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Genetic analysis of organoleptic quality in fresh market tomato. 2. Mapping QTLs for sensory attributes

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Abstract The organoleptic quality of fresh market tomato can be described by a set of attributes, including fruit appearance, taste, aroma and texture. Sensory analysis is the most-valid method to study organoleptic characteristics, particularly aroma and texture. A range of 144 recombinant inbred lines of tomato derived from a cross between a cherry tomato line and a large-fruited line was evaluated by descriptive sensory profiling. Taste was analyzed through sweetness and sourness, and aroma was analyzed through the overall aroma intensity, together with candy, lemon, citrus-fruit and pharmaceutical aroma. Texture was characterized by firmness, meltiness, mealiness, juiciness and difficulty to swallow the skin. A wide range of overall variation was shown for all the attributes and significant differences among genotypes were detected. The overall aroma intensity was positively correlated with sweetness and sourness, as well as with lemon, candy and citrus fruit aromas. It was negatively correlated with mealiness. Sweetness and sourness were negatively correlated together. Molecular markers were used to map quantitative trait loci (QTLs) for each sensory attribute. One to five QTLs were detected, by simple and composite interval mapping, per attribute. The percentage of phenotypic variation explained ranged from 9% to 45% per QTL. Clusters of QTLs were observed on chromosomes 2 and 9, involving QTLs for aroma, taste and texture attributes. Most of the favorable alleles came from the cherry tomato parent, showing the potential usefulness of this line for tomato organoleptic quality improvement.

Keywords Tomato · Sensory analysis · Organoleptic quality · QTL · Composite interval mapping

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Introduction

Since the 1970s, the yield and the yield stability of fresh market tomato has increased, together with adaptation to glasshouse conditions. Tomato fruit quality for the fresh market has also been strongly improved for 30 years. Fruit appearance and homogeneity were first improved. More recently, firmness and long shelf life, required for shipping to distant markets, retained the attention of fresh market breeders (Tigchelaar 1986). With the availability of tomato all year round and with the spread of long shelf life varieties, consumers began to complain about tomato flavor. Such criticisms seemed common to many countries such as the USA (Kader et al. 1977), Australia (Ratanachinakorn et al. 1997), the Netherlands (Janse and Schols 1995) and France (Decoene 1995). Consumers frequently associate recent varieties with a lack of flavor, although such an association could not be proven (Bruhn et al. 1991). Modifications in texture, mainly the increase in firmness observed in the modern varieties, are probably also responsible for consumer complaints. Taste-panel studies have shown that sweetness and sourness were the major determinants of tomato flavor preference (Stevens et al. 1977). Appearance, color, aroma, and texture are also major components of organoleptic quality.

Sensory analysis is the most-valid method to study organoleptic characteristics and has recently been used for the taste description of different fruits such as peach (Esti et al. 1997) or blackcurrant (Brennan et al. 1997). In tomato, Hobson et al. (1990) characterized the flavor of different tomato varieties by sensory profiling. They found strong differences between the flavor of cherry tomato and large-fruited tomatoes, the former being much

sweeter and showing a higher overall aroma intensity. The flavor of tomato was found to be influenced not only by the variety and nutritional regime of the plants (Hobson and Bedford 1989; Petersen et al. 1998), but also by the stage of ripening when picking fruit (Kader et al. 1977, 1978) and by post-harvest storage conditions (Ratanachinakorn et al. 1997). Kader et al. (1978) noted a decrease in the flavor of green-harvested or refrigerated fruits. Sensory analysis was also used to assay the perception of transgenic fruits with reduced polygalacturonase activity (Sozzi Quiroga and Fraschina 1997). Studies were performed to identify associations between fruit composition or physical characteristics and sensory traits (Baldwin et al. 1998). Sweetness and sourness were commonly found associated with sugar- and acid-content, respectively. Sugar- and organic acid-content, together with the sugar/acid ratio, were the major chemical compounds of consumer preference (Stevens 1979). Apparently the proper balance of these compounds is required to give optimal flavor, and a given sugar level corresponds to an optimal acid content (Malundo et al. 1995). Volatile compounds contribute to the tomato overall aroma intensity and numerous studies were devoted to identify the major constituents responsible for tomato aroma (Langlois et al. 1996; Baldwin et al. 1998; Krumbein and Auerswald 1998). Sweetness, sourness and overall aroma intensity are the three most-studied attributes (Jones and Scott 1984; Kader et al. 1977).

Most of the traits of interest, including the sensory attributes, have a continuous variation, strongly influenced by environmental conditions. The genetic variation of such traits has been attributed to the joint action of many genes. With the development of molecular markers, a number of saturated genetic maps have been constructed in plant species, which has allowed the location of loci (named QTLs for quantitative trait loci) controlling quantitative trait variation. Since the pioneer work of Paterson et al. (1988), QTL analysis has been applied to numerous species and traits. For most of these traits, a limited number of QTLs were detected, explaining a large part of the variation. In tomato, most of the studies concerned yield and quality traits (pH, soluble-solids content and fruit weight) of processing tomato (Paterson et al. 1988, 1991; Eshed and Zamir 1995), but also horticultural traits (Grandillo and Tanksley 1996; Bernacchi and Tanksley 1997; Fulton et al. 1997), as well as adaptation to abiotic stress (Foolad et al. 1997). Molecular markers are highly efficient for the evaluation of exotic germplasm (Tanksley and McCouch 1997), particularly in tomato where most of the molecular variability was found between related wild species rather than within the cultivated species. QTLs were detected with most of the species related to *Lycopersicon esculentum* (see Chen et al. 1999 for a recent review). QTL analysis was also applied to quality traits in peach (Dirlewanger et al. 1999), cucumber (Kennard and Havey 1995) and lemon (Fang et al. 1997). A recent publication reported the identification of QTLs associated with sensory preference in sweet corn (Azanza et al. 1996).

The purpose of the present paper is to study the inheritance of sensory attributes related to the fresh market tomato organoleptic quality and to describe the QTLs affecting these traits. We selected a remarkable cherry tomato line (Cervil) with strong aroma intensity, which was crossed to a large-fruit line. A segregating population was derived and assessed by a trained panel for 12 sensory attributes. The paper describes: (1) the analysis of sensory attributes in a large population size, (2) the study of the correlations between the various attributes, and (3) the location and characterization of QTLs.

Materials and methods

Mapping population

The studied population comprises 144 recombinant inbred F_7 lines (RILs) derived from the cross between a cherry tomato *L. esculentum* var. *cerasiforme* (Cervil, coded C) and a round larger-fruited tomato line (Levovil, coded L). The VILMORIN seed company provided both parental lines. The plant materials are described in Saliba-Colombani et al. (2000a).

Glasshouse trial

The 144 RILs were grown in a heated glasshouse during a spring crop (January–July) in a fully randomized trial. The two parental lines were each represented by three plots and the F_1 hybrid by nine plots. Each plot consisted of a single row of six plants. Ripe fruits were harvested daily during 6 weeks at the red stage, 1 day before fruit evaluation. Fruits with a homogeneous color were selected for sensory evaluation. Special care was taken to provide panelists with fruits at the same ripening stage.

Sensory profiling

Sensory analysis was performed with a panel of 54 trained panelists. Judges were grouped into four panels. Three were composed of seed company employees (CLAUSE, VILMORIN, TEZIER), with 20, 8 and 8 panelists, respectively. The fourth panel (DIJON) was composed of 18 volunteers already trained for sensory analysis with other products. This panel performed three assays per week, while the other three performed only one. Each panel was drawn by a leader. Panelists were trained during 13 assays before the experiment began. Attributes were selected after 2 years of sensory analyses with related tomato material. Taste attributes were sweetness (SWE) and sourness (SOU). Aroma attributes were overall aroma intensity (INT), candy aroma (CAN), lemon aroma (LEM), citrus-fruit (other than lemon) aroma (CIT) and pharmaceutical aroma (PHA). Texture attributes were flesh firmness (FIT), mealiness (MEA), meltiness (MEL), juiciness (JUI) and embarassing skin (SKI). Flavor descriptors were defined by reference solutions in mineral water: glucose (6 g/l) and fructose (6 g/l) for sweetness, citric acid (1 g/l) for sourness, lemon juice (30 ml/l) for lemon aroma, candy (40 g ground/l) for candy aroma, juice from half a pomelo and one orange for citrus-fruit aroma, and guaiacol (10 µl/l) for pharmaceutical aroma. Aroma intensity corresponded to the general impression of aroma before swallowing. Definition of texture attributes were as follow : mealiness – the sample is dry, mealy, powdery and non-sticky, saliva is necessary to swallow it; meltiness – the sample turns from solid to liquid easily, without chewing; juiciness – the sample liberates some juice when chewed, this juice comes from flesh and gel; firmness – the sample resists when chewed; embarrassing skin – the skin is difficult to swallow and tends to stay in the mouth. Panelists were instructed to cleanse their palate with bread and mineral water bet-

Table 1 Average values of sensory attributes of the parental lines Cervil and Levovil, and their F_1 hybrid. Significance level of the comparison test of Cervil vs. Levovil means (C vs. L). Average values, minima, maxima and standard error of the mean of the 144 RILs derived from the cross Levovil × Cervil

Attribute	SWE	SOU	ARO	LEM	CAN	CIT	PHA	FIT	MEL	JUI	MEA	SKI
Parent means												
Cervil	31.45	65.29	53.29	37.68	22.40	17.11	10.69	37.05	37.34	71.31	8.71	50.94
Levovil	29.23	19.95	27.53	11.97	8.85	16.21	18.77	24.10	68.45	65.52	18.97	46.19
C vs. L	ns	***	***	***	***	ns	ns	***	***	ns	ns	ns
F_1 hybrid	34.65	52.87	47.86	32.25	20.83	18.53	6.84	43.20	39.04	65.55	14.47	50.56
RIL												
Mean	36.36	41.11	41.65	22.49	16.65	15.82	11.41	44.67	40.60	57.52	18.92	50.44
Std. error	5.12	5.03	4.14	4.69	4.54	4.40	3.72	4.40	5.39	4.66	4.33	6.03
Min.	14.74	15.55	22.91	3.73	3.74	3.40	1.40	11.53	12.23	33.61	5.44	25.31
Max.	62.33	69.88	58.07	47.83	34.18	30.88	34.62	79.95	82.86	75.14	44.07	82.97

ns : non-significant; *** $P < 0.001$

ween each sample. Each attribute was rated on a 10-cm unstructured scale with anchor points (low-high) at each end. The data were converted to a 0–100 scale for analysis.

In a session, each panelist had to assay seven samples, ranked in a specific order. The last sample was always the hybrid control. Depending on fruit size, each sample (coded by three numbers) was represented by two or three fruits. Each line was evaluated once by about 18–23 judges in an incomplete randomized block design trial. As each panelist could not taste all the RILs, the experiment was designed following an incomplete block design (a block is an assay) to equilibrate the pairs of lines seen in the same assay and their rank of presentation. Pairs of consecutive lines were considered in order to minimize the carry over effect. Lines were also equilibrated over the weeks. As the experimental design was carefully respected, its strong equilibrium properties ensured the best estimations of the means per line.

Molecular map

The construction of the genetic map is described elsewhere (Saliba-Colombani et al. 2000a). For QTL mapping, a subset of 103 loci (one morphological, 84 RFLPs, two RAPDs, and 16 AFLPs) well distributed over the genome was selected. It covers 965 Kosambi cM, which corresponds to 85% of the genome, when compared to the saturated tomato-genome map (Tanksley et al. 1992).

Statistical analyses

Panelist performance and diversity among lines

The F_1 hybrid was used as a control in each assay. For each attribute, panelist performances were evaluated by the correlation coefficient between variances of the hybrid control and variances of RILs they assayed. Panelists showing extreme variances were discarded from the data set. The means of parental lines (represented each by three plots) were compared by analyses of variance. Differences among RILs, panelists, weeks and presentation rank were tested by analyses of variance. As the design was unbalanced, we used the GLM type-III procedure and only main effects were tested. Least square means of the RILs were then estimated with the panelist effect, in the model panelist + week + line, by an LSMEANS procedure. When the week-effect was significant, a linear regression was performed over the 6-week values. Pearson correlation coefficients were estimated among sensory attributes on the adjusted means of the RILs. All the statistical analyses were performed with the SAS (SAS Institute Inc. 1994) statistics package.

QTL analysis

For each attribute, a Lilliefors test was performed on the genotype means to assess for normality of the distributions. QTL detection was first performed with linear regression and simple interval mapping (IM). Composite interval mapping (CIM) was then performed. A forward-backward stepwise regression was used for the selection of co-factors. The five markers with highest *P*-values were added as co-factors in the composite interval mapping step (model 6, using a moving window size of 10 cM). Significance thresholds were evaluated for IM and CIM by 1000 permutations of each analysis, and an experiment-wise error threshold of 0.10 was retained. A QTL was thus detected when its LOD was higher than 2.36 for IM, and higher than 2.56 for CIM. When two QTLs were detected by CIM within less than 20 cM, only the most-significant was retained. The part of phenotypic variation explained by the QTL (R^2) was estimated in the model. All analyses were performed with the QTLCartographer software (Basten et al. 1997). Two-way interactions between pairs of markers were tested with two-factor ANOVAs. Tests were performed for the 84 RFLP markers of the framework map. A significant interaction was detected when $P < 0.0001$.

Results

Variation of sensory attributes

Fruits from Cervil were significantly more sour, exhibited a stronger overall aroma intensity, a higher lemon and candy aroma, and were firmer and less-melting than Levovil fruits (Table 1). The F_1 hybrid showed intermediate values between its two parental lines for eight attributes, although often closer to Cervil than to Levovil. It also showed higher means than both parents for sweetness, citrus-fruit aroma and firmness, and a lower mean for pharmaceutical aroma. The results of the analyses of variance on the data describing the RILs are summarized in Table 2. For each attribute, differences among the four panels were much-less significant than among panelists (data not shown). The 54 panelists were thus grouped as a unique panel. Comparable percentages of variation were observed among lines and among panelists, both highly significant. The variation among lines was higher than among panelists for sourness, firmness and meltiness. By contrast, cit-

Table 2 Percentage of variation attributable to line, panelist, week and order of presentation effects among the RIL fruits. Ratio of the sum of squares of factor over the total sum of squares (SS/SST) for sensory attributes and associated level of significance (PROB.)

Factor	*df*		SWE	SOU	ARO	LEM	CAN	CIT	PHA	FIT	MEL	JUI	MEA	SKI
Line	143	SS / SST	0.14	0.22	0.12	0.10	0.09	0.06	0.11	0.36	0.28	0.13	0.14	0.15
		PROB.	***	***	***	***	***	***	***	***	***	***	***	***
Panelist	48	SS / SST	0.22	0.18	0.17	0.23	0.25	0.20	0.15	0.12	0.21	0.30	0.22	0.28
		PROB.	***	***	***	***	***	***	***	***	***	***	***	***
Week	5	SS / SST	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.01	0.05	0.01
		PROB.	***	ns	ns	**	ns	ns	ns	***	*	***	***	***
Order	5	SS / SST	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.01
		PROB.	*	ns	**	***	ns	ns	***	ns	**	ns	ns	***
Error	2548	SS / SST	0.62	0.60	0.70	0.66	0.66	0.74	0.72	0.50	0.50	0.56	0.59	0.55

ns : non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3 Phenotypic correlations among sensory attributes in the RIL population. Only significant correlations are shown ($P < 0.05$)

Trait	SWE	SOU	ARO	LEM	CAN	CIT	PHA	FIT	MEL	JUI	MEA	SKI
SWE												
SOU	–0.41											
ARO	0.37	0.48										
LEM	–0.38	0.79	0.41									
CAN	0.66	ns	0.56	ns								
CIT	0.61	ns	0.50	ns	0.58							
PHA	ns	–0.22	ns	–0.25	–0.34	–0.27						
FIT	ns	0.30	ns	0.18	ns	ns	–0.20					
MEL	0.21	–0.39	ns	–0.22	ns	ns	ns	–0.90				
JUI	ns	ns	0.21	ns	ns	ns	ns	–0.19	ns			
MEA	–0.27	ns	–0.32	ns	–0.24	–0.35	ns	–0.27	0.28	–0.54		
SKI	ns	ns	ns	ns	0.20	ns	ns	ns	0.19	ns	0.25	

ns : non-significant

rus-fruit aroma showed the lowest *F*-value for the line factor. The ''week'' factor accounted for much-less variation and was not significant for all the attributes. Significant regressions over the 6 weeks were detected, negative for mealiness and positive for firmness and juiciness (data not shown). For the three other attributes showing significant differences among the week-values (sweetness, lemon aroma and embarrassing skin), no specific trends could be detected. Much-less variation was attributed to the rank of presentation than to the line effect. Most significant differences were shown for lemon aroma, pharmaceutical aroma and embarrassing skin. Pharmaceutical aroma and embarrassing skin had lower mean values in the first rank than in the five other positions in a session, while the contrary was shown for lemon aroma. Overall aroma intensity seemed over-rated in the first and last positions, as frequently observed in consumer trials (S. Issanchou, personal communication). Nevertheless, the equilibrium of the experimental design for rank factor protected against such an effect. Most of the RILs were distributed between the parental values for sourness, lemon and overall aroma intensity. Extreme transgressive attributes (more than 75% of the RILs outside the parental mean values) were sweetness, citrus-fruit aroma, firmness, juiciness and embarrassing skin. The other attributes showed intermediate situations, with only a few transgressive RILs.

Correlations between sensory attributes

The overall aroma intensity was positively correlated with both sweetness and sourness, as well as with lemon, candy and citrus-fruit aromas (Table 3). It was negatively correlated with mealiness. The taste and aroma attributes describing close flavor components, like sweetness and candy aroma, or sourness and lemon aroma, were strongly correlated. Citrus-fruit aroma seemed more related to sweetness and candy aroma than to sourness. Sweetness and sourness were negatively correlated, as were sweetness and lemon aroma. Pharmaceutical aroma was negatively correlated with the other aroma attributes, because of triangular rather than linear relationships. Actually, RILs with a high pharmaceutical aroma never had high lemon, citrus-fruit or candy aroma levels, but RILs with a low pharmaceutical aroma could exhibit either low or high lemon, citrus-fruit or candy aroma levels (Fig. 1). Texture attributes showed less-significant correlations, except for a strong negative relationship between firmness and meltiness, and a negative correlation between mealiness and juiciness. The strongest correlations between taste, or aroma, attributes and texture attributes were between meltiness and sourness, and between mealiness and citrus-fruit aroma.

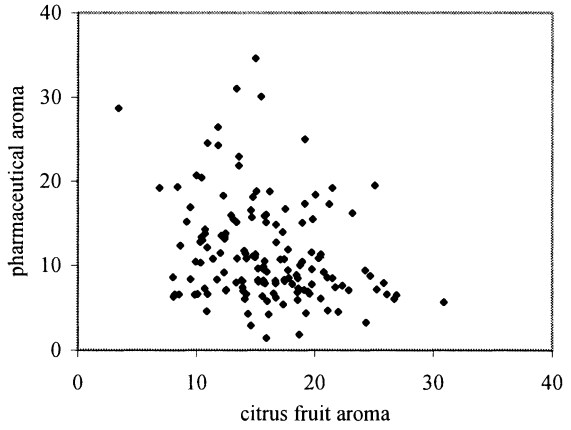

Fig. 1 Relationship between the pharmaceutical aroma and citrus fruit aroma of the 144 RILs

Detection of QTLs

Sweetness, mealiness and pharmaceutical aroma significantly deviated from normality. QTL analyses were thus performed on log values. Nevertheless, the QTL results did not differ and we thus present the results obtained with the raw data. For all the attributes, a total of 49 putative QTLs were identified, among which 27 were detected in common by IM and CIM (Table 4 and Fig. 2). Eleven QTLs were only detected by CIM, but in these cases, IM LOD-values were usually close to the significance threshold. Eleven QTLs were only detected by IM. Hereafter, we will focus on QTLs detected by CIM. In ten cases, CIM detected two linked QTLs within less than 20 cM, but we decided to present only the most significant one as the LOD decrease between the linked QTLs was not sufficient to declare the existence of two

Table 4 QTLs detected for sensory attributes based on CIM and IM analyses in the intraspecific RIL progeny. The most-closely associated marker locus is indicated. The column ''linked QTLs'' indicates the cases where two QTLs were detected by CIM in less than 20 cM. In such cases, only the most-significant was described. Position of the QTLs on the chromosomes are in cM (Kosambi distances) from the top of the chromosome. LOD is the log-likelihood at the specified position. Effect is the difference between the two allelic classes at the QTL, a positive effect indicating a higher value of the C allele. The parent whose allele at the QTL increase the trait value is shown in the Parent column. PVE is the percentage of phenotypic variation explained by the QTL. Data for non-significant effects in one method (ns) are indicated in italics. Markers introduced as co-factors in the CIM model are shown (COF) and, when a distance between the co-factor location and the QTL is observed, the exact position of the co-factor is indicated by the distance to the marker

Trait	QTL	Marker	Chr.	CIM						IM			COF
				Linked QTLs	Position	LOD	Effect	Parent	PVE	LOD	Effect	PVE	
Sweetness													
	swe2.1	CD035	2		58	3.09	5.26	C	9.2	2.58	5.56	8.9	–
	swe2.2	OPAE4–0.9C	2	2	68	5.16	7.04	C	18.3	3.60	6.63	11.9	cof
	swe3.1	H42M47–112L	3		84	4.55	–6.92	L	17.2	2.73	–6.28	10.7	cof +6
	swe9.1	H35M51–244C	9	2	36	3.05	–6.22	L	14.5	*1.84 ns*	*–6.43*	*11.3*	cof
	swe11.1	TG036	11		18	3.07	5.40	C	11.6	3.68	6.84	12.7	cof
Sourness													
	sou1.1	TG077	1		14	3.25	6.72	C	11.3	3.94	8.50	12.4	cof
	sou2.1	TG033	2	2	15	4.93	9.73	C	23.8	3.67	10.79	19.5	cof +8
	sou3.1	H42M47–112L	3		91	3.62	7.54	C	14.5	*2.10 ns*	*7.2*	*7.5*	cof
	sou9.1	CT032	9	2	2	7.62	10.66	C	24.7	5.13	10.04	16.8	cof
Aroma intensity													
	aro2.1	TG033	2		4	3.80	4.36	C	16.4	*2.35 ns*	*4.82*	*12.5*	cof
	aro2.2	CD035	2		58	*0.71 ns*	*0.46*	*C*	*2.8*	4.70	5.43	14.2	cof
	aro2.3	OPAE4_0.9C	2		68	8.37	5.97	C	26.2	7.45	6.68	24.1	cof
	aro9.1	H35M51–176C	9	2	12	6.19	5.74	C	24.3	*1.77 ns*	*3.75*	*7.3*	cof –7
	aro12.1	Sus3	12		28	3.87	4.58	C	17.6	2.83	4.84	12.5	cof
Lemon aroma													
	lem2.1	TG033	2	2	15	3.92	5.31	C	18.3	3.80	6.37	19.8	cof + 7
	lem3.1	H42M47–112L	3		86	4.13	4.54	C	13.5	*2.31 ns*	*3.92*	*7.2*	cof
	lem5.1	CT242	5		6	*2.48 ns*	*–3.34*	*L*	*7.8*	2.51	–4.47	10.1	cof
	lem9.1	H35M51–176C	9	2	8	3.58	4.77	C	14.3	*1.90 ns*	*3.56*	*6.1*	cof –5
Candy aroma													
	can2.1	CT103	2		42	*2.27 ns*	*4.05*	*C*	*8.4*	4.19	4.79	14.4	cof–13
	can2.2	OPAE4_0.9C	2	2	67	5.92	5.04	C	20.3	6.49	5.91	23	cof + 5
Citrus fruit aroma													
	cit2.1	OPAE4_0.9C	2		70	*2.22 ns*	*3.24*	*C*	*8.9*	2.42	2.92	9.5	cof
	cit4.1	TG287	4a		63	4.17	2.97	C	13	3.15	3.00	10	cof
	cit7.1	TG170	7		33	4.52	3.06	C	13.8	3.83	3.24	11.8	cof

Table 4 (continued)

Trait	QTL	Marker	Chr.	CIM						IM			COF
				Linked QTLs	Position	LOD	Effect	Parent	PVE	LOD	Effect	PVE	
Pharmaceutical aroma													
	pha2.1	TG014	2		42	*2.19 ns*	*–2.78*	*L*	*7.2*	3.03	–3.76	9.3	cof
	pha9.1	TG348	9		66	6.40	–4.93	L	20.6	8.45	–6.44	28.5	cof
	pha12.1	TG367	12		62	*1.58 ns*	*2.85*	*C*	*8.3*	2.95	4.56	14.2	cof
Firmness													
	fit2.1	TG484	2		65	2.78	7.16	C	9.3	*1.03 ns*	*5.92*	*3.8*	cof
	fit5.1	CT093	5		38	*0.24 ns*	*3.11*	*C*	*1.5*	2.62	9.40	9.6	–
	fit5.2	TG318	5		62	4.21	8.62	C	12.6	3.04	11.41	14	cof
	fit9.1	H35M51–176C	9		4	12.74	17.99	C	41.1	8.89	16.79	29	cof
	fit11.1	TG046	11		2	*1.94 ns*	*–6.39*	*L*	*7.4*	2.89	–10.00	11.2	cof
Meltiness													
	mel2.1	TG484	2		64	4.60	–8.70	L	13.9	2.61	–8.77	8.1	cof
	mel5.1	CD036	5		57	4.22	–8.83	L	14.4	3.04	–10.05	10.5	cof
	mel9.1	H35M51–176C	9		5	14.67	–18.93	L	45.5	9.44	–18.38	33.8	cof
	mel11.1	TG046	11		4	*2.06 ns*	*6.46*	*C*	*8.2*	3.28	11.12	13	cof
Juiciness													
	jui2.1	TG167	2	2	84	4.68	5.89	C	16.2	3.41	5.47	11.5	cof
	jui4.1	TG555	4b		4	2.93	–5.77	L	13.1	*2.07 ns*	*–5.62*	*9.3*	cof
	jui5.1	CT242	5		19	*1.61 ns*	*–3.17*	*L*	*5.9*	2.88	–6.44	15.6	–
	jui5.2	TG318	5		84	2.80	–4.49	L	9.9	*1.61 ns*	*–4.38*	*7*	cof
	jui12.1	TG367	12		57	*1.95 ns*	*4.47*	*C*	*9.9*	3.40	6.78	17	cof
Mealiness													
	mea2.1	TG492	2		79	8.65	–7.25	L	25.5	4.87	–6.90	17.1	cof + 4
	mea3.1	H42M47–112L	3		86	3.30	4.26	C	10.4	2.43	4.55	7.4	cof + 2
	mea4.1	TG287	4a		67	9.37	–8.01	L	29.7	3.98	–6.16	13.4	cof
	mea4.2	TG555	4b		4	2.90	5.10	C	13	*0.98 ns*	*4.34*	*5.3*	–
	mea9.1	H33M51–111C	9		26	0.49	–6.39	L	22.1	*1.02 ns*	*–4.46*	*6.1*	cof
Embarrassing skin													
	ski4.1	H38M62–188L	4a	2	62	3.47	–7.21	L	12.9	2.50	–7.37	9.9	cof +4
	ski6.1	TG356	6		45	2.95	–6.36	L	9.9	3.46	–7.86	11.3	cof
	ski8.1	TG045	8		12	3.93	–8.34	L	17.2	3.13	–7.29	9.8	cof
	ski8.2	Cel1	8		76	2.73	7.51	C	10.4	2.72	7.51	10.4	cof

QTLs. Two linked QTLs were retained for sweetness on chromosome 2, as they were separated by 33 cM and the scan plot clearly showed two peaks. Thus, between one and five QTLs were detected per attribute. QTLs explained between 9% and 45% of the phenotypic variation. QTLs with relatively major effects ($R^2 > 20\%$) were detected for 7 of the 12 attributes on chromosomes 2 (for sourness, aroma intensity, candy aroma and mealiness), 4 (for mealiness) and 9 (for sourness, firmness, meltiness, aroma intensity, mealiness and pharmaceutical aroma).

Five QTLs were detected for sweetness, the C allele contributing to the higher values for two linked QTLs on chromosome 2 and one on chromosome 11, while L alleles increased sweetness at the QTLs on chromosomes 3 and 9. The C allele increased sourness at the four detected QTLs on chromosomes 1, 2, 3 and 9. All together they accounted for 74% of the phenotypic variation. For the overall aroma intensity, the four QTLs detected by CIM showed high effects (all individual $R^2 > 15\%$). The C alleles increased the attribute values at the four QTLs. The three QTLs detected for lemon aroma were located close to QTLs for sourness on chromosomes 2, 3 and 9. On chromosome 5, a QTL detected only by IM was just below the LOD threshold by CIM. Only one major QTL was detected for candy aroma on chromosome 2, at the same location as the major QTL for sweetness. Two QTLs were detected for citrus-fruit aroma on chromosomes 4 and 7, and the C alleles increased the attribute values for both. Only one QTL was detected by CIM for pharmaceutical aroma on chromosome 9, showing a strong effect. The L allele increased the attribute values. For firmness and meltiness, three QTLs were detected, at the same locations, on chromosomes 2, 5 and 9. The C alleles provided higher values to the QTLs for firmness, and the contrary was shown for meltiness. On chromosome 9, QTLs exhibited very strong effects for both traits, explaining more than 40% of the variation. QTLs for juiciness were detected on chromosomes 2, 4b and 5. Both parental alleles contributed to higher attribute values. For mealiness, five QTLs were detected on chromosomes

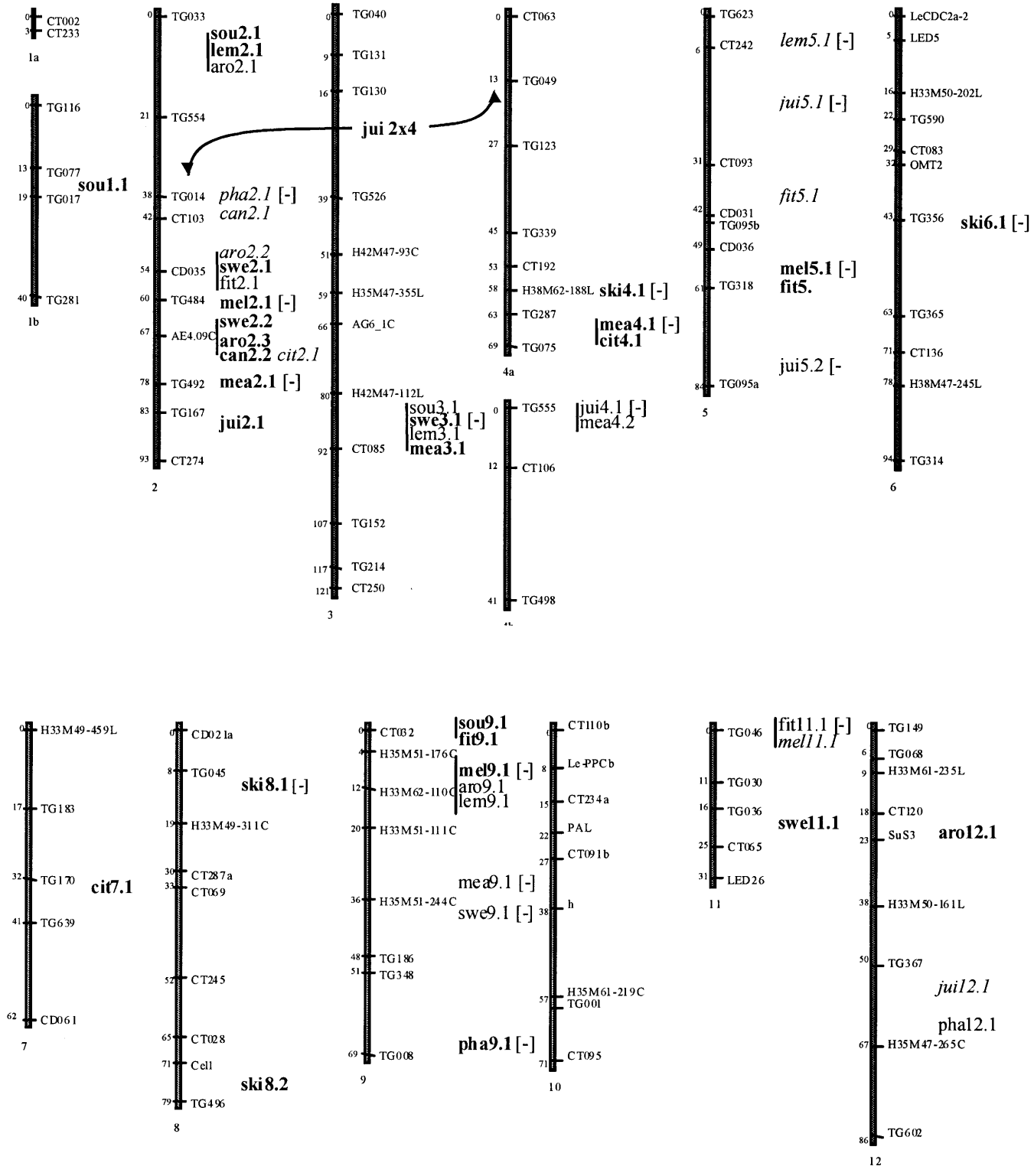

Fig. 2 Linkage map of tomato chromosomes based on an intraspecific RIL population of a cross between a cherry tomato and a large-fruit line. Names of the markers, on the right of chromosomes, are described in Saliba-Colombani et al. (2000a). Most-likely positions of QTLs detected for sensory attributes : sweetness (*swe*), sourness (*sou*), overall aroma intensity (*aro*), candy aroma (*can*), lemon aroma (*lem*), citrus-fruit aroma (*cit*), pharmaceutical aroma (*pha*), firm texture (*fit*), flesh mealiness (*mea*), meltiness (*mel*), juiciness (*jui*), and embarrassing skin (*SKI*). QTLs detected by CIM and IM are in *bold* in contrast to those detected only by CIM. QTLs only detected by IM are shown in *italics*. A *minus sign* after the QTL indicates that L alleles provided higher values for the attribute. The *arrow* indicates the two markers showing an epistatic interaction for juiciness

2, 3, 4a, 4b and 9. The three QTLs, where L contributed to higher values, on chromosomes 2, 4a and 9, also showed the strongest effects. The L alleles contributed to higher values for three of the four QTLs detected for embarrassing skin on chromosomes 4a, 6 and 8. Another QTL on chromosome 8 showed an opposite allelic effect.

Consistent with previous QTL mapping studies conducted in other tomato crosses (Paterson et al. 1988, 1991; de Vicente and Tanksley 1993; Grandillo and Tanksley 1996), only minimal evidence of epistasis was found. Two-locus interactions were screened between 84 RFLP markers, for a total of 3486 tests, by two-way tests. At a $P < 0.0001$ threshold, less than one significant test is expected by chance. Only one significant effect was detected for juiciness ($P < 10^{-6}$), between TG014 (chromosome 2) and TG049 (chromosome 4a), explaining 11% of the phenotypic variation (Fig. 2).

Discussion

Variation of sensory attributes

With 54 panelists in four panels and 144 RILs to assay, a total of 526 groups of seven tomatoes have been assessed. The comparison of 144 products is much bigger than the traditional experiment size and a specific experiment was designed. Overall, each RIL has been assayed about 20 times. As currently noted in quantitative descriptive sensory analysis, each panelist, on average, used his own level of the scale, but also his own range of scale. The presence of a hybrid control in each assay allowed us to evaluate the panelist's repeatability and discard the extreme data. The correlation coefficients between the variances of the hybrid control and the variances of the RILs, estimated for each assessor, showed a few panelists whose notations seemed randomly performed and which were therefore discarded from the data set. Sensory skills are known to vary not only from person to person, but also from one attribute to the other (Issanchou and Lesschaeve 1995). Three groups of attributes could be identified: (1) sourness, meltiness and firmness, with a high percentage of variation due to the line effect and a relatively low variation attributable to the panelist, (2) sweetness, candy aroma, lemon aroma, mealiness, juiciness and embarrassing skin, for which the line variation represented about 10–15% of the overall variation and for the panelist more than 20%, (3) citrus-fruit aroma, overall aroma intensity and pharmaceutical aroma, which showed the highest part of the residual variation. Citrus-fruit aroma had been added to the attributes because some panelists felt that lemon aroma was not sufficient to describe the Cervil aroma. Nevertheless, it was also judged as the most-difficult attribute to assess during panelist training.

Growing conditions have been shown to alter the sensory value of tomato (Hobson and Bedford 1989). Variation between fruits within a truss, between trusses, and between plants within a plot may have occured and each assay only concerned 1–3 fruits per genotype. Such levels of variation imposed an important number of repetitions per genotype in order to control, as well as possible, the external sources of variation. Fruit sweetness and sourness vary with ripening and also with light and temperature conditions (Davies and Hobson 1981). As sugar- and acid-content continue to evolve after ripening, special care was taken to assay fruits at the same ripening stage. Mealiness regularly decreased over the weeks, whilst firmness and meltiness increased. Such changes are currently observed in glasshouse-grown tomato. The evolution of texture attributes is due either to the age of the plant or to changes in the growing conditions (light and temperature). Although numerous sources of variation were identified, the large sample size and the number of repetitions per genotype allowed an accurate evaluation of line genotypic values to be obtained.

Differences between the parental lines

The fruits of the C parent, a cherry tomato line, appeared more sour and exhibited higher means for assumed positive aroma attributes (for the overall aroma intensity as well as for the lemon and citrus fruit aroma levels). It also appeared firmer in mouthfeel than L. These results confirmed the remarkable aromatic value of C, which seems to be interesting for tomato flavor improvement, as appreciated by breeders in a non-formal assay. Large-fruit varieties usually have a fruit composition distinct from Cherry tomato cultivars, which have higher dry matter, organic acid and sugar contents (Hobson and Bedford 1989). Moreover this group of cultivars (corresponding to *L. esculentum* var. *cerasiforme*) presents a higher genetic variability than modern varieties at the molecular level (Miller and Tanksley 1990). The C parental line differed from L for 30% of the tested RFLP probes (Saliba-Colombani et al. 2000a), which is among the highest distances within *L. esculentum*. It is thus extremely distant from the modern cultivars. Although C and L showed the same average value for sweetness, panelists detected a pharmaceutical aroma in L, which presumably completed the negative perception due to its low level of sourness and overall aroma intensity. The F_1 hybrid had intermediate values for most of the attributes, but showed heterosis for sweetness, citrus fruit aroma and firmness.

QTL accuracy

Analysis by CIM increased the control of the genetic background and the resolution of QTL mapping (Zeng 1993, 1994). Zeng (1994) showed that, in case of two linked QTLs, QTL mapping by IM is seriously biased. CIM helped to resolve situations where LOD-score profiles were spread over a large map distance indicating possible multiple QTLs in the region. For instance, on chromosome 9, significant associations for meltiness

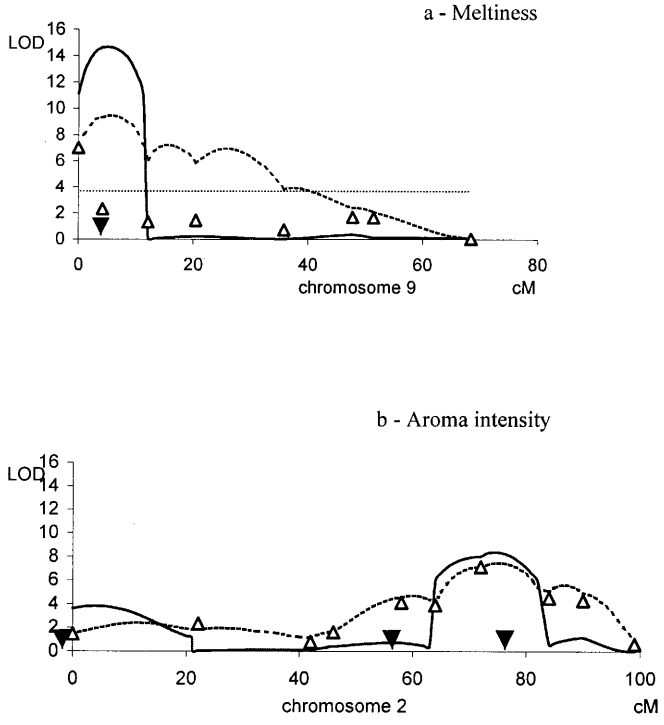

Fig. 3 Comparison of composite (CIM, *solid lines*) and simple interval mapping (IM, *dotted lines*). LOD-score plots along chromosome 9 for meltiness (**a**) and chromosome 2 for aroma intensity (**b**). The abscissa axis represents the chromosome in Kosambi cM. The *horizontal line* at LOD = 2.56 indicates the LOD threshold for detecting a QTL by CIM. *Black arrows* show the location of co-factors and *white arrows* the LOD value of the linear regression at the marker positions

spread over 50 cM by IM. CIM introduced the marker with the most-significant LOD-score as a co-factor, and the QTL was located at this position, with a confidence interval smaller than 20 cM (Fig. 3a). The number of detected QTLs is nevertheless a minimum number, as in the ten cases where CIM detected two linked QTLs within less than 20 cM, we decided to retain only the most significant one. Only a fine-mapping experiment could help to conclude the existence of two such linked QTLs. Most of the co-factors were detected close to the QTL location, sometimes at a small distance from the most-likely QTL location (Table 4). On chromosome 2, where many significant associations were detected, up to three markers were introduced by CIM as co-factors (Fig. 3b). Composite interval mapping appeared more efficient and more accurate to map QTLs than IM. Indeed, in most cases QTLs identified with CIM showed higher LOD scores and sharper peaks. Among the 27 QTLs significantly detected both by IM and CIM, the percentages of phenotypic variation explained were higher for two-thirds of the QTLs by CIM. Additive effects were higher only in eight CIM analyses, showing that additive-effect estimations are less over-estimated by CIM than by IM as test statistics at the QTL are not influenced by other QTLs (Zeng 1994).

QTL-allele effect and transgression

C provided favorable alleles for most of the attributes, in agreement with the expectations based on the phenotype of the parents. No significant differences between parents were detected for sweetness, juiciness, and mealiness, and both parents appeared to carry alleles with effects increasing these attributes. As suggested by de Vicente and Tanksley (1993), these QTLs may be responsible for the transgressive segregations observed for these attributes. All the alleles providing higher organoleptic quality are provided by C, except for sweetness, where the L alleles increased the attribute means on chromosomes 3 and 9, and for mealiness, where the L alleles reduced the trait value on chromosomes 3 and 4b. For juiciness, both parents provided alleles contributing to higher values, but the role of this attribute in consumer preference is not clear (data not shown). The overall percentages of variation explained by the QTLs were related to the part of the genetic variation estimated, and to the ability of the panelists to assess each attribute. Firmness and meltiness showed the highest amount of variation due to the line effect, and the strongest percentage of variation explained (PVE), whilst the aroma attributes, for which that part of the variation explained by QTLs was the lowest, had the highest residual variations. Mealiness, with a high PVE, seemed to be easily evaluated by panelists. In apple, mealiness was also well-described by panelists (Gomez et al. 1998).

Clusters of QTLs

Common or close locations of QTLs were frequently observed (Fig. 2) for correlated attributes. For instance, all the QTLs for lemon aroma were linked to QTLs for sourness, and the same sense and magnitude of QTL effects were detected. Except on chromosome 3, the major QTLs for sourness were located in different chromosomal regions than those for sweetness. The different locations of QTLs for sweetness and sourness revealed the possibility to improve both traits independently. The QTL for candy aroma corresponded to the major QTL for sweetness and overall aroma intensity. On chromosome 2, the QTL for overall aroma intensity and the QTL for sweetness were mapped at the same location. The contribution of sugars and acids not only to sweetness and sourness but also to the overall aroma intensity is well documented (Hobson and Bedford 1989). The QTLs for overall aroma intensity which mapped at the top of chromosome 2 and on chromosome 9 were close to the QTLs for sourness, while the QTLs at the bottom of chromosome 2 were close to the QTLs for sweetness. Only one common QTL location, on chromosome 3 (showing opposite allele effects), was responsible for the negative correlation detected between sweetness and sourness.

Mealiness and juiciness showed two common locations with opposite allele effects, C providing the favorable allele for mealiness on chromosome 2 and the opposite on

chromosome 4. The common QTLs, with opposite effects for firmness and meltiness, confirmed that the two attributes measured the same fruit characteristics but with opposite scales. By contrast, the partial correlations between mealiness and juiciness, or between lemon and citrus-fruit aroma, and the incomplete QTL co-localizations confirmed the usefulness of evaluating different attributes. Although sweetness and mealiness showed common QTL locations on chromosomes 3 and 9, with L providing higher values for both attributes, texture attributes were poorly correlated with taste and aroma attributes. QTLs on the top of chromosome 2 concerned only taste and aroma attributes, while QTLs for texture located on chromosomes 4b and 5 were independent from aroma QTLs. Three of the four QTLs for embarrassing skin were located far from the other QTLs, showing the different origin of this attribute. Texture attributes are secondarily important in fruit organoleptic quality, but once a good flavor is reached, a good texture will be required (Harker et al. 1997). A study of Janse and Schols (1995) showed that Dutch consumers preferred sweet and non-floury tomatoes. Firmness was not a major criterion in their decision. By contrast, firmness has been shown to be important by Winsor (1979). Wolters and van Gemerts (1990) also showed the role of sweetness, overall aroma intensity, and firmness in the mouth, the latter being negatively related to consumer responses. In their study, embarrassing skin and mealy mouthfeel were also found significant in consumer response. Mealiness, meltiness and juiciness may influence the sweetness feeling. Previous QTL studies in maize (Edwards et al. 1987) and tomato (Fulton et al. 1997) mentioned some regions of the genome which seemed to influence clusters of traits. We observed such a phenomenon mainly on chromosomes 2 and 9. Further genetic studies, such as fine mapping of these regions, are required to differentiate between closely linked multiple QTLs from the effect of pleiotropic genes.

Conclusion

The high number of repetitions and RILs allowed us to identify regions of the tomato genome with significant effects on organoleptic quality attributes, some of them with high effects. Although numerous publications relate to QTLs for the quality attributes of processing tomato, this is the first report concerning fresh market tomato. Comparison with other studies is thus difficult, as this is the only paper, to our knowledge, dealing with QTLs for sensory attributes in fresh market tomato. Chen et al. (1999) recently summarized the chromosome regions where QTLs for fruit weight and soluble-solid content were detected in the many interspecific progenies studied during the last 10 years. It is interesting to note that the QTLs detected in the present study for sourness and sweetness mapped within the few regions of the genome where QTLs for soluble solids frequently mapped in independent studies, on chromosome 2, 3, 9 and 11. These results will be used for marker-assisted selection in order to transfer the favorable alleles of the cherry tomato QTLs into elite lines. Furthermore, the progeny was also characterized for physical and chemical fruit traits and the QTLs were mapped (Saliba-Colombani et al. 2000b). Correlations between sensory, instrumental and compositional traits, together with QTL overlapping will be analyzed in a subsequent publication.

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