ORIGINAL PAPER

Mapping Architectural, Phenological, and Fruit Quality QTLs in Apricot

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Abstract The F1 population "Harostar"×"Rouge de
Mauves" was used to perform a quantitative trait loci (QTL)
mapping for tree architecture traits (i.e., tree diameter, total
branch number, tree shape); time to initial reproductive bud
break; and fruit quality traits (i.e., ground color, fruit form,
soluble solid content) using data collected from 2010 to 2012.
For architectural traits, interval mapping detected QTLs only
in "Rouge de Mauves" on linkage group 1 for trunk diameter
in 2010, on LG6 for total branch number in 2010, and on LG1
and LG5 for tree shape for both years 2010 and 2011 com-
bined. QTLs were detected only in "Harostar" for time to
initial reproductive bud break on LG1 and LG4 in 2011. For
fruit quality traits, data were collected in 2011 and 2012.
QTLs were identified on LG1 in 2011 and on LG4 in 2012
for soluble solid content, on LG3 for ground color in both
years, on LG7 only in 2011, and on LG3 for fruit form in both
years. The QTLs that we identified were compared to those
previously identified in other *Prunus* spp.

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Keywords Quantitative trait locus · *Prunus armeniaca* ·
Tree architecture · Time to reproductive bud break · Fruit
quality · Molecular breeding

Introduction

Apricot (*Prunus armeniaca* L.) is, along with peach and
plum, a major economically important *Prunus* crop, with
3.8 million tons produced worldwide in 2009 (FAOSTAT
2010). Although apricot is characterized by a non-surplus
production, critical limitations exist along the supply chain,
including climate adaptation, irregular seasonal production,
lack of resistant cultivars against pests and diseases, and a
rapid post-harvest ripening. Attention to a wide range of
agronomic traits in apricot breeding programs is required to
satisfy and keep up with grower and consumer demands
(Hormaza et al. 2007). Current breeding efforts and advan-
ces regarding disease resistance; adaptation to environment
(late frost susceptibility, extension of ripening time); tree
architecture; and fruit-related traits (productivity, quality,
resistance to handling) are reviewed in Zhebentyayeva et
al. (2012).

Tree growth, shape, and architecture have a direct influ-
ence on the training and pruning methods, on thinning and
harvesting management, and, consequently, on yield and
fruit quality (Laurens et al. 2000; Miller and Sorza 2010).
A biomechanical model performed by Alméras et al. (2004)
revealed that not only the initial geometry, especially slen-
derness and inclination, but also the distribution of the fruit
load along the shoot are involved in the apricot branch form.
However, although some apricot cultivars are well charac-
terized according to shoot slenderness and shoot bending
(Costes et al. 2006), the genetic determinism of tree shape
has been barely studied yet (Bassi and Audergon 2006). In
peach production systems, several important growth traits
have been found to be under a single gene control (e.g.,

branch angle or pillar growth form; Scorza and Sherman 1996; Sajer et al. 2012). The underlying genetics of complex tree architectural traits have been more extensively characterized in apple, for which the quantitative trait loci (QTLs) for geometric and topological traits were mapped (Liebhard et al. 2003; Kenis and Keulemans 2007; Segura et al. 2007).

Flowering time is another trait of importance in apricot production systems since spring frost can significantly damage inflorescence buds and flowers and consequently lead to an important yield reduction, particularly in continental producing regions. In apricot, chilling temperatures have a direct impact on the date of flowering, with late flowering varieties requiring more chilling units than early flowering varieties (Couvillon and Erez 1985; Andrés and Durán 1999; Ruiz et al. 2007; Campoy et al. 2012). Studies on flowering time (expressed in Julian days) in apricot and peach have revealed that this trait is quantitative. In the apricot cross "Z506-07"×"Currot", a QTL for flowering time was identified over 3 years of observation on LG5 by Campoy et al. (2011). In a backcross between peach and *Prunus davidiana*, Quilot et al. (2004) mapped over 2 years two QTLs for blooming date on LG1 and LG2, and two other QTLs were mapped over only 1 year on LG5 and LG6. In peach, Verde et al. (2002) consistently found a QTL for flowering time on LG4 over 5 years, and Fan et al. (2010) mapped two major QTLs for blooming date on LG1 and LG7, which co-localized with major QTLs for chilling requirement. More recently, QTLs for flowering date were identified in the three species—apricot, peach, and sweet cherry—on LG2, LG3, LG4, and LG7, with a major and stable QTL on LG4 in apricot (Dirlewanger et al. 2012). Candidate genes involved in chilling requirements for dormancy release have been studied in peach (Leida et al. 2010, 2012a, b), while the gene *ppLFL*, which is a *LEAFY/FLORICAULA* homolog, has been hypothesized to play a central role in peach flower induction (An et al. 2012).

Fruit quality is defined by organoleptic characteristics with aroma, sugar and acidity levels, and volatile compound contents; by physical characteristics with fruit size and color, firmness, texture, and resistance to handling; and by nutritional properties related to the health values of some components (Souty et al. 1990; Parolari et al. 1992). All these traits can be highly influenced by climatic conditions, agricultural practices, and storage treatments, but are also dependent on the genotype (Leccese et al. 2012). These traits are very often quantitative, and many genes can be involved in the genetic determinism of fruit quality traits. QTLs involved in fruit quality, including fruit weight, pH, titratable acidity, soluble solid contents (SSC), external color, and flesh color, were found in peach (Dirlewanger et al. 1999; Etienne et al. 2002; Eduardo et al. 2011) and in interspecific cross between peach and *P. davidiana* (Quilot

et al. 2004), recently reviewed by Infante et al. (2011). Many candidate genes for fruit quality have been assigned to linkage groups in peach and have been associated to QTLs (Etienne et al. 2002; Illa et al. 2011). In apricot, only Ruiz et al. (2010) reported preliminary results on the identification of QTLs for fruit weight, ground color, stone weight, sugars, acidity, and firmness in the two F1 populations, "Goldrich"×"Moniqui" and "Lito"×"BO81604311."

After the development of an inoculation technique for *Xanthomonas arboricola* pv. *pruni* and testing the technique on different apricot cultivars, we investigated the resistance against *X. arboricola* pv. *pruni* in an apricot F1 progeny comprising 101 individuals that were derived from the cross of "Harostar"×"Rouge de Mauves" (Socquet-Juglard et al. 2012a, b). Both linkage maps were constructed with a total of 81 microsatellite (SSR) markers and 136 amplified fragment length polymorphism (AFLP) markers. The "Harostar" linkage map is composed of the expected eight linkage groups and covers 553.6 cM; the linkage map of "Rouge de Mauves" is composed of nine linkage groups with two fragments belonging to LG2 and covers in total 684 cM. In this study, a QTL mapping in the same F1 population was performed for architectural habits, time to initial reproductive bud break (IRB), and fruit quality traits. We report QTLs for traits observed in field conditions over two consecutive years for architectural traits and fruit quality traits and over 1 year for time to IRB.

Materials and Methods

Plant Material

The apricot cultivars "Harostar" and "Rouge de Mauves" present differences in time to IRB, "Harostar" being a late-flowering cultivar and "Rouge de Mauves" a very late-flowering cultivar (Christen et al. 2006). Both cultivars widely contrast for their architecture, "Harostar" displaying a fastigiate growth habit (Layne and Hunter 2003) whereas "Rouge de Mauves" displays a drooping habit. "Harostar" produces fruits with a deep orange ground color, with crimson blush, and with high sugar and acidity levels (Lichou et al. 2003), whereas "Rouge de Mauves" produces fruits with a pale orange ground color, with few red punctuations, and with high sugar and acidity levels (D. Christen, unpublished). In early 2009, 102 seedlings were grown in a nursery and planted in spring on their own roots (4×1.70 m) in a field in Conthey, Valais, Switzerland. In order to study the tree architecture, trees were not pruned. Orchards were traditionally conducted following the guidelines of the Swiss integrated production and regularly irrigated by sprinklers. One tree died in 2009 and two died in 2010, resulting in a total of 101 and 99 individuals for assessments in 2010 and 2011, respectively.

Phenotyping

Tree Architecture

All trees were observed during two consecutive years in February 2010 and 2011. The trait "shape" was assessed according to the technical protocol for distinctness, uniformity, and stability tests of the Community Plant Variety Office (CPVO 2012). The scale used comprises six classes: (1) fastigiate, (2) upright, (3) upright to spreading, (4) spreading, (5) drooping, and (6) weeping. The total branch number was determined by counting long shoots and brindles of more than 10 cm; spurs were not taken into account. The total branch number and trunk diameter at 50 cm from the soil permitted to calculate the branch and diameter increments between 2010 and 2011. Trunk length was measured from the ground.

Phenology

Time to IRB was evaluated in 2011 every 2–3 days and expressed in Julian days from 1st January according to the BBCH scale developed for stone fruits by Meier et al. (1994). This trait was considered to correspond to a mark of 51 on the BBCH scale, when flower buds start to swell. Trees without flowers were excluded from the analysis. Maturity date was also expressed in Julian days from 1st January and corresponds to the date when half of the fruits of a tree were considered ripe and were harvested.

Fruit Traits

In 2011 and 2012, fruit batches were picked several times every 2–3 days, when fruits were considered as suitable for consumption and if enough fruits were available with the same maturity stage to constitute one full batch. Each tree was harvested separately and the fruits were grouped into eight fruits per batch, with one to ten batches per tree. Skin color was measured with a Minolta chromameter CR-400 (Konica Minolta, Osaka, Japan). From the values obtained for $a*$ ($-a*$, greenness; $+a*$, redness) and $b*$ ($-b*$, blueness; $+b*$, yellowness), the hue angle, $h°$, was determined according to McGuire (1992). With the filtered juice obtained from the batch, the SSC was measured using an ATAGO digital refractometer PR-1 (Atago, Tokyo, Japan). The SSC value was expressed in °Brix. Fruit form was estimated as the ratio between fruit height and width. Firmness was measured with a Durofel device, with a 0.10-cm^2 probe (Durofel, COPA-Technologie S.A./CTIFL). A titrimeter (Metrohm Titrino 719S, Herisau, Switzerland) was used to measure the titratable acidity. Five milliliters of filtered juice were titrated with NaOH (0.1 mol/l) and the results were expressed in milliequivalent per liter. Fruits and stones were weighed with a Mettler PE 360 Delta range balance (Mettler, Giessen, Germany), while flesh mass was calculated by subtracting the fruit weight from the stone weight.

Linkage Mapping and QTL Analysis

All QTL analyses were carried out with MapQTL® v.5.0 (van Ooijen 2004). The permutation test function (1,000 permutations) was used to calculate the logarithm of odds (LOD) score thresholds. Genome-wide thresholds were determined between 2.1 and 2.5 depending on the traits; however, since no QTL with a LOD score comprised in this interval was found, all QTLs with a LOD score above 2.5 were considered as significant. Kruskal–Wallis test (KW) and interval mapping (IM) were used for QTL analysis. For the Kruskal–Wallis test, only regions with several markers having a minimum significance linkage of $P<0.001$ with the trait of interest were considered. Interactions between different QTLs of the same trait were tested with the multiple QTL mapping (MQM) function when the LOD scores of QTLs found by interval mapping exceeded the significant thresholds. The mapping of the gene for time to IRB was performed with JoinMap 4.0 software (van Ooijen 2006), and the locus found was excluded while performing the QTL analysis of all traits.

Statistical Analysis

Data were checked for their distribution, and the results collected for fruits were subjected to an analysis of variance (ANOVA) to test the genotype effect on fruit quality traits. ANOVA, statistical analyses for Spearman correlations, and the associated P values were performed using the software JMP® v.8.0 (SAS Institute Inc., Carey, NC, USA).

Results

For the eight traits—trunk length; maturity date; titratable acidity; stone, fruit, and flesh weight; and firmness—no QTL was identified by interval mapping in any parent. Variation of the data, correlations obtained within architectural and fruit quality traits, as well as the results of the Kruskal–Wallis tests for these traits are presented in the Electronic supplementary material (ESM Tables S1, S2, S3, and S4).

Architectural Traits

The F1 population greatly varied for the different architectural traits measured, with trunk diameters ranging from 0.5 to 2.5 cm the first year and from 2.1 to

5.9 cm the second year (Table 1). Total branch number also widely varied from 5 to 57 branches in year 2010 and from 9 to 101 branches in year 2011. No weeping shape (class 6) was observed in the F1 population during both years of observation, so the population varied from fastigiate (class 1) to drooping (class 5) shapes. Tree diameter and total branch number were normally distributed, whereas skewed segregations toward the fastigiate tree shapes were obtained in both years (Table 1). Between-year correlations for trunk diameter, total branch number, and tree shape were significant and ranged from 0.47 for trunk diameter to 0.60 for tree shape (ESM Table S2). In both years 2010 and 2011, trunk diameter was significantly linked to all other architectural traits. A correlation depending on the years was found between tree shape and total branch number, for which both traits were significantly linked in 2010, but not in 2011. Because tree shape measured in 2010 and 2011 were highly correlated (ESM Table S2), the data of both years were pooled for further QTL analysis.

The Kruskal–Wallis analysis detected for all architectural traits, except trunk length, a significant linkage ($P<0.001$) to markers located on LG1 for "Rouge de Mauves" in both years (Table 2). Both Kruskal–Wallis and interval mapping tests detected a significant QTL for this parent, with a LOD score of 3.1 (14.5 % of the phenotypic variation explained, PVE) on LG1 for the trunk diameter in 2010, but no association was found in year 2011 (Table 2 and Fig. 1). Two QTLs for tree shape were mapped: one on LG1 (LOD=3.3, PVE=16.7 %) and one on LG5 (LOD=4.3, PVE=22.7 %). Finally, one QTL on LG6 was found for total branch number in 2010 (LOD= 2.9, PVE=14.6 %), but in 2011, only markers in this region were significantly linked by Kruskal–Wallis.

Concerning "Harostar", the Kruskal–Wallis test identified SSR marker UDAp-428A on LG2 as most significantly linked to trunk diameter in 2011. The Kruskal–Wallis test additionally identified SSR marker UDAp-487 on LG1 as linked to tree shape. Interval mapping did not confirm any QTL found by Kruskal–Wallis in "Harostar".

Table 1 Mean, minimum, maximum, and type of distribution of traits observed in the F1 population subdivided by year of observation

Trait	Year	n[a]	F1			Harostar			Rouge de Mauves			Distribution
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	
Architecture												
Trunk diameter (cm)	2010	101	1.7	0.5	2.5							Normal
	2011	99	4.2	2.1	5.9							Normal
Trunk diameter difference (cm)		99	2.5	0.5	3.8							Normal
Total branch number	2010	101	20.8	5	57							Normal
	2011	99	40.3	9	101							Normal
Total branch difference		99	20.4	5	80							Normal
Tree shape[e]	2010	101	2.6	1	5							Skewed toward fastigiate shape
	2011	99	2.5	1	5							Skewed toward fastigiate shape
Phenology												
Time to IRB[b]	2011	96	64.5	55	78							Bimodal
Fruit quality												
SSC (°Brix)	2011	47	15.1	10.2	19.5							Normal
	2012	70	13.6	6.2	19.1	15.7	15.3	16.3	10.6	9.6	11.4	Normal
Ground color[c]	2011	47	70.9	62.3	79.4							Normal
	2012	70	68.8	61.7	77.3	67.1	62.3	73.4	78.9	63.1	87.9	Normal
Fruit form[d]	2011	47	1.09	0.98	1.26							Normal
	2012	70	1.14	0.96	1.38	1.15	1.03	1.25	1.05	0.92	1.16	Normal

[a] Number of genotypes observed for each trait

[b] In Julian days from 1st January

[c] Hue angle as determined by $h°=\arc \tan(b*/a*)$: 0°=red/purple, 90°=yellow, 180°=bluish/green, 270°=blue (according to McGuire 1992)

[d] Ratio height/width

[e] No genotype in class 6 (weeping) was observed; for the parents, only one tree was observed. "Harostar" scored 1 and "Rouge de Mauves" scored 5

Table 2 Significant QTLs for tree architecture, phenology, and fruit quality traits detected by Kruskal–Wallis test and Interval Mapping (IM)

Traits	"Harostar"						Allele size[f]		Allele effect[f]		"Rouge de Mauves"						Allele size[f]		Allele effect[f]	
	LG	Position[a]	Marker[b]	KW[c]	LOD[d]	PVE[e]	0	1	0	1	LG	Position[a]	Marker[b]	KW[c]	LOD[d]	PVE[e]	0	1	0	1
Architecture																				
Trunk diameter, 2010											LG1	23.5	PaCITA5	***	3.1	14.5	137	214	1.5	1.8
											LG1	135.3	BPPCT011	*			0	196	1.6	1.8
Trunk diameter, 2011	LG2	13.4	UDAp-428A	**			123	121	3.9	4.4	LG1	99.3	E13-M12-201	*					4	4.3
Total branch number, 2010											LG1	77.2	E13-M12-107	*					18	23
											LG6	37.8	UDAp-492	***	2.9	14.6	192	214	16	24
Total branch number, 2011											LG1	99.3	E13-M12-201	**					35	45
											LG6	48.1	E13-M13-414	**					35	44
Tree shape, 2011/2012[g]	LG1	100.1	UDAp-487	*			130	179	1.6	1.9	LG1	14.1	E13-M13-193	***	3.3	16.7			1.8	2.7
											LG1	150.9	E13-M18-220	**					2.6	1.9
											LG5	37.8	E13-M13-439	***	4.3	22.7			2.7	1.9
Phenology																				
Time to IRB, 2011	LG1	60.8	UDAp-414	***	6.5	30.3	176	217	61	67.5	LG7	41.1	UDAp-407	**			194	176	62.3	66.5
	LG4	8.6	PaCITA25	***	3.1	14.1		216	62	66.5										
Single gene mapping IRB	LG1	72.3	IRB		5.0[h]				59	70.5										
Fruit quality																				
SSC, 2011	LG1	17.3	UDAp-415	***	3.1	26	164	0	15	16.7	LG3	54.9	UDAp-496	*			0	190	14.2	15.9
SSC, 2012	LG4	28.7	E13-M13-134		3.9	24.7			13	14.7	LG4	91.3	E13-M13-353	***	2.7	16.8			12.9	14
Ground color, 2011	LG3	35.9	E13-M18-296	***	6.7	50.9			73	68.1	LG3	59	E13-M18-252	**					68.6	72.2
	LG7	1.5	E13-M12-144	***	3.1	26.8			69	72.9	LG7	10.5	E13-M12-103	*					69.9	72.2
Ground color, 2012	LG3	55	E12-M13-70	***	9.8	51.5			65	72.7	LG3	34.35	UDAp-446	***	2.8	18.9			66.8	70.9
	LG7	3.9	E13-M18-249	***					66	71.8										
Fruit form, 2011	LG3	26.2	E13-M18-68	***	4.4	35.7			1.1	1.13	LG1	32.2	E12-M12-342	**					1.07	1.13
											LG5	30.8	E13-M13-349	**					1.06	1.12
Fruit form, 2012	LG3	64.09	E13-M18-200	***	3.5	20.7			1.1	1.17										

Kruskal–Wallis test indicates only the marker that most highly significantly linked to the trait

LG linkage group

[a] Location (in cM) of the QTL peak determined by interval mapping (not of the marker closest to the peak) or, in case interval mapping did not find a significant QTL, the location of the marker linked to the trait by the Kruskal–Wallis test. The most significantly linked marker per trait is reported only if other markers in the same region were also significantly linked to the same trait

[b] Marker information is available in Socquet-Juglard et al. (2012a)

[c] P value obtained by Kruskal–Wallis test: *$P<0.005$, **$P<0.001$, ***$P<0.0001$

[d] LOD score determined by interval mapping

[e] Phenotypic variance explained by the peak of the QTL (in percent)

[f] Segregating allele scored and mean value obtained for the progeny possessing either the "0" or "1" allele. For AFLPs, allele "1" corresponds to the size of the amplified fragment

[g] QTLs identified with both years' datasets combined

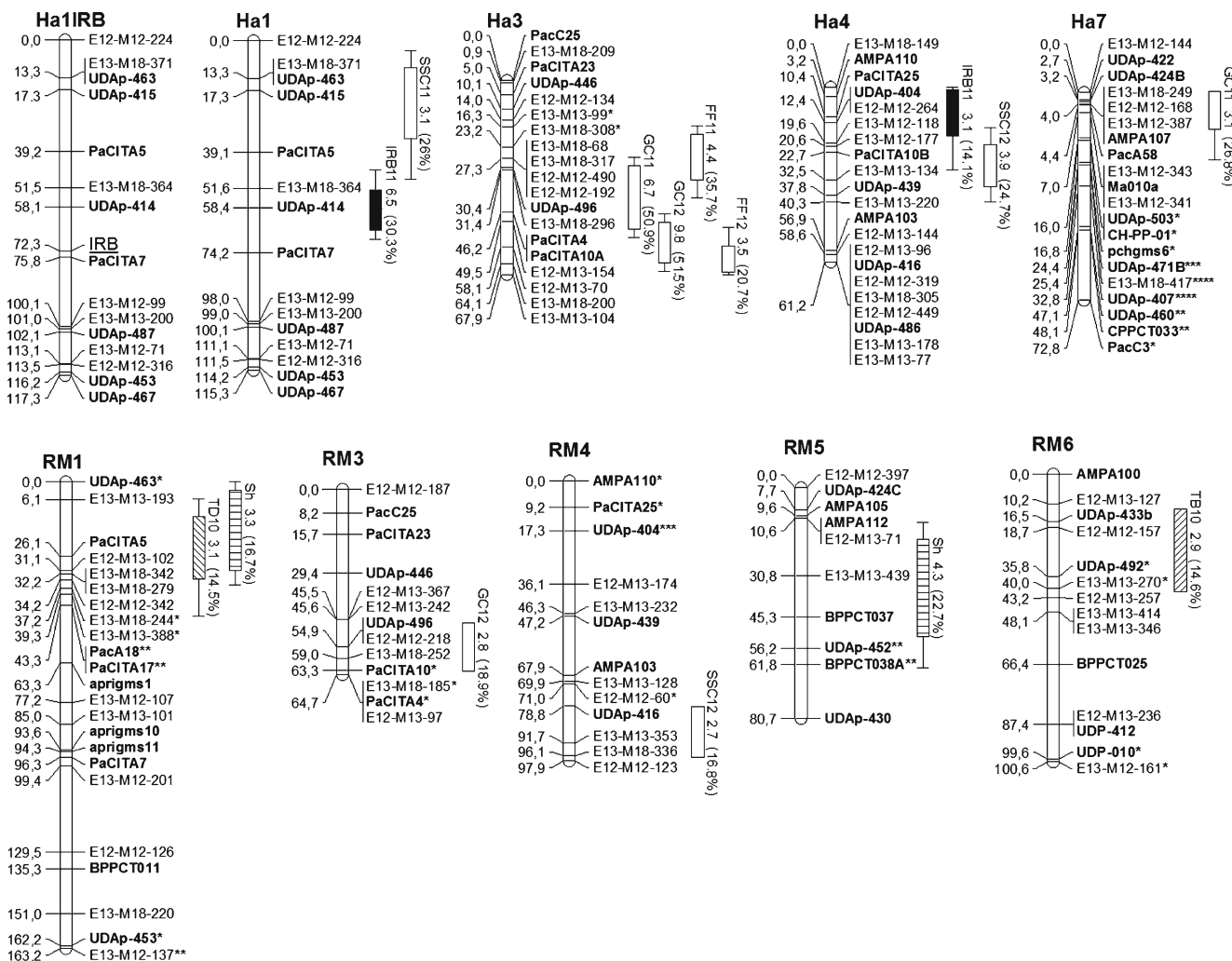[h] Maximal LOD score to which IRB was mapped at this position

Fig. 1 Location of QTLs determined by interval mapping controlling architectural, phonologic, and fruit quality traits in the F1 population "Harostar"×"Rouge de Mauves." Only the linkage groups for which QTLs were detected are represented. The names of the linkage groups (LG) correspond to the parents "Harostar" (Ha) and "Rouge de Mauves" (RM), and these LG are numbered according to the current *Prunus* linkage mapping nomenclature. Genetic distances are shown on the *left* of the linkage maps; names of the markers are indicated on the *right*. Microsatellite markers are indicated in *bold*. Markers showing segregation distortion are indicated by *asterisks*: significant distortion at P<0.05, **P<0.01, ***P<0.005, and **** P<0.001. QTLs are represented alongside the right of the corresponding linkage groups.

Striped boxes indicate architectural QTLs, *black boxes* indicate QTLs for phenology, and *white boxes* indicate QTLs for fruit quality. The LOD scores are indicated after abbreviations of corresponding traits as trunk diameter (*TD*), total branch number (*TB*), tree shape (*Sh*), time to IRB (*IRB*), soluble solid content (*SSC*), ground color (*GC*), and fruit form (*FF*). Phenotypic variation explained is provided in *brackets*. *10*, *11*, and *12* indicate the years 2010, 2011, and 2012, respectively. Time to IRB (*IRB*) locus is *underlined* and is indicated in Ha1IRB. Confidence intervals of 2 LOD are represented with *lines*. *Boxes* represent a 1 LOD confidence interval. When the LOD score was <3, only the 1 LOD confidence interval was drawn

Phenology

The F1 population varied greatly for time to IRB, with a difference of 23 days between the first and last tree which produced flower buds and ranged from 24th February to 19th March. A bimodal distribution was observed for this trait (Table 1 and Fig. 2). This distribution allowed us to divide the population into two classes (fast and slow time to IRB) and to map the time to IRB as a qualitative trait. The group "fast IRB" is composed of plants having a time to

IRB shorter than 65 days, while the "slow IRB" group is composed of plants with a time to IRB greater than 69 days. Five progeny plants identified with the frequency distribution in between the two groups were excluded from the single gene mapping since it was not clear to which group the genotypes had to be assigned. This trait was mapped on LG1 of "Harostar" at about 3.5 cM above the SSR marker PaCITA7 (Ha1IRB; Fig. 1).

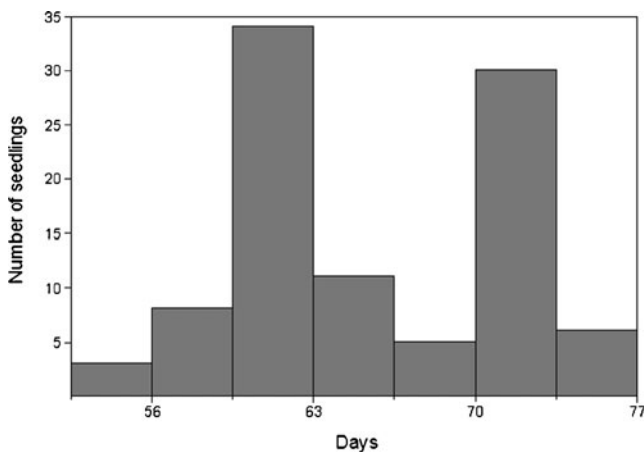In "Rouge de Mauves", the Kruskal–Wallis test identified one linkage group, LG7, with SSR UDAp-407 most

Fig. 2 Frequency distribution of the time to IRB in 2011 in the "Harostar"×"Rouge de Mauves" population

significantly linked to time to IRB. In "Harostar", when considering time to IRB as a quantitative trait, both Kruskal–Wallis and interval mapping tests identified two QTLs: one on LG1 (marker UDAp-414) close to the locus identified by single gene mapping accounting for 30.3 % of the PVE (LOD=6.5) and the second one on LG4 accounting for 14.1 % of PVE (LOD=3.1; Table 2 and Fig. 1). The MQM analysis performed did not permit identifying any multiple linked QTL.

Fruit Quality Traits

Forty-seven trees in 2011 and 70 in 2012 produced a sufficient number of fruits to perform statistical analysis for fruit quality traits. All traits related to fruit quality were normally distributed (Table 1), and ANOVA revealed highly significant genotype effects for all those traits ($P<0.0001$, ESM Table S5). An important variability in SSC was observed, which ranged from 10.2 to 19.5°Brix in 2011 and from 6.2 to 19.1 in 2012 (Table 1). Hue angle, which was the value used for ground color, also greatly varied in orange tones from 62.3° to 79.4° in 2011 and from 61.7° to 77.3° in 2012. Fruit form expressed as the ratio between height and width ranged from round fruits (0.98) to a more cylindrical form (1.26) in 2011 and from 0.96 to 1.38 in 2012. High correlations among years for ground color, fruit form, stone weight, and titratable acidity were found, ranging from 0.51 for titratable acidity to 0.70 for ground color, whereas SSC, firmness, and fruit and flesh weights were not correlated among years (ESM Table S3).

For "Rouge de Mauves", the Kruskal–Wallis test identified in 2011 marker UDAp-496 on LG3 as linked to SSC; two markers, E13-M18-252 and E13-M12-103, linked to ground color on LG3 and LG7, respectively; and two AFLP markers, E12-M12-342 and E13-M13-349, linked to fruit

form on LG1 and LG5, respectively. No QTL was found at a genome-wide significance by interval mapping for "Rouge de Mauves" in 2011. In 2012, both Kruskal–Wallis and interval mapping tests identified one QTL for SSC on LG4 accounting for 16.8 % of the PVE (LOD=2.7) and one QTL for ground color on LG3 accounting for 18.9 % of the PVE (LOD=2.8; Table 2 and Fig. 1).

Concerning "Harostar", in 2011, the Kruskal–Wallis and interval mapping both identified the same regions involved in SSC, ground color, and fruit form (Table 2 and Fig. 1). One QTL on LG1 was associated with SSC and explained 26 % of the PVE (LOD=3.1). Two QTLs were mapped for ground color on LG3 and LG7, explaining 50.9 and 26.8 % of the PVE (with LOD of 6.7 and 3.1, respectively). Finally, one QTL was identified on LG3 for fruit form and explained 35.7 % of the PVE (LOD=4.4). In 2012, a QTL for SSC accounting for 24.7 % of the PVE (LOD=3.9) was mapped on LG4, a QTL for fruit form accounting for 20.7 % of the PVE (LOD=3.5) was identified on LG3, and a major QTL on LG3 was detected for ground color in a region close to the one found in 2011 and accounted for 51.5 % of the PVE (LOD=9.8). The QTL found for ground color on LG7 in 2011 was not detected by interval mapping in 2012, but markers in the exact same region were significantly linked by the Kruskal–Wallis test to the trait. MQM mapping did not reveal any multiple linked QTL.

Discussion

Despite an important research in *Prunus* for architectural traits, fruit quality traits, and flowering time, information about the genetic determinism of these traits in apricot is scarce. In peach, many architectural traits (bushy, brachytic dwarf, pillar, compact shape, and weeping shape) are controlled by single genes (Lammerts 1945; Mehlenbacher and Scorza 1986; Chaparro et al. 1994; Monet et al. 1996), and their effects are well characterized (Scorza 2002; Werner and Chaparro 2005); however, to our knowledge, only the recessive gene *br* controlling pillar growth has been mapped on LG2 (Sajer et al. 2012). The data obtained for tree shape permitted identifying in our population different genomic regions linked to more fastigiate or more drooping architectural types. Because trees did not produce any fruit in 2009 and 2010, tree shape was not influenced by the load of the fruits, resulting, as expected, in high correlations obtained between 2010 and 2011 for this trait. This allowed the pooling of the data before performing a QTL analysis in order to reduce the environmental effect and evaluator bias.

Two QTLs were mapped in "Rouge de Mauves" for tree shape: one on LG1 and one on LG5. The shape of the trees

possessing the combination of the 2 alleles for drooping shape (allele "1" of E13-M13-193 on LG1 and allele "0" of E13-M13-439 on LG5; Table 2) was significantly more drooped (mean value of 3.2) than the shape of the trees possessing only one of the alleles for drooping shape (mean value of 2.7). Inversely the shape of the trees possessing the combination of the 2 alleles for fastigiate shape (allele "0" of E13-M13-193 and allele "1" of E13-M13-439) was also significantly more fastigiate (mean value of 1.6) than the shape of trees possessing only one of the alleles for fastigiate shape (mean values of 1.8 and 1.9). The two intermediate combinations gave intermediate results (both 2.1). Therefore, the QTLs involved in tree shape have an additive effect in both directions. From an agronomic point of view, the control of plant size and shape is an important goal to achieve in tree species because it has a direct impact on yield and on the amount of labor required for pruning, with consequences for the successful management of diseases (Costes et al. 2004; Fournier et al. 2004; Segura et al. 2007). The QTLs we identified for tree shape and their additive effects should help breeders to give trees a more fastigiate or spreading shape depending on the production system requirements.

In this study, the correlations obtained for the studied architectural traits showed that the traits we measured are related. This was verified with the detection of a region on the bottom of LG1 of "Rouge de Mauves" (from marker E13-M12-107 to marker E13-M18-220) which was involved in the variation of all architectural traits. This region on LG1 is located close to a homologous region in peach where the evergrowing gene evg was mapped (Bielenberg et al. 2008). Although QTLs were not always confirmed by interval mapping in the second year, markers linked to the traits in close regions were identified by the Kruskal–Wallis test in the second year for total branch number and trunk diameter, indicating that these QTLs could be stable.

Flowering time has been widely studied in Prunus, and QTL mappings performed have identified several regions, scattered on most linkage groups (Joobeur et al. 1998; Dirlewanger et al. 1999, 2012; Verde et al. 2002; Fan et al. 2010; Cao et al. 2012). Exceptionally warm temperatures in 2011 during the evaluations between bud break and flowering time greatly accelerated the flowering time of the slowest individuals, provoking the full bloom of all F1 progeny in a very short time. This phenomenon induced a very low variation in the progeny population, which did not permit to perform a QTL analysis for blooming date in Julian days; instead, we used the time to IRB, which led to the detection of the IRB locus and of QTLs located in similar regions where QTLs for flowering time have been previously identified in peach. We identified two QTLs involved in time to IRB in "Harostar". The QTL on LG1 is located downstream from the region where QTLs for blooming date (Quilot et al. 2004) and for flowering date (Dirlewanger et al. 2012) were previously identified. In addition, the region where we identified IRB by single gene mapping, as well as the QTL for time to IRB is close to the homologous region in peach containing the gene PrpMADS5 involved in flowering time and floral organ development (Xu et al. 2008). The second region involved in time to IRB on top of LG4 is in a similar position to the regions identified by Cao et al. (2012) in peach, by association mapping, and corresponds to the region where the Late bloom gene (Lb) was mapped in almond (Ballester et al. 2001). Both QTLs on LG1 and LG4 also correspond to regions found in peach by Fan et al. (2010) and by Dirlewanger et al. (2012) in peach, apricot, and sweet cherry. In apricot, Ruiz et al. (2010) also found one major QTL on LG4, although they did not indicate its precise position on the map. In our study, an additive effect was observed for trees possessing both alleles for early IRB (alleles "0" of markers UDAp-414 and PaCITA25) or late IRB (alleles "1" of the same markers), with IRB averages of 59 or 69 days, respectively. Trees with intermediate allele combination (early/late or late/early) had a time to IRB of 63–65 days. The difference of pyramiding the two alleles inducing early or later IRB compared to the presence of only one of these alleles is only approximately 2 days. This difference looks rather small to be considered by breeders. The IRB locus, identified by single gene mapping, has a very similar effect (59.2 vs. 70.5 days) to the combination of the 2 early or late alleles of the QTLs for time to IRB (Table 2). The marker closest to the IRB locus is the SSR marker PaCITA7 at 3.5 cM. The alleles of this marker associated to early and late IRB have a size of 213 bp for early IRB and 196 bp for late IRB. Since this marker is an SSR and the effects are similar to those obtained by pyramiding both QTLs, we advise using this marker for the selection of early or late IRB genotypes. However, marker PaCITA7 cannot be used to delay or fasten the ripening date since no correlation was found between time to IRB and the maturity date in our study (data not shown), in accordance with results previously observed in peach (Quilot et al. 2004; Layne and Bassi 2008; Cao et al. 2012).

Marker-assisted selection for fruit quality traits represents a very cost-effective technique to discard at a very early stage genotypes for which fruit qualities do not meet grower and consumer expectations. When price is not taken into account, fruit size, shape, and skin color are key factors that will determine the purchase choice made by consumers (Moreau-Rio and Roty 1998; Moreau-Rio 2006). In addition, consumers prefer apricot fruits with a high sugar content, over 12°Brix (Azodanlou et al. 2003), and this characteristic by far prevails over other criteria such as "juicy", "melting", or "acidulous" (Moreau-Rio 2006). The large variability of soluble solid contents (SSC) observed in our F1 progeny (Table 1) allowed the identification of a QTL on LG1 in 2011 and on LG4 in 2012. In peach, significant year effects were previously reported (Brooks

et al. 1993; Dirlewanger et al. 1999; Cantìn et al. 2009), and QTLs for SSC have been identified on LG2, LG3, LG4, and LG6 (Dirlewanger et al. 1999; Eduardo et al. 2011). Similarly, in our study, this trait did not correlate among years, and we could consequently not confirm the QTLs. The lack of correlation could be due to the differences in climate between years or to a different fruit load on the trees (as hypothesized by Cantìn et al. 2009).

Although consumers prefer fairly round fruits (Moreau-Rio 2006), fruit shape has not previously been an important criterion of study in apricot as it has been in peach breeding. A QTL for fruit shape was mapped on LG3 in 2011 and was detected in 2012 in a close region. To our knowledge, this would be the first report of the identification of a QTL for fruit shape in apricot. Concerning the trait "ground color", two QTLs were identified on LG3 and LG7 in 2011 and were confirmed in 2012 by interval mapping for the first and by Kruskal–Wallis test for the second. When scored as a qualitative trait, the *Sc* locus for red or green color has been mapped in peach on LG6 (Yamamoto et al. 2001; Dirlewanger et al. 2004), and QTLs with a low repeatability over 2 years of observation were mapped on LG3, LG6, and LG7 by Eduardo et al. (2011), whereas Dirlewanger et al. (1999) did not find any QTL for skin color. In apricot, Ruiz et al. (2010) identified QTLs on LG2, LG3, and LG6 for ground color. Our results are in agreement with Ruiz and Egea (2008) who hypothesized that apricot skin color could have an important genetic determinism since year-by-year differences were not observed during their 2 years of observations. With the dataset of 2011, when combining both alleles for a more yellow/orange color (allele "0" of marker E13-M18-296 on LG3 and allele "1" of marker E13-M12-144 on LG7; Table 2) or for a more orange/red tone (allele "1" of marker E13-M18-296 and allele "0" of marker E13-M12-144), no significant difference in hue angle was observed (73.8 and 67.9, respectively), with values similar to the effect of an allele alone (approximately 73° for yellow tones and 68° for red tones; Table 2). This shows that these QTLs have no additive effects. Ruiz et al. (2005) showed that there was a linear correlation between hue angle and the carotenoid content of the fruits measured by HPLC. Consequently, with the QTLs identified for ground color, breeders could have an interesting tool for the selection of fruits with both higher nutritional properties and a more orange color.

Additional traits were scored in our population. For architectural traits, trunk length was measured and was correlated with other architectural traits for which QTLs were identified (ESM Table S2). For fruit quality traits, stone mass, fruit mass, flesh mass, titratable acidity, and firmness were measured in both years (ESM Table S1). Although all these architectural and fruit quality traits greatly varied in our progeny population during both years of observation, the interval mapping performed did not permit to identify any QTL linked to one of these traits; however, markers were found to be linked with these traits only by the Kruskal–Wallis test (ESM Table S5). The significant genotype effect for fruit quality traits indicates that there is a possibility to breed for an increased fruit quality (ESM Table S4). A too small population size, especially for the fruit quality traits, could explain why we did not detect any QTL for these traits. In addition, if both alleles of one parent have a similar contribution to a trait, no QTL can be detected.

In this study, several QTLs were identified over 1 year for phenology and over 2 years for architectural and fruit quality traits. QTLs identified for the same or similar traits as the ones previously described in peach were often detected in regions comparable to the ones identified in peach by other authors; this reflects the high synteny within the *Prunus* species and between peach and apricot, in particular.

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