42	13.72	0.30	SNP_IGA_400572	32.13
	qSSC.V-Ch4-2009b	SSC 09-b	44	6.49	2.15	27.6	12.89	14.45	1.57	SNP_IGA_407115	44.03
	qSSC.V-Ch4-2010	SSC 10-a	54	3.85	2.10	21.4	12.73	14.51	1.78	SNP_IGA_440110	54.65
	qSSC.V-Ch4-Mean	SSC X-a	44	4.02	2.20	22.0	12.85	14.22	1.37	SNP_IGA_407115	44.03
	qSSC.BT-Ch5-2009	SSC 09-c	21	3.02	2.23	17.1	12.70	14.18	1.48	SNP_IGA_572589	24.39
	qSSC.BT-Ch5-2010	SSC 10-b	33	2.60	2.14	15.2	12.80	13.98	1.18	SNP_IGA_585182	35.73
	qSSC.BT-Ch5-Mean	SSC X-b	29	2.32	2.18	13.5	12.82	13.86	1.04	SNP_IGA_572589	24.39

Supplementary Table 4. (Continued)

Trait	QTL name	QTL code	Pos cM	LOD score	Threshold	Genetic Variance VG %	Geno. AA	means AB	Allele_effect a	Nearest Marker	Dist cM
pH	qpH.BT-Ch5-2007	pH 07	4	15.17	2.36	52.2	3.36	3.75	0.40	SNP_IGA_544961	2.94
	qpH.BT-Ch5-2009	pH 09	3	27.96	2.48	85.3	3.52	4.10	0.58	SNP_IGA_544961	2.94
	qpH.BT-Ch5-2010	pH 10	4	21.42	2.55	75.7	3.27	3.80	0.53	SNP_IGA_544961	2.94
	qpH.BT-Ch5-Mean	pH X	3	26.66	2.62	84.0	3.35	3.86	0.51	SNP_IGA_544961	2.94
TA	qTA.BT-Ch5-2007	TA 07-a	3	12.67	2.63	60.4	0.57	1.00	0.43	SNP_IGA_544961	2.94
	qTA.BT-Ch5-2009	TA 09	3	25.4	2.56	82.5	0.80	0.42	-0.37	SNP_IGA_544961	2.94
	qTA.BT-Ch5-2010	TA 10	2	14.8	2.54	62.6	1.02	0.44	-0.59	SNP_IGA_544961	2.94
	qTA.BT-Ch5-Mean	TA X	3	27.63	2.53	84.6	0.81	0.35	-0.46	SNP_IGA_544961	2.94
RI (SSC/TA)	qRI.BT-Ch5-2007	RI 07	0	7.55	2.45	42.4	14.72	29.29	14.57	SNP_IGA_543368	0.00
	qRI.BT-Ch5-2009	RI 09	3	17.41	2.56	69.8	16.67	33.72	17.06	SNP_IGA_544961	2.94
	qRI.BT-Ch5-2010	RI 10	4	11.38	2.54	53.1	15.28	34.86	19.58	SNP_IGA_548597	5.93
	qRI.BT-Ch5-Mean	RI X	3	21.55	2.51	76.8	15.41	32.78	17.52	SNP_IGA_544961	2.94
Total sugars	qTSU.V-Ch2_2-2009	TSU 09-b	0	2.52	2.14	15.5	84.98	96.64	11.66	SNP_IGA_140938	0.00
	qTSU.BT-Ch4-2010	TSU 10	34	2.20	2.05	14.9	82.48	97.68	15.20	SNP_IGA_477941	33.97
	qTSU.BT-Ch5-2009	TSU 09-c	19	3.15	2.23	16.6	83.37	95.38	12.01	SNP_IGA_559057	14.84
	qTSU.BT-Ch5-Mean	TSU X-c	23	2.43	2.01	15.1	81.30	91.40	10.10	SNP_IGA_572589	24.39
Sucrose	qSUC.V-Ch4-2010	SUC 10	11	2.37	2.13	18.9	62.77	51.04	-11.73	SNP_IGA_378159	11.02
	qSUC.BT-Ch5-2007	SUC 07	5	2.87	2.16	18.6	60.85	47.99	-12.86	SNP_IGA_548597	5.93
	qSUC.BT-Ch5-2009	SUC 09	17	4.21	2.19	22.0	54.03	64.79	10.89	SNP_IGA_559057	14.84
	qSUC.BT-Ch5-Mean	SUC X	3	6.14	2.13	30.4	50.84	61.45	10.61	SNP_IGA_544961	2.94
Glucose	qGLU.V-Ch4-2007	GLU 07	48	4.07	2.06	23.8	9.18	11.51	2.33	SNP_IGA_408981	45.50
Sorbitol	qSOR.V-Ch4-2007	SOR 07	46	12.88	2.14	51.2	3.15	7.65	4.50	SNP_IGA_408981	45.50
	qSOR.V-Ch4-2008	SOR 08	49	5.75	2.02	27.3	3.92	8,27	4.35	SNP_IGA_437516	51.66
	qSOR.V-Ch4-2009	SOR 09	46	18.59	2.27	57.7	4.06	10.54	6.48	SNP_IGA_408981	45.50
	qSOR.V-Ch4-2010	SOR 10a	54	5.62	2.16	36.8	5.32	9.14	3.82	SNP_IGA_440110	54.65
	qSOR.V-Ch4- Mean	SOR X	47	22.22	2.12	60.5	3.96	8.66	4.71	SNP_IGA_408981	45.50
	qSOR.BT-Ch5-2010	SOR 10b	40	2.56	2.16	20.5	4.60	7.32	2.72	SNP_IGA586202	40.28

Supplementary Table 4. (Continued)

Trait	QTL name	QTL code	Pos cM	LOD score	Threshold	Genetic Variance VG %	Geno. AA	means AB	Allele_effect a	Nearest Marker	Dist cM
Fructose	qFRU.V-Ch2_1-2008	FRU 08-a	3	2.90	2.00	13.2	14.67	12.54	-2.13	SNP_IGA_249849	2.98
	qFRU.V-Ch4-2007	FRU 07-a	48	2.73	2.14	17.6	9.95	11.75	1.80	SNP_IGA_408981	45.50
	qFRU.BT-Ch1_2-2008	FRU 08-b	23	2.62	2.21	16.5	12.54	14.21	2.27	SNP_IGA_25403	23.04
	qFRU.BT-Ch1_2-Mean	FRU X-b	23	2.48	2.26	15.9	11.47	12.88	1.41	SNP_IGA_25403	23.04
	qFRU.BT-Ch5-2007	FRU 07-b	54	3.57	2.28	22.7	9.71	11.75	2.03	SNP_IGA_595212	53.74
Total Phenolics	qPHE.V-Ch2_2-2009	PHE 09-a	0	2.32	2.16	14.3	19.37	23.55	4.18	SNP_IGA_140938	0.00
	qPHE.V-Ch4-Mean	PHE X	45	2.67	2.18	15.8	30.66	35.37	4.71	SNP_IGA_408981	45.50
	qPHE.BT-Ch2-2009	PHE 09-b	1	2.50	2.21	15.0	23.55	19.37	-4.18	SNP_IGA_141612	1.47
Flavonoids	qFLV.V-Ch2_2-2010	FLV 10-a	1.5	2.76	1.82	17.0	6.31	10.91	4.59	SNP_IGA_185060	1.47
	qFLV.V-Ch3-2008	FLV 08-c	3	2.18	2.02	10.1	24.23	19.26	-4.97	SNP_IGA_298154	2.98
	qFLV.V-Ch4-2008	FLV 08-a	53	4.40	2.02	17.8	18.81	26.03	7.22	SNP_IGA_437516	51.66
	qFLV.V-Ch7-2008	FLV 08-b	0	4.04	2.02	18.6	24.84	17.38	-7.45	SNP_IGA_787282	0.00
	qFLV.BT-Ch2-2010	FLV 10-b	0	2.86	1.93	17.1	10.91	6.31	-4.59	SNP_IGA_161939	0.00
Anthocyanins	qANT.BT-Ch5-2009	ANT 09	3	3.24	1.93	18.7	6.45	2.61	-3.84	SNP_IGA_544961	2.94
	qANT.BT-Ch5-2010	ANT 10	3	5.28	2.19	27.6	7.03	2.88	-4.15	SNP_IGA_544961	2.94
	qANT.BT-Ch5-Mean	ANT X	3	6.02	2.14	30.0	2.29	4.27	1.98	SNP_IGA_544961	2.94
RAC	qRAC.V-Ch4-2009	RAC 09-a	46	7.47	2.14	34.9	274.23	391.40	117.17	SNP_IGA_408981	45.50
	qRAC.V-Ch4-Mean	RAC X	54	3.58	2.03	20.2	415.58	498.13	82.55	SNP_IGA_440110	54.65
	qRAC.BT-Ch8-2009	RAC 09-b	82	2.72	2.28	9.3	358.26	298.65	-59.61	SNP_IGA_884538	81.39