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QTL analysis of fruit quality in fresh market tomato: a few chromosome regions control the variation of sensory and instrumental traits

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Abstract

The organoleptic quality of tomato fruit involves a set of attributes (flavour, aroma, texture) that can be evaluated either by sensory analyses or by instrumental measures. In order to study the genetic control of this characteristic, a recombinant inbred line (RIL) population was developed from an intraspecific cross between a cherry tomato line with a good overall aroma intensity and an inbred line with medium flavour but bigger fruits. A total of 38 traits involved in organoleptic quality were evaluated. Physical traits included fruit weight, diameter, colour, firmness, and elasticity. Chemical traits were dry matter weight, titratable acidity, pH, and the contents of soluble solids, sugars, lycopene, carotene, and 12 aroma volatiles. A panel of trained assessors quantified sensory attributes: flavour (sweetness and sourness), aroma (overall aroma intensity, together with candy, lemon, citrus fruit, and pharmaceutical aromas) and texture (firmness, meltiness, mealiness, juiciness, and skin difficult to swallow). RILs showed a large range of variation. Molecular markers were used to map a total of 130 quantitative trait loci (QTL) for the 38 traits. They were mainly distributed in a few chromosome regions. Major QTLs (R^2 >30%) were detected for fruit weight, diameter, colour, firmness, meltiness, and for six aroma volatiles. The relationships between instrumental measures and sensory traits were analysed with regard to the QTL map. A special insight was provided about the few regions where QTLs are related to multiple traits. A few examples are shown to illustrate how the simultaneous analysis of QTL segregation for related traits may aid in understanding the genetic control of quality traits and pave the way towards QTL characterization.

Key words: Aroma, *Lycopersicon esculentum*, organoleptic quality, QTL, sensory analysis, texture.

Introduction

Consumers have complained about tomato flavour for more than ten years in many countries of Europe (Decoene, 1995; Janse and Schols, 1995) as well as in the USA (Kader *et al*., 1977) and Australia (Ratanachinakorn *et al*., 1997). Organoleptic quality involves taste and aroma, but also the colour and texture of the fruit. It can be evaluated either by instrumental measures or by sensory analysis, the latter being the most efficient way to describe organoleptic characteristics. In tomato, Hobson *et al*. (1990) characterized the flavour of different tomato varieties by sensory profiling and showed the potential of cherry tomato, which have sweeter fruits and higher overall aroma intensity than large-fruited tomatoes. The flavour of tomato was influenced not only by varietal differences and the 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

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conditions (Ratanachinakorn *et al*., 1997). Sensory analyses showed that sweetness and sourness were the major determinants of tomato flavour preference (Stevens *et al*., 1977). On the other hand, modifications in texture (Harker *et al*., 1997), mainly the increase in the firmness of modern varieties, are also responsible for consumer complaints.

Several associations were found between tomato fruit composition (for a review, see Davies and Hobson, 1981) and physical characteristics and sensory traits (Baldwin *et al*., 1998). Flavour mainly relies on sugar and acid contents (Stevens, 1979), and a given sugar level corresponds to an optimal acid content (Malundo *et al*., 1995). More than 400 aroma volatiles were identified in tomato fruit (Petro-Turza,1987), but they are not all equally important to the development of tomato aroma (Baldwin *et al*., 1998; Krumbein and Auerswald, 1998). Variety (Langlois *et al*., 1996), ripening stage (Baldwin *et al*., 1991) and storage conditions (Stern *et al*., 1994) may influence the content of aroma volatiles, but little is known about their genetic control (Stevens, 1986) and the genes responsible for their variation.

Most of the quality traits show a continuous variation, strongly influenced by environmental conditions. The genetic variation of such traits was attributed to the joint action of many genes (QTLs, for Quantitative Trait Loci), which can be mapped on the genome with genetic markers. A QTL approach has previously been used to localize genomic regions controlling quality traits of processing tomato. QTLs for tomato fruit weight, soluble solid content, pH, fruit colour, and fruit firmness were detected in several segregating populations derived from interspecific crosses (Paterson *et al*., 1988; Goldman *et al*., 1995; Eshed and Zamir, 1996; Tanksley *et al*., 1996; Bernacchi *et al*., 1998; Chen *et al*., 1999).

In order to analyse the genetic control of organoleptic quality in fresh market tomatoes, the genetic variation of physical, chemical and sensory attributes of fruit were studied in a population derived from a cross between a cherry tomato line, which exhibited a high overall aroma intensity, and a large-fruited line with poor taste. Physical components concerned fruit weight, firmness and colour. Chemical components were dry matter weight, sugar content, titratable acidity, pH, and also the contents of several aroma volatiles and pigments. Sensory components included taste, aroma and texture attributes. A genetic map was constructed (Saliba-Colombani *et al*., 2000). In two previous papers, the QTL locations were described separately for physical and chemical traits (Saliba-Colombani *et al*., 2001) and sensory traits (Causse *et al*., 2001). In the present paper, the relationships between instrumental assays and sensory traits are presented in order to evaluate the relevance of each group of traits in the evaluation of quality and to estimate how instrumental measures may replace sensory profiles. The relationships among traits were analysed with regard to the QTL map. A special insight is provided about the few regions where QTLs are related to multiple traits.

Materials and methods

Mapping population and glasshouse trial

The population consisted of 144 recombinant inbred F_7 lines (RILs) derived from the cross between a cherry tomato line *L. esculentum* var. *cerasiforme* (Cervil, coded C) and a round larger-fruited tomato line *L. esculentum* (Levovil, coded L). The Vilmorin seed company provided both parental lines. Plant materials are described in Saliba-Colombani *et al*. (2000). The RILs were grown in a heated glasshouse during the spring (January–July) in a fully randomized trial. Each plot consisted of a single row of six plants. The two parental lines were each represented by three plots and the F_1 hybrid by nine plots. Ripe fruits were harvested daily for 6 weeks at the red stage, one day before fruit evaluation.

Sensory profiling

Sensory analysis was performed by a panel of 54 trained assessors, as described in Causse *et al*. (2001). 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 how difficult skin was to swallow (SKI). Each assessor had to assay seven samples during a session. The last sample was always the hybrid control. Two or three sessions were performed per week for 6 weeks.

Physical and chemical measures

The physical and chemical analyses were completed as described in Saliba-Colombani *et al*. (2001). Each fruit was first evaluated for physical traits: fruit weight (FW), diameter (FD), firmness (FIR), elasticity (ELA), and external colour (L, a and b, measured by a Minolta chromameter). Several chemical measurements were then taken from bulk fruit: total dry matter weight (DMW), soluble solids content (SSC), sugar content (SUC), titratable acidity (TA), pH, lycopene content (LYC), carotene content (CAR), and the content of 12 aroma volatiles—pentanal (PNA), 2-methylbut-2-enal (BEA), hexanal (HXA), 3-methylpentan-1-ol (MNO), hex-3-en-1-ol (X3O), 2-(methylthio)ethanol (MEO), 3-(methylthio)propanal (MTA), 6-methylhept-5-en-2-one (MHN), 2-isobutylthiazole (IBT), 2-phenylethanal (PEA), orthomethoxyphenol (MYP), eugenol (EUG). Aroma volatiles were separated and quantified by a combined gas chromatography-mass spectrometry system (GC-MS) as described by Langlois *et al*. (1996) and by Bertin *et al*. (2000). These volatiles were chosen, after an exhaustive analysis of parental lines, because (1) the two parental lines had different contents, (2) they were representative of different metabolic pathways and (3) they had characteristic odours, putatively important in tomato aroma, as described in Saliba-Colombani *et al*. (2001). Overall, six measurements (15 fruits per measurement per RIL) were taken on chemical traits during the 6 weeks of harvest (one measurement per week). Only three measurements of aroma volatiles content were performed.

Molecular map

The construction of the genetic map has been described elsewhere (Saliba-Colombani *et al*., 2000). For QTL mapping, a subset of 103 loci (1 morphological, 84 RFLP, 2 RAPD, and 16 AFLP) well

distributed over the genome was selected. The map covered 965 Kosambi cM, which corresponded to about 85% of the genome, when compared to the saturated tomato genome map (Tanksley *et al*., 1992).

QTL analysis

QTL detection was performed with simple interval mapping (IM) and composite interval mapping (CIM), as described in Saliba-Colombani *et al*. (2001). Significance thresholds were evaluated by 1000 permutations, and an experiment-wise error threshold of 0.10 was retained. The part of phenotypic variation explained by the QTL (R^2) was estimated in the model. All analyses were performed with the QTL Cartographer software (Basten *et al*., 1997). The multitrait QTL analysis was performed with MultiQTL software (Korol *et al*., 2001). Epistasis was tested by two-way ANOVAs.

Results and discussion

Genetic variation in quality traits

Fruits from the cherry tomato (C) line were significantly more sour, exhibited a stronger overall aroma intensity, higher lemon and candy aroma, and were firmer and less melting than fruits from the large-fruited parent (L). C also showed higher levels than L for traits describing fruit composition (in % of fresh mass). These results confirmed the remarkable aromatic value of this cherry tomato line. L showed higher levels for the physical traits and for four aroma volatiles. The F_1 hybrid had values intermediate between the two parent means for most of the traits, but it showed higher means than both parents for sweetness, citrus fruit aroma and firm texture, and a lower mean for pharmaceutical aroma. RILs showed a very large range of variation for all the traits, with high heritabilities (>0.5) for all the physical traits and most of the chemical traits, with the exception of the contents of lycopene, carotene and some aroma volatiles which showed lower heritabilities (<0.3). Continuous variation was usually shown, except for the content of the aroma volatile MYP, which showed a bimodal distribution. For most of the attributes, RILs were distributed between the parental values, with only a few transgressive RILs. Extreme transgressive attributes (more than 75% of the RILs outside the parental mean values) were MNO content, sweetness, citrus fruit aroma, firm texture, juiciness, and embarrassing skin.

Relationships among traits

Several instrumental traits appeared correlated together (Table 1, adapted from Saliba-Colombani *et al*., 2001). Fruit weight was positively correlated to fruit elasticity. Fruit elasticity was positively correlated with colour parameters. Among the chemical traits, the strongest positive correlations were observed between dry matter weight on the one hand and soluble solid content, sugar content and titratable acidity on the other hand. Aroma volatiles presented a complex but relaxed network of correlations. A few correlations were significant between aroma volatiles and other chemical traits. MHN and EUG were negatively correlated with the major chemical components of the fruit, while MNO was positively correlated with these traits. Lycopene and carotene contents were positively correlated together and to PNA, IBT, and HXA. Lycopene content was also positively correlated to the MHN content. Fruit weight and fruit elasticity were negatively correlated to most of the chemical traits.

Among the sensory traits (Table 2, adapted from Causse *et al*., 2001), the overall aroma intensity was positively correlated with both sweetness and sourness, as well as with lemon, candy and citrus fruit aromas. It was

Table 1. *Phenotypic correlations among major instrumental measures in the RIL population (adapted from Saliba-Colombani* et al. *2001)*

Only significant correlations are shown (P <0.05).

	FW	ELA	L	SSC	TA	LYC	CAR	PNA	BEA	HXA	MNO	X3O	MEO	MTA	MHN	IBT	PEA	MYP	EUG
ELA	0.54																		
L	0.23	0.56																	
SSC	–0.56	–0.53	–0.43																
TA	–0.58	–0.64	–0.46	0.59															
LYC	–0.32	ns[a]	0.20	ns	ns														
CAR	–0.41	–0.35	ns	0.33	0.20	0.48													
PNA	–0.20	ns	ns	0.25	ns	0.33	0.28												
BEA	–0.19	ns	0.25	ns	ns	0.24	ns	ns											
HXA	ns	0.32	0.45	–0.21	–0.21	0.26	0.20	0.45	0.24										
MNO	ns	–0.38	–0.37	0.21	0.43	–0.18	ns	ns	ns	–0.18									
X3O	–0.19	–0.32	–0.30	0.19	0.24	ns	0.22	0.21	ns	ns	0.46								
MEO	–0.17	ns	ns	ns	ns	ns	0.27	0.18	0.21	0.21	ns	–0.18							
MTA	ns	ns	ns	–0.21	ns	ns	ns	ns	0.56	ns	ns	–0.20	0.43						
MHN	ns	0.19	0.32	–0.45	–0.24	0.29	ns	ns	ns	0.25	ns	ns	ns	ns					
IBT	ns	ns	ns	ns	ns	0.33	0.39	ns	ns	ns	ns	ns	ns	ns	0.19				
PEA	ns	0.26	0.35	ns	–0.23	ns	ns	ns	0.40	0.18	–0.34	–0.46	0.52	0.68	0.19	ns			
MYP	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		
EUG	0.36	0.18	ns	–0.32	–0.22	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.40	

[a] ns: Non-significant.

Table 2. *Phenotypic correlations among sensory attributes in the RIL population (adapted from Causse* et al. *2001)*

Only significant correlations are shown (P <0.05).

	SWE	SOU	ARO	LEM	CAN	CIT	PHA	FIT	MEL	MEA	SKI
SWE	–										
SOU	–0.41	–									
ARO	0.37	0.48	–								
LEM	–0.38	0.79	0.41	–							
CAN	0.66	ns[a]	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	–		
MEA	–0.27	ns	–0.32	ns	–0.24	–0.35	ns	–0.27	0.28	–	
SKI	ns	ns	ns	ns	0.20	ns	ns	ns	0.19	0.25	–

[a] ns: Non-significant.

Table 3. *Phenotypic correlations between sensory traits and major physical and chemical traits in the RIL population*

Only significant correlations are shown (P <0.05). No significant correlations were observed with HXA, X3O, MEO, MTA, IBT, and PEA, which do not appear in the table.

	Sensory attributes											
	SWE	SOU	ARO	LEM	CAN	CIT	PHA	FIT	MEL	JUI	MEA	SKI
Physical traits												
FW		–0.45	–0.53	–0.39	–0.44	–0.24	0.25	–0.21	0.33	–0.20	0.19	
FIR								0.29				
ELA		–0.47	–0.48	–0.40	–0.33					–0.32		
L		–0.37	–0.36	–0.23	–0.31			–0.20	0.32			
Chemical traits												
SUC	0.64		0.65		0.67	0.55	–0.23				–0.24	
DMW	0.38	0.48	0.76	0.35	0.62	0.42	–0.23	0.24	–0.32			–0.20
pH		–0.26		–0.28							–0.24	–0.27
LYC					0.20							
CAR			0.24		0.25					0.20	–0.25	
TA	–0.22	0.82	0.56	0.70				0.21	–0.30	0.20		0.20
Volatiles												
PNA	0.27		0.21		0.25	0.20						
BEA		0.24	0.20							0.20		
MNO		0.32		0.31							0.26	0.39
MHN	–0.25		-0.31		–0.22						0.23	
MYP	0.25	–0.24		–0.28			0.72					
EUG		–0.23	–0.25	–0.20	–0.30	–0.25	0.50					–0.26

negatively correlated with mealiness. The taste and aroma attributes describing close flavour components, like sweetness and candy aroma, or sourness and lemon aroma, were strongly correlated. Citrus fruit aroma seemed more related to sweetness and to candy aroma than to sourness. Sweetness and sourness were negatively correlated, as were sweetness and lemon aroma. Texture attributes showed less significant correlations, except a strong negative relationship between firm texture 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.

Correlations between sensory and instrumental traits

Significant correlations between sensory and the major instrumental traits are shown in Table 3. Negative correlations between flavour descriptors and fruit weight suggest a dilution effect, as illustrated by the negative correlation between chemical fruit composition (in sugars, acids and pigments) and fruit weight. Nevertheless, fruit weight was not correlated to sweetness, although it was correlated to sugar content. A positive but loose correlation was detected between instrumental firmness and firm texture. Colour parameters were mainly negatively correlated to the overall aroma intensity, and to the candy and lemon aromas. As all the fruits were harvested at the same stage, this correlation must correspond to genetic differences, the parent L being slightly more orange (higher L and b) than C.

Some correlations were expected, such as between sweetness, overall aroma intensity, or candy aroma, for example, and sugar or dry matter content. A positive correlation was also detected between sourness and titratable acidity. The correlation between sourness and

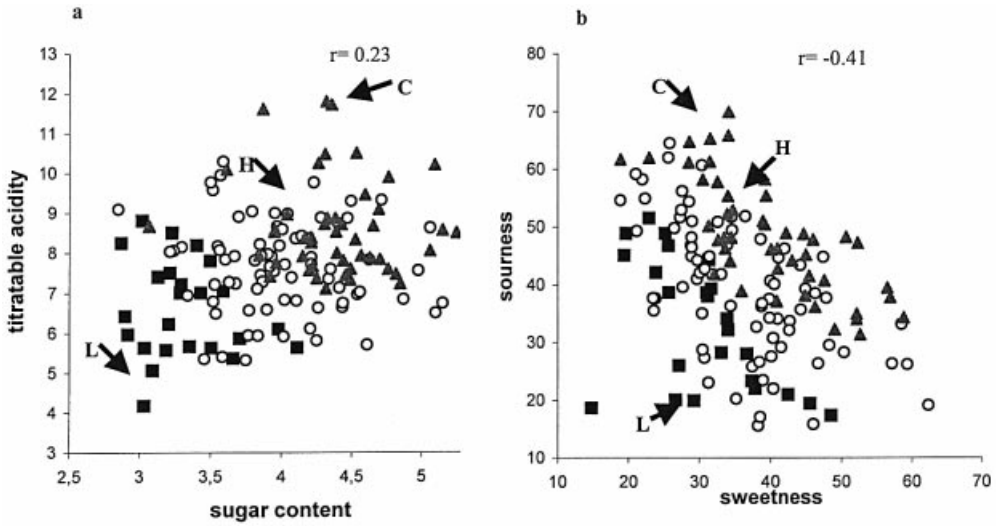

Fig. 1. (a) Relationships between overall aroma intensity, sugar content and titratable acidity. (b) Relationships between overall aroma intensity, sweetness and sourness. In each plot, three classes of aroma intensity are shown (black squares, ARO <35; white circles, ARO 35–45; black triangles, ARO >45). The average values of the parental lines (C and L) and their hybrid (H) are shown with an arrow.

pH was lower, as previously seen by Kader *et al*. (1977) and Stevens (1979). This low correlation was also due to the low variability of the pH in the population.

The levels and sense of the correlations between sugar content and acidity (r=0.23) and between sweetness and sourness (r= –0.41) were not comparable. Such a result can be attributed to the perception of sweetness and sourness, which are not independent (Stevens *et al*., 1977). The C line had high sugar content and acidity, to the opposite of L. Figure 1 shows that both sugar content and titratable acidity contributed to the overall aroma intensity, in an equal manner. This result is consistent with the observations of Stevens (1979) and Kader *et al*. (1977). The lemon aroma was positively correlated to the titratable acidity, contrary to the citrus fruit aroma, which was only correlated to the sugar content. Very few correlations were detected between the texture traits and chemical traits. The strongest was between melting texture and dry matter weight (r= –0.32).

Correlations between the volatile contents and the aroma descriptors were low when significant, with the exception of the pharmaceutical aroma which was strongly correlated to the content in two phenolic compounds, orthomethoxyphenol (MYP) and eugenol (EUG). The analysis by trained sniffers of these two compounds associated their presence with odours of clove and camphor, which can be related to the pharmaceutical aroma. Another correlation can be mentioned, between the pentanal (PNA) content and the descriptors related to sweetness (SWE, ARO, CAN, CIT). In the same way, the 3-methylpentan-1-ol (MNO) content was related to sourness and lemon aroma. Baldwin *et al*. (1998) noted a positive correlation between sourness and the hexanal (HXA) content, which was not observed here. Baldwin *et al*. (1998) also observed a positive correlation between aroma intensity and the content in X2A, BIO and X3O. None of these correlations were significant in the studied population. The overall aroma intensity was only positively correlated to two volatile compounds, the 2-methylbut-2-enal (BEA) and the pentanal (PNA). The only common correlation between this study and that of Baldwin *et al*. (1998) concerned the negative correlation between MHN and sweetness. These results do not mean that the other compounds do not interfere with the tomato aroma, but their role is less obvious as shown by the QTL map. Besides, it is known that some compounds have a threshold effect, which might be difficult to detect by linear relationship analysis and the aroma perception results from the overall interaction among volatiles in the mouth.

QTL detection

A total of 130 putative QTLs were detected for all traits (Saliba-Colombani *et al*., 2001; Causse *et al*., 2001). Between one and six QTLs were detected per attribute. The individual percentage of explanation of the phenotypic variation (R^2) varied between 87% for the aroma volatile MYP and 8% (the lowest limit of detection). Twenty-five QTLs showed an R^2 lower than 10%, 70 QTLs an R^2 between 10% and 20%, 21 QTLs an R^2 between 20% and 30%, and 14 QTLs an R^2 higher than 30%. These last QTLs could be considered as major genes. They control fruit weight (on chromosomes 2 and 3) and diameter (on chromosomes 2 and

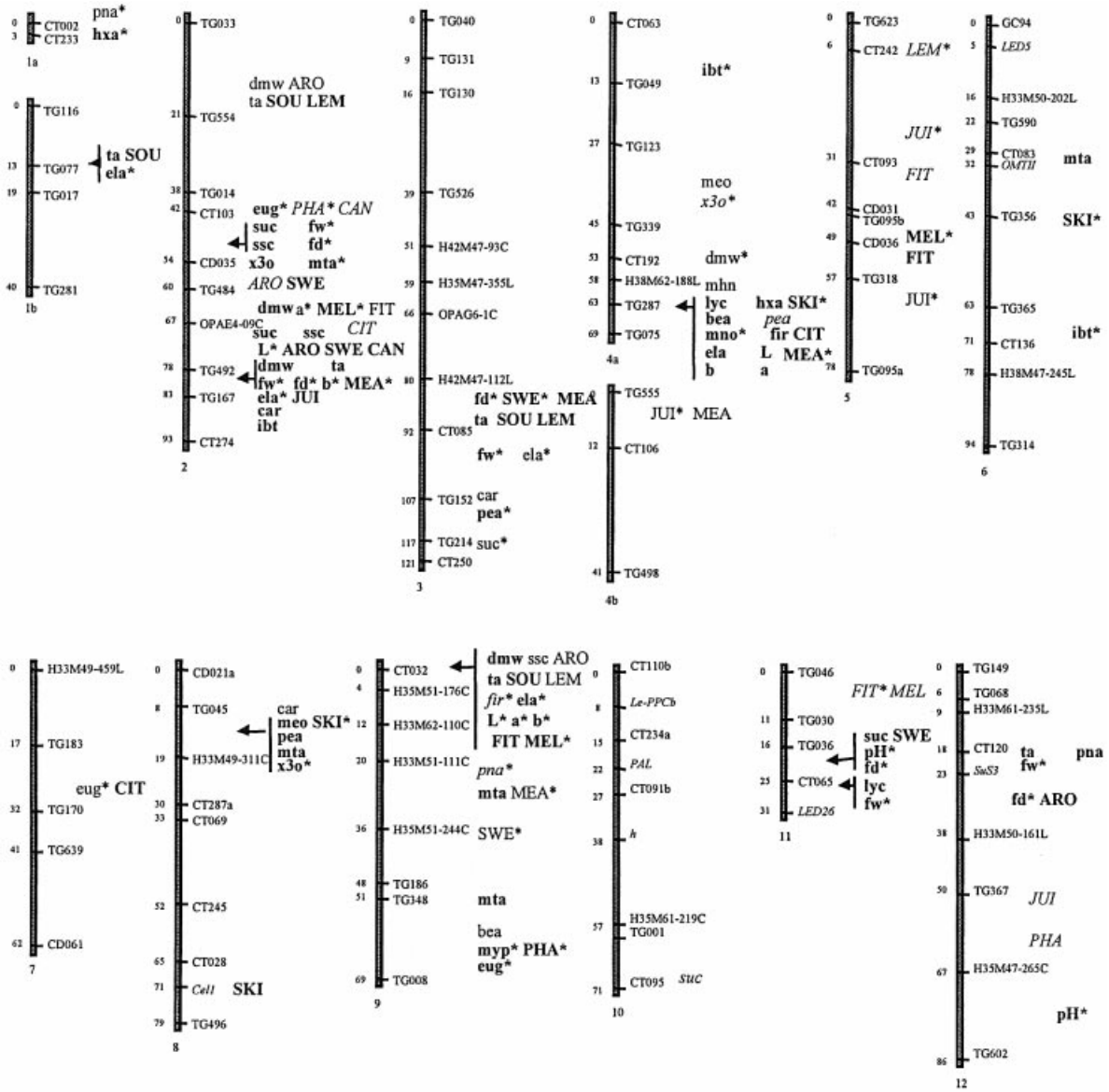

Fig. 2. QTL map for organoleptic quality attributes, based on an intraspecific RIL population derived from a cross between a cherry tomato line and a large fruit line. Names of the markers, on the right of chromosomes are described in Saliba-Colombani *et al*. (2000). Distances in Kosambi cM are on the left of chromosomes. QTLs detected by composite interval mapping (CIM) and simple interval mapping (IM) are in bold, those only detected by CIM are in normal letters and those only detected by IM are in italics. Stars indicate the QTL where the L allele increased the trait value. An arrow was added when a few QTLs mapped on the same locus.

11), fruit firmness and colour (both on chromosome 4), the aroma volatiles MNO, IBT (both on chromosome 4), MEO, PEA (both on chromosome 8), EUG (on chromosome 2), MYP (on chromosome 9), and sensory traits (firm texture and meltiness, on chromosome 9). C provided favourable alleles for most of the attributes (except for physical attributes), in agreement with the expectations based on the phenotype of parents, but 27 of the 130 QTLs (21%) showed an effect opposite to that expected from the means of the parents. All the alleles providing higher organoleptic quality were provided by C except for sweetness, where the L alleles increased the attribute mean on chromosomes 3 and 9, and for mealiness where L alleles reduced the trait value on chromosomes 3 and 4. For juiciness, both parents provided alleles contributing to higher values.

Clusters of QTLs

Several clusters of QTLs were identified (Fig. 2), mainly on chromosomes 1, 2, 3, 4, 8, 9, 11, and 12. A total of 86 QTLs (66%) mapped to about 14% of the map length. Previous QTL studies in tomato mentioned that some regions of the genome seemed to influence several traits (Fulton *et al*., 1997). These clusters may reveal either a fortuitous linkage, or the segregation of a unique QTL

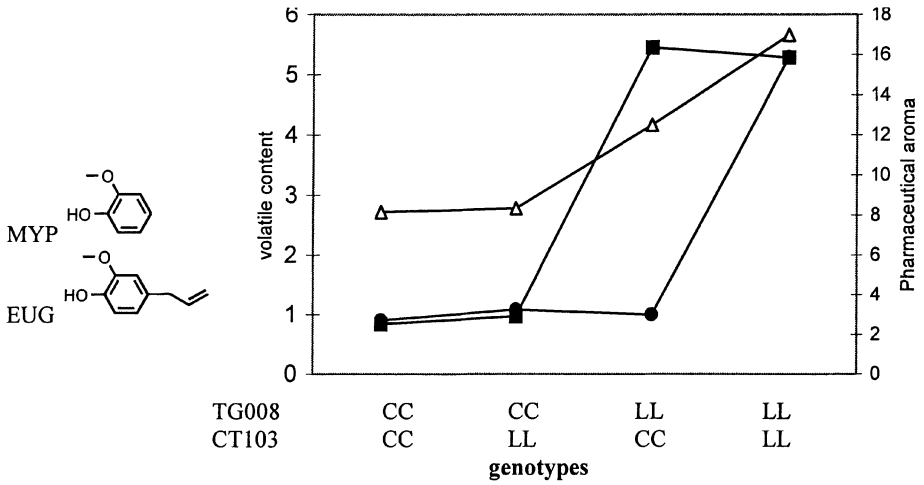

Fig. 3. Relationships between the average content in ortho-methoxyphenol (MYP, black squares, in μg 100 g^{-1} FW), in eugenol (EUG, black circles, in μg kg^{-1} FW) and the pharmaceutical aroma intensity (white triangles), depending on the genotype at TG008 (chromosome 9) and CT103 (chromosome 2) markers. Each point represents the average of the RILs with a specific combination of alleles.

controlling two traits because of a causal relationships among traits or of related metabolisms. These co-locations could be compared to the correlations, as two related traits are expected to share common QTLs. QTL co-locations were observed for related sensory and instrumental traits. For instance, QTLs of titratable acidity, sourness and lemon aroma were in the same regions on chromosomes 1, 2, 3, and 9. QTLs for sugar content and sweetness mapped in the same regions on chromosomes 2 (two regions) and 11. A QTL for fruit weight with an opposite effect was also detected in each of these three regions. Only one common QTL location, on chromosome 3 could be responsible for the negative correlation detected between sweetness and sourness. The contribution of sugars and acids, not only to sweetness and sourness, but also to the overall aroma intensity (Hobson and Bedford, 1989), was confirmed. The QTLs for overall aroma intensity which mapped on chromosomes 2 (top), 9 and 12 were close to QTLs for sourness, while QTLs at the bottom of chromosome 2 were close to QTLs for sweetness.

Only a few co-locations between aroma descriptors and volatile content were expected, based on the low correlations observed. The strong correlation between phamaceutical aroma and the eugenol and ortho-methoxyphenol, two compounds with medicinal odours, was corroborated by two co-locations, one on chromosome 2 (EUG with PHA) and one on chromosome 9 (PHA with EUG and MYP). The content in eugenol was dependent on the two loci with an epistatic interaction. Both L alleles were necessary to detect a significant quantity of eugenol. By contrast, the MYP content only depended on a major gene close to TG008 on chromosome 9. As these two phenolic compounds only differ by a methyl group (Fig. 3), one can think that EUG is derived from the methylation of MYP, such a change being possible only for lines carrying an L allele at the QTL close to CT103. Both of these compounds seemed to be responsible for the pharmaceutical aroma and in an additive manner (Fig. 3).

With the exception of sweetness and mealiness, which showed common QTL locations on chromosomes 3 and 9 (L alleles providing higher values for both attributes), co-locations of QTLs of texture attributes and taste or aroma attributes were not frequent. QTLs on the top of chromosome 2 affected only taste and aroma attributes, while QTLs for texture located on chromosomes 4 and 5 were independent from aroma QTLs.

Fine mapping and multitrait QTL analysis

The region characterized by the largest cluster of QTLs was at the lower end of chromosome 2 (a region of 50 cM). QTLs with strong effect for fruit weight, fruit elasticity, colour, sourness, aroma intensity, candy aroma, mealiness, dry matter weight, soluble solids, sugars, and eugenol content were localized in this cluster. Furthermore, for several traits, more than one QTL was detected in the region. Further genetic studies, such as fine mapping of this region were required to differentiate between closely linked multiple QTLs from the effect of pleiotropic genes. A substitution mapping experiment was thus conducted and near isogenic lines differing only by a short region of this chromosome were evaluated for quality traits. It was thus possible to dissect the region around CD035 and identify at least three different QTLs, one controlling fruit firmness, one controlling sugar and soluble solids content and one controlling fruit weight (L Lecomte *et al.*, unpublished results). By contrast, at the bottom of chromosome 2, the QTLs of fruit weight, elasticity and sugar content remained linked in an interval of 10 cM. This

Table 4. *Multitrait QTL analysis in regions where several QTLs were detected*

The most likely location of the QTL (location) is indicated in cM from the top of the linkage group, followed by the confidence interval (CI) of this location. LOD and percentage of variation explained (PVE) by the QTL are indicated both for multitrait analysis and simple interval mapping. The traits significantly contributing to the multitrait QTL were identified following the procedure proposed by the MultiQTL software (Korol *et al*., 2001).

Multitrait QTL					Individual QTLs	
Chromosome	Location (CI)	LOD	PVE	Traits	LOD	PVE
2 (group 1)	42 (35–53)	18.3	51%	PHA	3.0	9.3%
				EUG	11.3	37.9%
				MTA	3.5	11.2%
				SSC	8.3	26.5%
2 (group 2)	81 (78–88)	19.0	48%	FW	14.0	40.9%
				DMW	11.3	31.8%
				IBT	2.9	10.6%
				MEA	4.9	17.1%
3	85 (73–97)	16.1	44.5%	SWE	2.7	10.7%
				SOU	2.1	7.5%
				TA	4.7	17.3%
				FW	5.4	20.2%
				MEA	2.4	7.4%
4a (group 1)	66 (64–69)	35.1	67.5%	CIT	3.1	10.0%
				BEA	7.1	23.6%
				MNO	21.6	55.2%
				PEA	5.6	17.9%
4a (group 2)	66 (63–69)	23.8	53%	L	6.8	20.5%
				LYC	4.6	13.8%
				MEA	3.9	13.4%
				SKI	2.5	9.9%
				FIR	9.8	31.9%
8	8 (4–13)	18.2	44%	SKI	3.1	9.8%
				X3O	3.5	14.1%
				MEO	13.3	42.2%
9	3 (0–6)	19.3	44%	SOU	5.1	16.8%
				ARO	1.8	7.3%
				MEL	9.4	33.8%
				FIR	3.2	9.8%
				ELA	2.9	10.3%
11	24 (17–29)	12.5	33%	SWE	3.7	12.7%
				pH	4.7	16.3%
				LYC	5.5	17.8%
12	23 (10–38)	12.5	32%	FD	5.1	22.8%
				FW	3.7	12.4%
				PNA	3.6	11.5%

last QTL could be allelic to the fw2.2 QTL controlling fruit weight variation in several genetic backgrounds (Frary *et al*., 2000).

As it was not possible to set up fine mapping experiments for all the clusters of QTLs, the multitrait QTL analysis described by Korol *et al*. (2001) was applied. This method simultaneously takes into account the variation of several traits, extracting some residual information from the covariance among traits. The application of multivariate QTL analysis increases the QTL detection power, and also increases the power of discriminating among hypotheses concerning the genetic control of complex traits, such as linkage versus pleiotropy (Korol *et al*., 2001). Table 4 presents the results of the multitrait QTL analysis based on this approach. In each cluster, the most likely position of the QTL and the associated LOD are shown. Permutation tests were performed to test the significance of the whole trait complex and the traits contributing to the QTL. Several multitrait QTLs were detected in the cluster regions. Such analyses allowed the confidence interval around the QTLs to be reduced and the strong interactions between all the components of fruit quality was corroborated. Two different QTLs were identified in the same location on chomosome 4, corresponding to two distinct sets of traits. The first group corresponded to the citrus fruit aroma and to three aromas which could contribute to this aroma: BEA, MNO and PEA. Indeed, MNO and BEA have a related chemical structure (Fig. 4) and a gene close to TG075 could be responsible for the conversion of BEA into MNO, with different effects of the C and L alleles. Plants with the C allele do not accumulate MNO, whatever the BEA concentration, in contrast to the plants with the L allele for which the two volatiles are strongly related (Fig. 4).

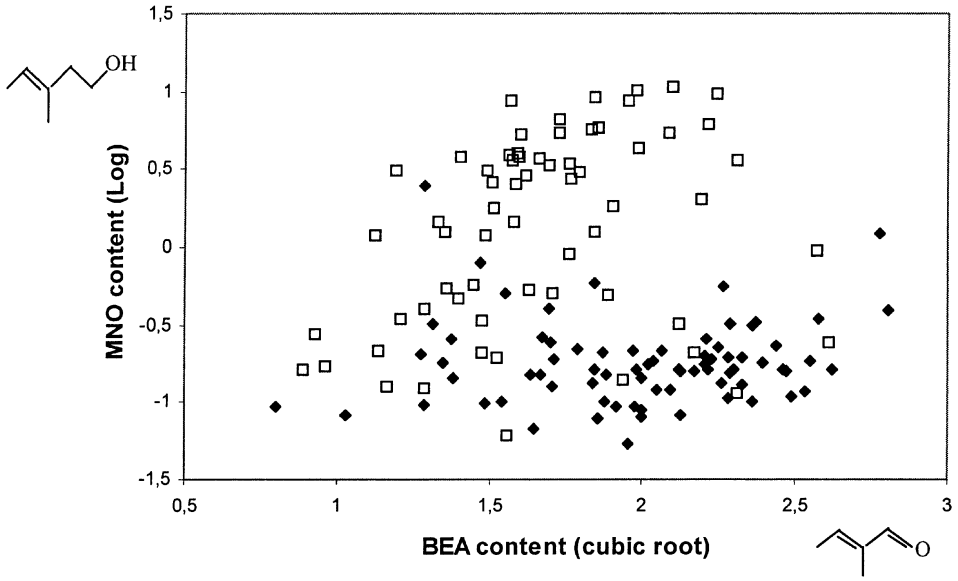

Fig. 4. Relationships between the 2-methylbut-2-enal (BEA) and 3-methylpentan-1-ol (MNO) content (μg kg^{-1} FW, transformed by cubic root or Log to improve the normality of the distributions), related to the Levovil (white squares) or Cervil (black diamonds) genotype at the marker TG075.

The second multitrait QTL on chromosome 4 corresponded to texture traits, involving mealiness, skin, firmness, and colour parameters. Another region on chromosome 9 (top) seemed to control the variation of a texture trait (meltiness) and its related instrumental components (firmness and elasticity). Finally, the region on chromosome 3 is interesting as it is the only one where the L alleles simultaneously increased fruit weight and sweetness, and decreased mealiness and sourness.

Conclusion

The organoleptic quality of fresh market tomatoes can be described by a set of attributes, including fruit appearance, taste, aroma, and texture. A wide variation was found in the progeny for most of the traits. Numerous relationships among sensory traits and instrumental or compositional traits have been shown. While flavour traits (sweetness and sourness) are well described by the sugar content and titratable acidity, the prediction of aroma and texture traits seem much more uncertain because of the lack of precision in the instrumental measures and the interactions among traits.

This is the first study comparing the QTL location for sensory and instrumentally measured traits of fresh market tomato. Several QTLs were detected for all the components of organoleptic quality, some of them with strong effects. Chen *et al*. (1999) recently summarized the chromosome regions where QTLs for fruit weight and soluble solid content were detected in several interspecific progenies studied during the 10 past years. It is interesting to note that the QTLs detected in the present study for sourness and sweetness mapped on chromosomes 2, 3, 9, and 11 within the few regions of the genome where QTLs for soluble solid content frequently mapped in independent studies. Several QTL clusters were detected and it was shown that multivariate analysis could help in describing these clusters. Fine mapping experiments are, nevertheless, much more efficient in dissecting such clusters. These analyses provide the bases for QTL characterization, following either a candidate gene approach (Pflieger *et al*., 2001) or through positional cloning (Frary *et al*., 2000).

Tomato breeders need selection criteria both efficient and easy to assess for organoleptic quality breeding. Physical and chemical traits could be an alternative approach for routinely measuring some of the quality traits, but molecular markers will provide a much more efficient tool. These results will be used for marker-assisted selection in order to transfer pleasant flavour characteristic of the cherry tomato line into elite lines with bigger fruits. As few clusters were detected and some QTLs showed strong effects, genetic progress is expected.

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