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# Genetic analysis of organoleptic quality in fresh market tomato. 1. Mapping QTLs for physical and chemical traits

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**Abstract** Improving organoleptic quality is an important but complex goal for fresh market tomato breeders. A total of 26 traits involved in organoleptic quality variation were evaluated, in order to understand 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 a common taste but with bigger fruits. Physical traits included fruit weight, diameter, color (L,a,b), 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. RILs showed a large range of variation for most of the traits and many of them were transgressive. Some correlations between aroma volatiles were in accordance with the metabolic pathway they originated from. A total of 81 significant QTLs were detected for the 26 traits by simple and composite interval mapping. They were mainly distributed in a few regions on chromosomes 2, 3, 4, 8, 9, 11 and 12. Major QTLs ($R^2$>30%) were detected for fruit weight, diameter, and color, and for six aroma volatiles. Co-localization of QTLs controlling correlated traits was mainly found on chromosome 2. QTLs for fruit weight and sugar content or dry matter weight were often co-localized. However, a QTL for soluble-solids content and dry matter weight have been detected on chromosome 9 in a region without fruit weight QTLs. QTLs for seven aroma volatiles, lycopene content and fruit color were also co-localized. The QTL localizations were compared with those detected in crosses between *Lycopersicon esculentum* and wild tomato species.

**Keywords** Tomato · Quality · QTL · Aroma · Composite interval mapping

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## Introduction

The considerable efforts of tomato breeders have mainly emphasized yield, fruit size, fruit appearance (lack of defects and attractive color), disease resistance and, more recently, fruit firmness and shelf life (to allow long-travel trading). Currently, however, consumers complain about the lack of pleasant sensory qualities of tomato fruit. According to a recent market survey, the sensory quality of a food product has been ranked higher than its nutritional value, price or safety, from a consumer point of view (Berger 1996).

Organoleptic characteristics of a fruit are the sensations perceived by the five senses while consuming it. Organoleptic quality thus involves taste and aroma (both named flavor, since their distinction is sometimes difficult to make) but also the color and the texture of the fruit. Many studies on tomato described the chemical composition of the fruit (for a review see Davies and Hobson 1981). Flavor mainly depends on sugar and acid contents but also on the sugar/acid ratio (Dennison et al. 1953; Stevens 1972). However, the weak correlation between the tomato-like flavor and sugar and acid contents justified the study of volatile composition. Many researchers have identified and quantified aroma volatiles essential to tomato flavor (reviewed in Petro-Turza 1987). With the advent of combined gas chromatography-mass spectrometry systems (GC-MS), analysis of food aroma was greatly facilitated, particularly the isolation and the identification of volatiles (Adda and Richard 1991). More than 400 aroma volatiles were identified in tomato fruit but they are not all equally important for the development of tomato flavor (Petro-Turza 1987). The

influence of variety (Langlois et al. 1996), ripening stage (Baldwin et al. 1991) and storage conditions (Stern et al. 1994) on the most important aroma volatiles was proved, but little is known about their genetic control and the genes responsible for their variation.

Several attempts have been made to improve the sugar/acid ratio and to increase dry matter weight. However, breeding for organoleptic quality has been severely restricted by the lack of efficient selection criteria and by the polygenic nature of the trait. One of the present preoccupations of tomato breeders is to associate high fruit firmness, shelf life, a good flavor, and many disease resistance genes in the same variety. For this purpose, both efficient and easy to measure criteria are needed. Sensory analysis can efficiently describe flavor and texture, but is not of practical use for breeders since large trained panels are necessary for several weeks of analysis. Physical and chemical methods can also be used to evaluate components of texture and flavor, like fruit firmness, and the contents of sugars, acids and aroma volatiles.

Genetic markers have been an important tool to enhance the knowledge of the genetic control of complex quantitative traits. During the past several years, DNA-based markers have been successfully used to map loci controlling quantitative trait variation. Quantitative trait loci (QTLs) were detected in tomato for many important traits such as yield (Eshed and Zamir 1995), disease resistance (Mutschler et al. 1996), tolerance to abiotic stress (Foolad et al. 1998) and plant architecture (de Vicente and Tanksley 1993; Paran et al. 1997). The QTL approach was mainly used to localize genomic regions controlling the quality traits of processing tomato (Paterson et al. 1988). QTLs for fruit weight, dry matter weight, soluble-solids content, pH, fruit color and fruit firmness have been detected in several segregating populations derived from interspecific crosses (Paterson et al. 1988; Goldman et al. 1995; Eshed and Zamir 1996; Grandillo and Tanksley 1996; Bernacchi et al. 1998; Chen et al. 1999). However, no previous effort has been made to map and characterize QTLs contributing to the organoleptic quality of fresh market tomato.

In order to better understand the genetic control of the organoleptic quality of fresh market tomato, we studied the genetic variation of physical, chemical and sensory components. The physical components involved texture and fruit appearance. The chemical components were dry matter weight, sugar content, titratable acidity, pH, and also aroma volatiles and pigment contents. The sensory components will be detailed in a companion paper (Causse et al. 2000). A genetic map was constructed using a population derived from a cross between a cherry tomato line, which exhibited a high overall aroma intensity, and a large-fruited line with common taste (Saliba-Colombani et al. 2000). The purposes of the present study were: (1) to study the phenotypic correlations among and between physical and chemical components of organoleptic quality for fresh, market tomato, and (2) to identify the chromosomal localization and genetic effects of QTLs involved in the variation of these components.

## Materials and methods

### Plant material

The plant material employed was described in Saliba-Colombani et al. (2000). $F_7$ recombinant inbred lines (RILs) were developed from an intraspecific cross between two inbred lines Cervil (C) and Levovil (L). Cervil is a cherry tomato [*Lycopersicon esculentum*, var. *cerasiforme* (Dun.) Gray] with small fruits (6–10 g). It was chosen for its good taste and high aroma intensity. Levovil (*L. esculentum* Mill.) is a line with bigger fruits (90–160 g) and a common taste. A subset of 144 RILs, from the 153 RILs used for map construction, was chosen for QTL detection.

### Evaluation of the RILs

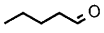
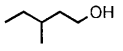
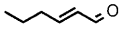
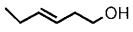
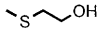
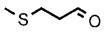
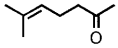
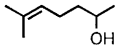
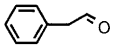
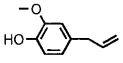
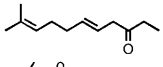
The 144 RILs were grown in a heated greenhouse from February to June 1996 in a fully randomized trial at Châteaurenard (Southern France). A plot of six $F_7$ plants represented each RIL. The parental lines (three plots each) and their $F_1$ hybrid (nine plots) were included as controls to evaluate the environmental variation.

During 6 weeks (from May to June), fruits were harvested daily in bulk on the six plants of each plot. Fruits were harvested on the basis of their red color so that we could compare them at a homogeneous ripening stage. Thirty two physical and chemical traits were measured on a total of 90 fruits per RIL (15 fruits per week). Fruit by fruit evaluation was first achieved for physical traits: fruit weight (FW), fruit diameter (FD), fruit firmness (FIR), and fruit elasticity (ELA). Fruit firmness and fruit elasticity were evaluated by a penetrometer developed at INRA-Montfavet by F. Duprat. The fruit was compressed between two steel plates. A force was applied by the upper plate to deform the fruit by 5% of its diameter and the resulting deformation was measured. FIR is the force by surface unit needed to deform the fruit by 5% of its initial diameter. ELA measures the extent of the fruit deformation after its compression (force/deformation). External color was measured by a Minolta chromameter which resulted in three parameters: lightness (L), and chromaticity coordinates (''a'', a green-to-red scale, and ''b'', a blue-to-yellow scale). The fruits were then cut and frozen (–30°C) for further chemical analyses. Chemical analyses were achieved on fruit frozen powder derived from blending fruits with liquid $N_2$. Chemical traits were total dry matter weight (DMW), soluble-solids content (SSC), sugar content (SUC), titratable acidity (TA), pH, lycopene content (LYC) and carotene content (CAR). Chemical analyses were achieved as recommended in Lime et al. (1957) and the SCAR Agro-Food tomato Working Group (1991). The contents of 18 aroma volatiles, which were quantitatively different between the two parents or representative of a major metabolism, were analyzed for each RIL as described by Bertin et al. (2000). In order to inhibit enzymes involved in the aroma volatile degradation, ammonium sulphate was added to tomato purée. The serum was extracted with pentane-dichloro-methane. Aroma volatiles were separated and quantified by a combined Gas Chromatography-Mass Spectrometry (GC-MS) system as described by Langlois et al. (1996). Table 1 shows the aroma volatiles analyzed, their origin, their chemical structure and their associated odor evaluated by combined hedonic response measurement (CHARM) analyses (Acree et al. 1984). Aroma volatile quantities were expressed as micrograms of the internal standard (used in extraction) per kilogram of fresh fruit. Overall, six measurements (15 fruits per measurement per RIL) were achieved on physical and chemical traits during the 6-week harvest (one measurement per week). Only three measurements of aroma volatile content were performed corresponding each to fruits harvested during 2 weeks (30 fruits per measurement per RIL).

### Data analysis

The mean, standard deviation, environmental and genetic variances of each trait were estimated for the two parents, their $F_1$ hybrid

**Table 1** The 18 studied aroma volatiles. Codes, metabolism, origin and equivalent odor indicated by combined hedonic response (CHARM) analysis

| Volatile aroma | Code | Metabolism | Structure | CHARM equivalent odor |
|---|---|---|---|---|
| Pent-1-en-3-one | N3N | Fatty acids |  | Chemical, green note, plastic |
| Pentanal | PNA | Fatty acids |  | |
| Pentan-3-one | PNN | Unknown |  | |
| 2-Methylbut-2-enal | BEA | Amino acids |  | |
| Hexanal | HXA | Fatty acids |  | Green, green tomato, grass |
| 3-Methylpentan-1-ol | MNO | Amino acids |  | |
| (E)-Hex-2-enal | X2A | Fatty acids |  | Apple, almond |
| Hex-3-en-1-ol | X3O | Fatty acids |  | Green |
| 2-(Methylthio)ethanol | MEO | Unknown |  | |
| 3-(Methylthio)propanal | MTA | Amino acids |  | Potato |
| 6-Methylhept-5-en-2-one | MHN | Lycopene |  | Green bean, parsley |
| 6-Methylhept-5-en-2-ol | MHO | Lycopene |  | |
| 2-Isobutylthiazole | IBT | Unknown |  | |
| 2-Phenylethanal | PEA | Amino acids |  | Flower, rose, green |
| Orthomethoxyphenol | MYP | Phenol |  | Mint, green note, camphor, clove |
| Eugenol | EUG | Phenol |  | Spices, banana, clove |
| Geranylacetone | GYN | Lycopene |  | Green, fried fat |
| Beta-ionone | BIO | Carotenoids |  | |

and the RILs. There was no plot repetition for the RILs, but each of the 6-week measurements (three measurements for aroma volatiles) was considered as a repetition. Differences among lines and among weeks were tested by ANOVA. Heritabilities were estimated as follows:

$h^2 = \sigma^2_G / \sigma^2_G + \sigma^2_e$ , where $\sigma^2_G = \sigma^2_P - \sigma^2_{Plot}$

with $\sigma^2_G$ the genetic variance, $\sigma^2_P$ the phenotypic variance, $\sigma^2_{Plot}$ the residual variance estimated on controls (when a significant difference was detected between control plots), and $\sigma^2_e$ the residual variance. The average values of the repetitions over weeks were used for subsequent analyses. Phenotypic correlations among traits were estimated by Spearman coefficient. Transgressions were investigated by calculating the number of RILs higher or lower than the highest or lowest parent by at least 2-fold the standard deviation (SD) of the parents. For traits deviating from normality, several transformations (log, square root and cubic root) were tested. The transformation that gave the least-skewed result was used for the QTL analysis.

### Map construction and QTL analysis

Molecular markers analyses were as reported in Saliba-Colombani et al. (2000). Linkage analysis was performed with the software package MAPMAKER/EXP version 3.0 (Lander et al. 1987; Lincoln et al. 1992). Recombination fractions were converted into map distances in centimorgans (cM) using the Kosambi mapping function (Kosambi 1944).

Averages of the 6-week values (three for aroma volatiles) for each RIL were used for QTL analyses. QTL detection was performed by interval mapping (IM) (Lander and Botstein 1989) and composite interval mapping (CIM) (Zeng 1993, 1994) using QTL Cartographer software (Basten et al. 1997). A Forward-Backward stepwise regression was performed to choose co-factors before performing QTL detection by CIM. Five co-factors, with the highest *F* values, were taken into account. A window size of 10 cM around the test interval, where the co-factors were not considered, was chosen (model 6 of QTL Cartographer). A permutation test was performed with QTL Cartographer to estimate appropriate significant thresholds for both IM and CIM models. After 1000 permutations, LOD thresholds of 2.36 and 2.56 were chosen for IM and CIM, respectively, corresponding to a genome-wise significance level of $\alpha = 0.10$. When two QTLs were detected by CIM within less than 20 cM, only the most significant one was retained. For each QTL, the position, the additive effect, and the percentage of phenotypic variation explained were estimated. Epistatic interactions between the 84 RFLP markers present in the framework map were analyzed by two-way analyses of variance for all pairwise combinations of marker loci. Only interactions with $P < 0.0001$ were considered.

## Results

### Distribution of phenotypic traits

The 32 physical and chemical traits studied showed continuous variation (Table 2). The content of the aroma volatile MYP (detailed codes in Table 1) showed a bimodal distribution. Analyses of variance indicated highly significant differences among the 6 weeks of harvest for many traits (data not shown). Significant differences were also detected among the 144 RILs for all traits except six aroma compounds (N3N, PNN, X2A, MHO, GYN and BIO), which were removed from the subsequent analyses. The parental lines showed significant differences

**Table 2** Variation of physical and chemical traits. Average values of the parent lines and their $F_1$ hybrid are detailed. Significance level of the comparison test of Cervil vs. Levovil means is indicated by (C vs. L). Recombinant inbred lines are described by mean, standard deviation (SD), range of variation and heritability. The transformation used for QTL detection, and the number of lines showing transgression (see Materials and methods), are indicated. fm = fresh matter

| Item | Trait | Code | Parents and $F_1$ hybrid | | | | RILs | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Cervil | Levovil | Hybrid | C vs. L | Mean (SD) | Range | Heritability | Transformation | Transgression |
| Physical traits | Fruit weight | FW (g) | 7.38 | 125.20 | 29.56 | *** | 24.36 (4) | 10.8–71.3 | 0.75 | Log | No |
| | Fruit diameter | FD (cm) | 2.46 | 6.27 | 3.92 | *** | 3.66 (0.2) | 2.77 – 5.28 | 0.86 | Log | No |
| | Fruit firmness | FIR (Pa) | 35 080 | 34 920 | 32 430 | ns | 39 990 (4842) | 28 130–57 280 | 0.63 | Log | 21 |
| | Fruit elasticity | ELA (N/cm) | 12.41 | 34.37 | 19.37 | *** | 22.40 (2.2) | 16.9–38.4 | 0.78 | Log | No |
| | L | | 38.12 | 42.13 | 38.03 | *** | 38.85 (1.01) | 36.8–43.5 | 0.55 | Log | No |
| | a | | 14.87 | 15.96 | 13.33 | ns | 13.98 (1.9) | 6.10–20.8 | 0.68 | No | 29 |
| | b | | 17.43 | 24.83 | 16.54 | *** | 18.06 (1.7) | 14.3–26.1 | 0.55 | Log | No |
| Chemical traits | Dry matter weight | DMW (g/100 g fm) | 10.59 | 5.35 | 8.74 | *** | 8.36 (0.46) | 5.5–10.8 | 0.85 | No | No |
| | Soluble-solids content | SSC (Brix) | 8.80 | 5.06 | 7.27 | *** | 7.18 (0.71) | 4.4–9.4 | 0.58 | No | No |
| | Sugar content | SUC (g/100 g fm) | 4.32 | 3.09 | 4.04 | *** | 4.01 (0.42) | 2.9–5.3 | 0.61 | No | No |
| | Titratable acidity | TA (meq/100 g fm) | 11.80 | 5.06 | 8.96 | *** | 7.82 (0.62) | 4.2–11.7 | 0.81 | Square root | 1 |
| | pH | | 4.20 | 4.23 | 4.19 | ns | 4.22 (0.00) | 4.1–4.4 | 0.51 | No | 12 |
| | Lycopene content | LYC (µg/100 g fm) | 1949 | 1935 | 2017 | ns | 2024 (834) | 981–3199 | 0.10 | No | No |
| | Carotene content | CAR (µg/100 g fm) | 1350 | 962.90 | 1126 | *** | 1183 (244) | 877–1786 | 0.25 | Square root | No |
| Aroma volatiles | Pent-1-en-3-one | N3N (µg/kg) | 12.18 | 3.34 | 2.09 | ns | 8.34 (15) | 0.3–75.5 | – | – | – |
| | Pentanal | PNA (µg/kg) | 26.06 | 20.42 | 23.09 | ns | 23.27 (12.2) | 4.5–63 | 0.23 | Square root | 2 |
| | Pentan-3-one | PNN (µg/kg) | 0.42 | 0.35 | 0.24 | ns | 0.40 (0.24) | 0.1–1.7 | – | – | – |
| | 2-Methylbut-2-enal | BEA (µg/kg) | 21.12 | 1.44 | 7.57 | *** | 6.27 (6.15) | 0.5–22 | 0.19 | Cubic root | No |
| | Hexanal | HXA (µg/kg) | 46.40 | 136.80 | 56.86 | *** | 61.26 (40) | 15.7–255.7 | 0.30 | Square root | No |
| | 3-Methylpentan-1-ol | MNO (µg/kg) | 2.24 | 0.94 | 0.50 | ns | 0.24 (0.79) | 0.05–10.8 | 0.88 | Log | 99 |
| | (E)-Hex-2-enal | X2A (µg/kg) | 74.94 | 49.88 | 49.15 | ns | 62.18 (43) | 6.4–339.7 | – | – | – |
| | Hex-3-en-1-ol | X3O (µg/kg) | 12.27 | 11.71 | 9.64 | ns | 11.60 (3.7) | 4.7–29.9 | 0.53 | Log | 10 |
| | 2-(Methylthio)ethanol | MEO (µg/kg) | 412.20 | 13.66 | 106.50 | *** | 133.70 (56) | 16.2–557.4 | 0.78 | Cubic root | 1 |
| | 3-(Methylthio)propanal | MTA (µg/kg) | 99.00 | 15.60 | 58.53 | *** | 61.98 (33) | 6.6–662 | 0.76 | Log | 9 |
| | 6-Methylhept-5-en-2-one | MHN (µg/kg) | 6.28 | 8.92 | 9.58 | ns | 5.95 (3.53) | 1.9–16.4 | 0.14 | Square root | No |
| | 6-Methylhept-5-en-2-ol | MHO (µg/kg) | 0.12 | 0.36 | 0.08 | ns | 0.19 (0.20) | 0.006–1.3 | – | – | – |
| | 2-Isobutylthiazole | IBT (µg/kg) | 0.04 | 0.58 | 0.07 | * | 0.05 (0.05) | 0.006–0.3 | 0.47 | Log | No |
| | 2-Phenylethanal | PEA (µg/kg) | 43.90 | 7.51 | 19.55 | *** | 26.43 (14.9) | 2.5–169.8 | 0.72 | Cubic root | 8 |
| | Orthomethoxyphenol | MYP (µg/kg) | 2.88 | 55.72 | 1.63 | *** | 18.34 (13.4) | 1–194 | 0.87 | Log | 7 |
| | Eugenol | EUG (µg/kg) | 0.89 | 5.39 | 0.47 | *** | 0.89 (1.05) | 0.5–14.8 | 0.82 | Log | 6 |
| | Geranylacetone | GYN (µg/kg) | 0.94 | 1.07 | 0.90 | ns | 0.93 (0.63) | 0.03–4.4 | – | – | – |
| | Beta-ionone | BIO (µg/kg) | 0.34 | 0.25 | 0.05 | ns | 0.26 (0.26) | 0.003–0.8 | – | – | – |

**Table 3** Phenotypic correlations among physical and chemical traits in the RIL population. Only significant correlations are shown (P < 0.05 and * P < 0.01). ns (non significant)

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **FW** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **FD** | 0.98* | **FD** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **FIR** | –0.22* | –0.22* | **FIR** | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **ELA** | 0.54* | 0.56* | 0.66* | **ELA** | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **L** | 0.23* | 0.26* | 0.41* | 0.56* | **L** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **a** | ns | ns | 0.47* | 0.40* | 0.68* | **a** | | | | | | | | | | | | | | | | | | | | | | | | | |
| **b** | 0.25* | 0.27* | 0.49* | 0.64* | 0.90* | 0.78* | **b** | | | | | | | | | | | | | | | | | | | | | | | | |
| **DMW** | –0.67* | –0.70* | ns | –0.65* | –0.56* | –0.31* | –0.56* | **DMW** | | | | | | | | | | | | | | | | | | | | | | | |
| **SSC** | –0.56* | –0.58* | ns | –0.53* | –0.43* | –0.29* | –0.46* | 0.90* | **SSC** | | | | | | | | | | | | | | | | | | | | | | |
| **SUC** | –0.45* | –0.48* | ns | –0.40* | –0.33* | ns | –0.33* | 0.79* | 0.78* | **SUC** | | | | | | | | | | | | | | | | | | | | | |
| **TA** | –0.58* | –0.59* | –0.22* | –0.64* | –0.46* | –0.30* | –0.50* | 0.67* | 0.59* | 0.23* | **TA** | | | | | | | | | | | | | | | | | | | | |
| **pH** | 0.27* | 0.26* | ns | ns | ns | –0.17 | ns | ns | ns | ns | –0.26* | **pH** | | | | | | | | | | | | | | | | | | | |
| **LYC** | –0.32* | –0.31* | 0.25* | ns | 0.20 | 0.51* | 0.27* | ns | ns | 0.27* | ns | ns | **LYC** | | | | | | | | | | | | | | | | | | |
| **CAR** | –0.41* | –0.44* | ns | –0.35* | ns | ns | –0.18 | 0.34* | 0.33* | 0.26* | 0.20 | ns | 0.48* | **CAR** | | | | | | | | | | | | | | | | | |
| **PNA** | –0.20 | –0.22* | ns | ns | ns | ns | ns | 0.19 | 0.25* | 0.22* | ns | –0.34* | 0.33* | 0.28* | **PNA** | | | | | | | | | | | | | | | | |
| **BEA** | –0.19 | –0.18 | ns | ns | 0.25* | 0.33* | 0.23* | ns | ns | ns | ns | –0.25* | 0.24* | ns | ns | **BEA** | | | | | | | | | | | | | | | |
| **HXA** | ns | ns | 0.40* | 0.32* | 0.45* | 0.38* | 0.41* | –0.23* | –0.21 | ns | –0.21 | ns | 0.26* | 0.20 | 0.45* | 0.24* | **HXA** | | | | | | | | | | | | | | |
| **MNO** | ns | ns | –0.37* | –0.38* | –0.37* | –0.38* | –0.34* | 0.30* | 0.21 | ns | 0.43* | ns | –0.18 | ns | ns | ns | –0.18 | **MNO** | | | | | | | | | | | | | |
| **X3O** | –0.19 | –0.23* | –0.21 | –0.32* | –0.30* | –0.39* | –0.31* | 0.24* | 0.19 | ns | 0.24* | ns | ns | 0.22* | 0.21 | ns | ns | 0.46* | **X3O** | | | | | | | | | | | | |
| **MEO** | –0.17 | ns | ns | ns | ns | 0.19 | ns | ns | ns | ns | ns | ns | ns | 0.27* | 0.18 | 0.21 | 0.21 | ns | –0.18 | **MEO** | | | | | | | | | | |
| **MTA** | ns | ns | ns | ns | ns | ns | ns | ns | –0.21 | ns | ns | –0.20 | ns | ns | ns | 0.56* | ns | ns | –0.20 | 0.43* | **MTA** | | | | | | | | | |
| **MHN** | ns | 0.22* | ns | 0.19 | 0.32* | 0.48* | 0.35* | –0.39* | –0.45* | –0.28* | –0.24* | ns | 0.29* | ns | ns | ns | 0.25* | ns | ns | ns | ns | **MHN** | | | | | | | | |
| **IBT** | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.20 | ns | ns | 0.33* | 0.39* | ns | ns | ns | ns | ns | ns | ns | 0.19 | **IBT** | | | | | | |
| **PEA** | ns | 0.18 | ns | 0.26* | 0.35* | 0.41* | 0.31* | ns | ns | ns | –0.23* | ns | ns | ns | ns | 0.40* | 0.18 | –0.34* | –0.46* | 0.52* | 0.68* | 0.19 | ns | **PEA** | | | | | |
| **MYP** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | **MYP** | | | | |
| **EUG** | 0.36* | 0.35* | ns | 0.18 | ns | ns | ns | –0.34* | –0.32* | –0.31* | –0.22* | 0.19 | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.40* | **EUG** | | |

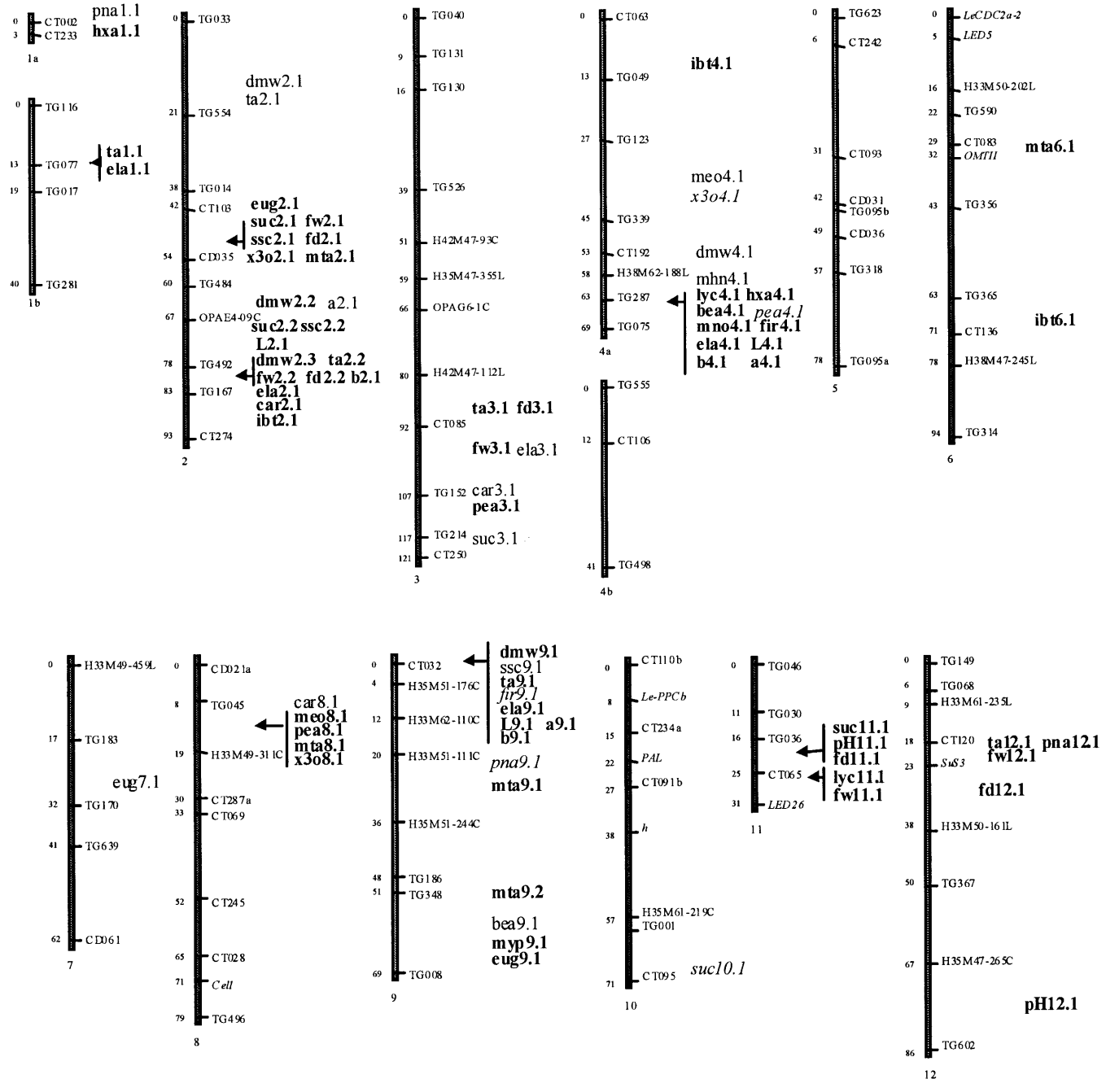



**Fig. 1** Linkage map of the tomato genome based on an intraspecific RIL population of a cross between a cherry tomato line and a large fruit line. Names of the markers, on the right of chromosomes, are described in Saliba-Colombani et al. (2000). QTLs detected by CIM and IM are in *bold*, those only detected by CIM are in *normal letters*, and those only detected by IM are in *italics*. QTL codes are followed by two *numbers*: first the chromosome number and second the number of the QTL on the chromosome. An arrow was added when a few QTLs mapped to the same locus

for most of the traits (Table 2). Cervil showed higher levels than Levovil (by at least two standard-deviation units) for traits describing fruit composition. Conversely, Levovil showed higher levels for the physical traits and for four aroma volatiles (by at least three standard-deviation units). The $F_1$ hybrid had values intermediate between the two parent means for most of the traits. Compared to Cervil, all the RILs showed bigger, firmer, and more-elastic fruits. The RILs showed higher values than Levovil for contents of soluble solids, sugar, and MEO and MTA aroma volatiles. RILs showed a very large range of variation for the 12 retained aroma volatiles. For example, the MNO content varied in RILs from 0.05 to 10.75 µg/kg, and the MTA content varied from 6.6 to 662 µg/kg. Based on extreme values of RILs, transgressive segregations were detected in both directions for most of the traits. Nevertheless, only nine traits showed transgressive segregation with means that were higher or lower than the highest or lowest parent by at least 2 SDs, re-

spectively (Table 2). Heritabilities were high (> 0.5) for all the physical traits and most of the chemical traits (Table 2). The contents of lycopene, carotene and some aroma volatiles showed low heritability (< 0.3). Deviation from normality characterized most of the traits (Table 2). None of the tested transformations completely restored the normality of MYP and EUG.

## Correlations

Phenotypic correlations among the 26 traits are detailed in Table 3. Fruit weight and fruit diameter, both highly correlated, were positively correlated to fruit elasticity but negatively correlated to fruit firmness. Both fruit firmness and elasticity were positively correlated with color parameters. Among the chemical traits, the strongest positive correlations were observed between dry matter weight on one hand and soluble-solids content, sugar content and titratable acidity on the other hand. Aroma volatiles presented a complex network of correlations. A few correlations were significant between aroma volatiles and other chemical traits. MHN and EUG were negatively correlated to the major chemical components of the fruit, while MNO was positively correlated to these traits. Lycopene and carotene contents were positively correlated together, as well as to PNA, IBT and HXA. Lycopene content was positively correlated to the MHN content. Some correlations were also observed between physical and chemical traits like fruit weight and fruit elasticity which were negatively correlated to most of the chemical traits. Fruit-color parameters L and b were also negatively correlated to dry matter components. The color parameter a was positively correlated to lycopene content but also to the aroma volatile MHN.

## Map construction and QTL analysis

The complete map included one morphological, 132 RFLP, 33 RAPD and 170 AFLP markers (Saliba-Colombani et al. 2000). A framework map with 103 markers (one morphological, 84 RFLPs, two RAPDs, and 16 AFLPs) and an average interval of 10 cM, was selected for QTL analyses. Regions in the middle of chromosomes 1 and 4 were still not covered. The map covered about 85% of the tomato genome when compared to the high-density genetic map of tomato (Tanksley et al. 1992).

QTLs were detected for all traits (Fig. 1). The results of analyses performed on transformed data are reported. A total of 81 significant associations between molecular markers and phenotypic data were detected by IM and CIM (Table 4 and Fig. 1). This corresponded to a minimal number of QTLs, as in 35 cases, two QTLs closely linked (d < 20 cM) were detected by CIM, but we only retained the most significant one. IM and CIM almost detected the same QTLs but the LOD-score values were not identical with the two methods, especially when two QTLs were detected on the same chromosome. Among the 81 QTLs, 14 were only significant by CIM and five were only significant by IM. However, their LOD-scores in IM and CIM, respectively, fell just below the thresholds (2.36 for IM and 2.56 for CIM) or else their closest marker effects were among the five most-significant effects detected by multiple regression.

Sixteen (28%) of the eighty one QTLs showed an effect opposite to that expected from the means of the parents. A maximum of six QTLs (for titratable acidity) and a minimum of one QTL (for aroma volatiles MNO, MYP and MHN) controlled each trait. The individual percentage of explanation for the phenotypic variation ($R^2$) varied between 87.4% for the aroma volatile MYP and 8.3% (the lowest limit of detection) for the a color parameter. Nine QTLs showed a $R^2$ lower than 10%, 60 QTLs a $R^2$ between 10% and 30% and 12 QTLs a $R^2$ between 30% and 87%. Hereafter, only QTLs detected by CIM will be detailed.

Fruit weight and fruit diameter each involved five QTLs on chromosomes 2 (two QTLs), 3, 11 and 12. All these QTLs had allelic effects in the expected direction with the Levovil allele increasing the diameter and weight of the fruit. The most significant QTLs *fw2.2* and *fd2.2* explained 46% and 38% of the fruit-weight and fruit-diameter phenotypic variation. Fruit firmness was affected by one QTL on chromosome 4, while five QTLs were detected for fruit elasticity on chromosomes 1, 2, 3, 4 and 9. The color parameters L, a and b were each affected by three QTLs on chromosomes 2, 4 and 9.

For dry matter weight, five QTLs were detected on chromosomes 2 (three QTLs), 4 and 9, with the most-significant QTL *dmw2.2* explaining 25% of the phenotypic variation. The Cervil allele increased the dry matter weight as expected for all QTLs, with one exception on chromosome 4. Three QTLs controlled the soluble-solids content, two on the same regions as QTLs for dry matter weight on chromosome 2 and one on chromosome 9. Variation of the sugar content was explained by four QTLs on chromosomes 2 (two QTLs), 3 and 11. As expected, the Cervil allele increased the sugar content at three QTLs, while the Levovil allele increased the trait value at the QTL on chromosome 3. Titratable acidity was controlled by six QTLs with the most significant one (*ta9.1*) accounting for 22% of the phenotypic variation. As expected, Cervil alleles at all these QTLs increased the titratable acidity. Lycopene content was controlled by two QTLs on chromosomes 4 and 11; and three QTLs controlled carotene content on chromosomes 2, 3 and 8. QTLs for aroma volatiles were mainly localized on chromosomes 2, 4, 8 and 9 (Fig. 1). Among the 26 QTLs detected for aroma volatiles, the $R^2$ was lower than 10% in two cases, it varied from 10% to 30% for 18 QTLs, and was higher than 30% for six QTLs. Some aroma-volatile variations were mostly explained by one major QTL, as for the MYP and MNO contents with *myp9.1* and *mno4.1* accounting for 87% and 63% of the phenotypic variation, respectively. By contrast, three and five QTLs were involved in the variation of EUG and MTA contents, respectively. Levovil alleles increased aroma-volatile values for half of the QTLs.

**Table 4** QTLs detected for physical and chemical traits based on CIM and IM analyses in the RIL progeny. The most-closely associated marker locus is indicated. When more than one QTL per trait was detected by CIM in less than 20 cM, the number of QTLs is indicated in the column ''linked QTLs'', but only the most significant is described. The distance of the QTL in cM (Kosambi) from the nearest marker is indicated by Pos. LOD is the log-likelihood at that position. Effect is the absolute value of the difference (after transformation) of the two allelic classes at the QTL. PVE is the percentage of phenotypic variation explained by the QTL. The parent increasing the trait value is shown in the parent column. Data for non-significant (ns) effects in one method are indicated in italics. Markers introduced as co-factors in the CIM model are designated by cof. When the co-factor was different from the marker QTL, the distance (in cM) between the co-factor and the QTL localization was added (cof +)

| Trait | QTL | Marker | Chr. | Composite interval mapping | | | | | | | Interval mapping | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Linked QTLs | Pos. | LOD | Effect | PVE | Parent | COF | Pos. | LOD | Effect | PVE |
| **Fruit weight** | **fw2.1** | CT103 | 2 | 2 | 5.19 | 4.32 | 0.10 | 17.4 | L | cof | 8 | 3.37 | 0.13 | 13.3 |
| | **fw2.2** | TG492 | 2 | | 3.94 | 17.62 | 0.19 | 46.2 | L | cof+1 | 2 | 13.99 | 0.22 | 40.9 |
| | **fw3.1** | CT085 | 3 | | 1.78 | 10.85 | 0.14 | 31.8 | L | cof | 6 | 5.39 | 0.15 | 20.2 |
| | **fw11.1** | CT065 | 11 | | 0.11 | 10.46 | 0.13 | 29.3 | L | cof | 0 | 4.45 | 0.13 | 13.9 |
| | **fw12.1** | CT120 | 12 | 2 | 1.74 | 3.73 | 0.08 | 13.2 | L | – | 2 | 3.69 | 0.12 | 12.4 |
| **Fruit diameter** | **fd2.1** | TG484 | 2 | 2 | 2.01 | 6.29 | 0.04 | 22.4 | L | cof | 7 | 12.65 | 0.07 | 35.0 |
| | **fd2.2** | TG492 | 2 | | 4.94 | 13.72 | 0.06 | 38.3 | L | cof | 2 | 14.70 | 0.08 | 42.4 |
| | **fd3.1** | H42M47–112L | 3 | 2 | 10.23 | 9.11 | 0.04 | 27.8 | L | cof+2 | 7 | 4.38 | 0.05 | 16.5 |
| | **fd11.1** | TG036 | 11 | 2 | 2.91 | 11.52 | 0.05 | 34.5 | L | cof+6 | 7 | 4.34 | 0.05 | 14.7 |
| | **fd12.1** | *SuS3* | 12 | 2 | 5.95 | 3.66 | 0.03 | 17.5 | L | – | 8 | 5.08 | 0.06 | 22.8 |
| **Firmness** | **fir4.1** | TG287 | 4 | | 5.14 | 10.85 | 0.07 | 33.3 | C | cof+1 | 4 | 9.78 | 0.07 | 31.9 |
| | **fir9.1** | CT032 | 9 | | *0.00* | *2.25 ns* | *0.03* | *10.35* | *L* | *cof* | 0 | 3.20 | 0.04 | 9.8 |
| **Elasticity** | **ela1.1** | TG077 | 1 | | 2.10 | 3.03 | 0.05 | 10.2 | L | | 2 | 3.03 | 0.05 | 10.3 |
| | **ela2.1** | TG167 | 2 | 2 | 0.88 | 7.67 | 0.06 | 24.9 | L | cof | 1 | 6.13 | 0.07 | 20.1 |
| | **ela3.1** | CT085 | 3 | 2 | 0.78 | 3.52 | 0.04 | 11.3 | L | cof | *8* | *2.18 ns* | *0.04* | *8.7* |
| | **ela4.1** | TG287 | 4 | | 4.14 | 2.68 | 0.04 | 9.8 | C | cof+2 | 2 | 2.68 | 0.05 | 9.2 |
| | **ela9.1** | CT032 | 9 | 2 | 1.01 | 4.17 | 0.05 | 13.9 | L | cof | 1 | 2.88 | 0.05 | 10.3 |
| **L** | **L2.1** | OPAE4–0.9C | 2 | | 4.98 | 5.76 | 0.01 | 20.1 | L | cof | 7 | 3.40 | 0.87 | 13.0 |
| | **L4.1** | TG287 | 4 | | 1.14 | 6.56 | 0.01 | 19.8 | C | cof | 1 | 6.83 | 1.11 | 20.5 |
| | **L9.1** | CT032 | 9 | 2 | 1.01 | 5.17 | 0.01 | 16.5 | L | cof | 1 | 4.83 | 0.98 | 15.7 |
| **a** | **a2.1** | TG484 | 2 | | 3.01 | 3.88 | 1.64 | 14.1 | L | cof | *3* | *1.87 ns* | *1.49* | *7.3* |
| | **a4.1** | TG287 | 4 | | 2.14 | 10.35 | 2.77 | 30.8 | C | cof | 1 | 8.59 | 2.77 | 24.7 |
| | **a9.1** | CT032 | 9 | | 0.00 | 2.66 | 1.32 | 8.3 | L | cof | 0 | 2.65 | 1.61 | 8.2 |
| **b** | **b2.1** | TG492 | 2 | | 4.94 | 5.06 | 0.03 | 15.7 | L | cof | 5 | 3.30 | 0.03 | 10.4 |
| | **b4.1** | TG287 | 4 | | 5.14 | 6.23 | 0.04 | 19.3 | C | cof+1 | 2 | 6.25 | 0.04 | 19.4 |
| | **b9.1** | CT032 | 9 | 2 | 1.00 | 8.82 | 0.04 | 26.5 | L | cof | 1 | 7.02 | 0.05 | 22.1 |
| **Dry matter weight** | **dmw2.1** | TG033 | 2 | | 9.01 | 2.94 | 0.62 | 16.0 | C | – | *15* | *2.05 ns* | *0.71* | *10.0* |
| | **dmw2.2** | TG484 | 2 | 2 | 4.01 | 7.38 | 0.96 | 25.6 | C | cof+3 | 7 | 11.30 | 1.25 | 31.8 |
| | **dmw2.3** | TG492 | 2 | 2 | 3.95 | 2.88 | 0.63 | 9.9 | C | cof+2 | 1 | 10.25 | 1.21 | 29.7 |
| | **dmw4.1** | CT192 | 4 | | 0.11 | 3.11 | 0.51 | 9.5 | L | cof | *0* | *2.10 ns* | *0.58* | *6.5* |
| | **dmw9.1** | CT032 | 9 | | 0.00 | 5.70 | 0.71 | 16.8 | C | cof | 0 | 2.84 | 0.67 | 8.8 |
| **Soluble solids content** | **ssc2.1** | CT103 | 2 | 2 | 5.19 | 3.58 | 0.59 | 14.7 | C | cof+7 | 10 | 8.26 | 0.94 | 26.5 |
| | **ssc2.2** | OPAE4–0.9C | 2 | 2 | 3.98 | 4.57 | 0.68 | 18.6 | C | cof | 2 | 10.26 | 1.01 | 31.9 |
| | **ssc9.1** | CT032 | 9 | 2 | 0.00 | 4.36 | 0.52 | 13.3 | C | cof | *2* | *2.14 ns* | *0.49* | *7.3* |
| **Sugar content** | **suc2.1** | CT103 | 2 | | 6.20 | 2.66 | 0.34 | 11.9 | C | cof | 11 | 7.62 | 0.53 | 22.5 |
| | **suc2.2** | OPAE4–0.9C | 2 | | 2.98 | 7.40 | 0.47 | 25.3 | C | cof | 2 | 9.19 | 0.59 | 29.0 |
| | **suc3.1** | TG214 | 3 | | 0.00 | 2.78 | 0.25 | 8.8 | L | cof | *1* | *1.90 ns* | *0.28* | *6.5* |
| | **suc10.1** | TG001 | 10 | | *9.00* | *2.39 ns* | *0.26* | *9.3* | *C* | *cof* | 11 | 2.94 | 0.34 | 9.5 |
| | **suc11.1** | TG036 | 11 | 2 | 6.90 | 3.32 | 0.29 | 11.2 | C | cof+2 | 5 | 3.42 | 0.39 | 12.5 |
| **Titratable acidity** | **ta1.1** | TG077 | 1 | | 0.20 | 3.70 | 0.12 | 11.2 | C | cof | 0 | 4.89 | 0.18 | 14.9 |
| | **ta2.1** | TG033 | 2 | 2 | 14.01 | 3.22 | 0.14 | 17.3 | C | – | *14* | *2.24 ns* | *0.17* | *12.4* |
| | **ta2.2** | TG492 | 2 | 2 | 3.94 | 5.46 | 0.15 | 17.2 | C | cof | 3 | 4.50 | 0.18 | 14.3 |
| | **ta3.1** | H42M47–112L | 3 | | 8.23 | 4.88 | 0.16 | 18.1 | C | cof+4 | 7 | 4.70 | 0.19 | 17.3 |
| | **ta9.1** | CT032 | 9 | 2 | 0.00 | 7.80 | 0.19 | 22.4 | C | cof | 0 | 3.76 | 0.16 | 11.5 |
| | **ta12.1** | CT120 | 12 | 2 | 3.74 | 2.97 | 0.12 | 10.6 | C | cof+1 | 2 | 2.79 | 0.15 | 9.7 |
| **pH** | **pH11.1** | TG036 | 11 | 3 | 4.91 | 5.97 | 0.06 | 20.0 | L | – | 5 | 4.75 | 0.06 | 16.3 |
| | **pH12.1** | H35M47–265C | 12 | | 9.01 | 3.93 | 0.06 | 19.1 | L | cof+10 | 11 | 3.33 | 0.06 | 15.8 |
| **Lycopene content** | **lyc4.1** | TG287 | 4 | | 0.14 | 3.86 | 265 | 11.7 | C | cof | 0 | 4.65 | 330 | 13.8 |
| | **lyc11.1** | CT065 | 11 | | 1.11 | 5.60 | 336 | 18.0 | C | cof | 1 | 5.46 | 370 | 17.8 |
| **Carotene content** | **car2.1** | TG167 | 2 | 2 | 4.88 | 3.87 | 1.66 | 14.1 | C | cof | 4 | 3.08 | 1.82 | 13.8 |
| | **car3.1** | TG152 | 3 | 2 | 5.77 | 3.30 | 1.55 | 12.8 | C | cof | *5* | *1.87 ns* | *1.31* | *7.2* |
| | **car8.1** | TG045 | 8 | 2 | 0.83 | 3.07 | 1.44 | 10.7 | C | cof | *0* | *1.74 ns* | *1.16* | *5.6* |

**Table 4** (continued)

| Trait | QTL | Marker | Chr. | Composite interval mapping | | | | | | | | | Interval mapping | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Linked QTLs | Pos. | LOD | Effect | PVE | Parent | COF | Pos. | LOD | Effect | PVE |
| **Pentanal content** | **pna1.1** | CT002 | 1 | | 2.01 | 2.62 | 0.49 | 8.5 | L | cof+1 | *2* | *2.09 ns* | *0.51* | *6.8* |
| | **pna9.1** | H33M51–111C | 9 | | *5.40* | *2.14 ns* | *0.57* | *11.3* | *L* | *cof* | 3 | 2.68 | 0.76 | 14.5 |
| | **pna12.1** | CT120 | 12 | 2 | 0.74 | 3.39 | 0.57 | 10.9 | C | cof | 1 | 3.61 | 0.67 | 11.5 |
| **2-Methylbut-2-enal content** | **bea4.1** | TG287 | 4 | 2 | 1.14 | 8.84 | 0.42 | 27.1 | C | cof | 4 | 7.10 | 0.42 | 23.6 |
| | **bea9.1** | TG348 | 9 | | 3.97 | 3.33 | 0.27 | 13.6 | C | cof | *8* | *2.01 ns* | *0.26* | *9.2* |
| **Hexanal content** | **hxa1.1** | CT002 | 1 | | 0.00 | 9.90 | 2.12 | 29.1 | L | cof | 1 | 8.09 | 2.11 | 25.2 |
| | **hxa4.1** | TG287 | 4 | 3 | 2.14 | 4.27 | 1.36 | 15.7 | C | – | 0 | 4.70 | 1.6 | 14.3 |
| **3-Methylpentan-1-ol content** | **mno4.1** | TG287 | 4 | | 3.14 | 25.90 | 1.00 | 63.2 | L | cof | 3 | 21.56 | 0.94 | 55.2 |
| **Hex-3-en-1-ol content** | **x3o2.1** | CD035 | 2 | | 0.07 | 3.01 | 0.08 | 9.6 | C | cof | 0 | 2.38 | 0.09 | 7.5 |
| | **x3o4.1** | TG123 | 4 | | *11.00* | *1.17 ns* | *0.07* | *6.4* | *L* | *cof* | 12 | 3.66 | 0.13 | 16.5 |
| | **x3o8.1** | TG045 | 8 | | 2.83 | 3.40 | 0.09 | 12.2 | L | cof | 5 | 3.53 | 0.12 | 14.1 |
| **2-(Methylthio) ethanol content** | **meo4.1** | TG123 | 4 | | 9.18 | 2.69 | 0.72 | 14.2 | C | cof | *9* | *2.32 ns* | *0.88* | *12.1* |
| | **meo8.1** | TG045 | 8 | 2 | 2.83 | 15.98 | 1.61 | 48.8 | C | cof | 3 | 13.3 | 1.62 | 42.2 |
| **3-(Methylthio) propanal content** | **mta2.1** | CT103 | 2 | | 10.19 | 3.75 | 0.19 | 12.7 | L | cof+2 | 11 | 3.50 | 0.21 | 11.2 |
| | **mta6.1** | CT083 | 6 | | 2.12 | 6.65 | 0.24 | 21.0 | C | cof+1 | 2 | 4.60 | 0.23 | 15.1 |
| | **mta8.1** | TG045 | 8 | | 7.83 | 3.01 | 0.18 | 12.2 | C | cof+3 | 6 | 2.94 | 0.21 | 12.1 |
| | **mta9.1** | H33M51–111C | 9 | 2 | 11.93 | 3.51 | 0.21 | 18.4 | C | – | 8 | 2.45 | 0.23 | 13.7 |
| | **mta9.2** | TG348 | 9 | | 1.00 | 3.20 | 0.17 | 11.0 | C | | 0 | 2.67 | 0.18 | 8.5 |
| **6-Methylhept-5-en-2-one content** | **mhn4.1** | H38M62–188L | 4 | | 4.60 | 4.62 | 0.58 | 14.2 | C | cof | *3* | *1.92 ns* | *0.26* | *6.5* |
| **2-Isobutylthiazole content** | **ibt2.1** | TG167 | 2 | | 5.88 | 3.89 | 0.22 | 14.6 | C | cof+4 | 7 | 2.96 | 0.23 | 10.6 |
| | **ibt4.1** | CT063a | 4 | | 11.01 | 9.60 | 0.35 | 31.2 | L | cof+2 | 11 | 6.26 | 0.33 | 21.4 |
| | **ibt6.1** | TG365 | 6 | 2 | 5.97 | 5.71 | 0.25 | 18.7 | L | cof+2 | 6 | 4.99 | 0.29 | 16.4 |
| **2-Phenylethanal content** | **pea3.1** | TG152 | 3 | | 0.77 | 4.36 | 0.46 | 15.1 | L | cof | 4 | 2.63 | 0.51 | 9.6 |
| | **pea4.1** | TG287 | 4 | | *4.60* | *2.24 ns* | *0.44* | *8.3* | *C* | *cof+1* | 5 | 5.64 | 0.69 | 17.9 |
| | **pea8.1** | TG045 | 8 | 2 | 6.83 | 15.38 | 1.04 | 56.4 | C | cof+4 | 7 | 9.97 | 0.96 | 34.6 |
| **Orthomethoxy-phenol content** | **myp9.1** | TG348 | 9 | | 12.97 | 47.95 | 1.18 | 87.4 | L | cof+5 | 13 | 45.7 | 1.23 | 86.8 |
| **Eugenol content** | **eug2.1** | CT103 | 2 | 2 | 4.19 | 10.84 | 0.66 | 42.3 | L | cof | 3 | 11.31 | 0.47 | 37.9 |
| | **eug7.1** | TG183 | 7 | | 10.60 | 3.17 | 0.19 | 11.9 | L | cof+4 | *9* | *1.39 ns* | *0.18* | *5.8* |
| | **eug9.1** | TG348 | 9 | | 14.97 | 4.62 | 0.39 | 22.9 | L | cof+3 | 17 | 4.01 | 0.33 | 20.8 |

### Epistatic interactions

Epistatic interactions were tested between the 84 RFLP markers of the framework map for all the traits. With 3486 tests per trait, a significance threshold of $P < 0.0001$ was chosen. Thus, less than one (0.348) interaction could occur by chance. At this threshold 14 significant associations were detected (Table 5). Significant interaction was detected for MNO between CT85 on chromosome 3 and TG339 on chromosome 4 (20 cM apart from a QTL for MNO). RILs with the Cervil allele on CT85 and the Levovil allele on TG339 showed the highest MNO content. Seven associations concerned EUG on two genomic regions of chromosomes 2 and 9. The most significant one was between CT103 on chromosome 2 and TG8 on chromosome 9, where the two major QTLs for EUG were detected (Fig. 1). Individuals with Levovil alleles at both markers contained 5-fold more EUG than individuals with the three other allele combinations.

## Discussion

Breeding for the organoleptic quality of tomato is difficult due to the complexity of this characteristic. In order to understand the genetic control of organoleptic quality, the major physical and chemical components responsible for its variation were evaluated. Fruit quality has often been studied for processing tomato. The major traits examined were fruit weight, soluble-solids content, and pH. These traits are not sufficient to describe fresh market tomato and so additional chemical traits were also studied. Titratable acidity and pH are both important criteria for tomato eating quality (Kader et al. 1977; Baldwin et al. 1991). The contents of pigments, such as lycopene and carotene, are related to fruit color but also to nutritional quality, since carotene is a precursor of vitamin A and the benefits of lycopene have been shown by Rao and Agarwal (1998). Moreover, the aroma volatiles are responsible for the tomato-like flavor. Many studies concerned the qualitative and quantitative composition of aroma volatiles in tomato fruits (Buttery

**Table 5** Significant epistatic interactions ($P < 0.0001$) detected between the 84 RFLP markers. The Prob. (probability), the $R^2$ (percentage of the phenotypic variation explained) of the epistatic interaction, and the means of the four genotype classes are detailed

| Trait | Marker 1 | Marker 2 | Chromosomes | Prob. | R2 | CC | LC | CL | LL |
|---|---|---|---|---|---|---|---|---|---|
| ELA | TG365 | TG314 | 6–6 | 9.40E-05 | 12.8 | 20.75 | 24.40 | 24.62 | 22.19 |
| b | TG077 | LED5 | 1–6 | 7.81E-05 | 14.0 | 18.90 | 17.76 | 17.41 | 19.49 |
| b | OPAE4–0.9C | H33M62–110C | 2–9 | 5.34E-05 | 9.1 | 17.64 | 18.31 | 18.02 | 21.50 |
| SSC | TG365 | TG314 | 6–6 | 7.58E-05 | 13.2 | 7.35 | 6.85 | 6.61 | 7.41 |
| pH | Cel1 | TG030 | 8–11 | 9.32E-05 | 12.7 | 4.18 | 4.23 | 4.27 | 4.23 |
| MNO | CT085 | TG339 | 3–4 | 3.34E-05 | 17.0 | 0.57 | 1.59 | 4.46 | 0.96 |
| EUG [(a)] | CT103 | TG008 | 2–9 | 5.29E-08 | 14.2 | 0.90 | 1.08 | 1.00 | 5.29 |
| EUG | CD036 | TG348 | 5–9 | 5.05E-06 | 16.1 | 1.31 | 1.13 | 1.72 | 6.12 |

[(a)] Seven epistatic associations between linked markers on chromosomes 2 (to CT103) and 9 (to TG008) were detected for EUG, but only the most significant one is indicated

et al. 1987; Baldwin et al. 1991; Krumbein and Auerswald 1998) but poor knowledge of their genetic control is available.

## Trait distribution and transgression

Parent values were significantly different for 18 of the 32 studied traits. Cervil showed higher values especially for traits related to dry matter weight and for some aroma volatiles. This was expected since Cervil was chosen for its high aroma intensity and good flavor. Levovil did not show any special aroma characteristics but had higher values for three aroma volatiles, HXA, MYP and EUG. MYP and EUG contents corresponded to odors generally not appreciated (pharmaceutical odors). HXA could improve the aroma of tomato juice in the concentration range of 0.1–0.5 ppm, but above a 0.5-ppm concentration its flavor is similar to rancid vegetable fats (Kazeniac and Hall 1970). It was not possible to compare HXA concentration to that mentioned in Kazeniac and Hall (1970) due to differences in the quantification method. The $F_1$ hybrid was intermediate between the two parent values for several traits such as fruit elasticity, dry matter weight and carotene content, suggesting additivity of these traits. The $F_1$ hybrid value was close to the lower parent for fruit weight, diameter and color, pH, and for the aroma volatiles HXA and IBT. This implied the dominance of the small values.

Low heritability (< 0.3) of some traits (as for lycopene and carotene content) corresponded to high variation between the repetitions (over the 6 weeks) and could result either from the effect of climate variation or from the physiological variation induced by change of the plant with age. In contrast, traits like sugar content and titratable acidity showed high heritabilities (> 0.5), suggesting a minimal effect of the environment under greenhouse-controlled conditions. Six of the eighteen aroma volatiles significantly different between the parent lines did not show any significant differences between RILs, because of strong variation between the three repetitions. Transgression, observed for 12 of the 26 traits, could be explained by the presence of complementary QTL alleles in the two parental lines. In many cases, transgression was associated with the detection of QTLs having allelic effects opposite to those predicted by the parents. However, some traits like the aroma volatiles MEO, MYP and EUG, despite their transgressive segregation, did not show such QTLs with an effect opposite to the parents. Transgression proved that Levovil contains QTL alleles increasing some pleasant volatile contents despite its common flavor, but also increasing L, a, b, dry matter weight, and sugar-content values.

## Relationships between traits

Some correlations were due to physiological relationships between traits. Positive correlations were observed, as expected, between the major components of dry matter. Fruit weight was negatively correlated to soluble-solids content as in Tanksley et al. (1996), Bernacchi et al. (1998) and Chen et al. (1999). However, in Grandillo and Tanksley (1996) this correlation was positive.

Low fruit pH of tomato allows the reduction of processing time. The pH value is also important for the flavor of fresh market tomato as variation in sour taste was shown to be due to pH and titratable acidity (Kader et al. 1977). The correlation between these traits was positive or negative depending on the samples studied (Davies and Hobson 1981). In our study, titratable acidity and pH were negatively correlated. Actually, relationships between these traits are complex and several buffers can interact with them (Paulson and Stevens 1974). Stevens (1986) proposed that both traits should be measured for evaluating the quality of fresh market tomato. Color parameters were negatively correlated to soluble-solid content. This result is in contradiction to the findings of Fulton et al. (1997) and Tanksley et al. (1996) from interspecific crosses. A positive correlation between color parameters (L and b) and fruit weight was found in our study, which is consistent with the results of Fulton et al. (1997). Tanksley et al. (1996) and Bernacchi et al. (1998) reported an opposite correlation between these traits in progenies involving *Lycopersicon pimpinellifolium* and *Lycopersicon hirsutum*. A positive correlation was detected between fruit weight and elasticity while a poor negative correlation

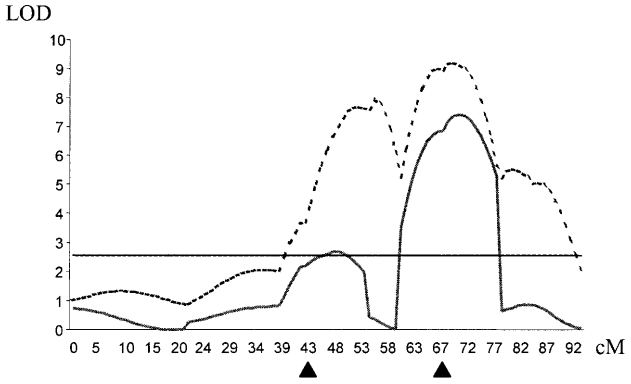



**Fig. 2** Comparison of the LOD-score plot for sugar content along chromosome 2 estimated by IM (dotted lines) and CIM with a 10 cM window size (*solid line*). The abscissa axis represents the chromosome distance in Kosambi cM. The *horizontal line* at LOD = 2.56 indicates the LOD threshold for detecting a QTL by CIM. *Black arrows* show the localization of co-factors

was detected between fruit weight and firmness, as in Fulton et al. (1997). This implied that large fruits were more elastic and less firm than small fruits. Actually, the lower elasticity of small fruits was also suggested by the higher number of cracks observed (data not shown). For aroma volatiles, some correlations were in accordance with the metabolic pathway they originated from. For instance, PNA, HXA and X3O, which derived from fatty acids, were expected to exhibit correlated contents. PNA content was positively correlated to HXA and X3O, but HXA and X3O were not correlated. For aroma volatiles deriving from amino acids, positive correlations were found between MTA, BEO and PEA contents, and between MNO and PEA contents. EUG and MYP contents were positively correlated since both are phenolic compounds (Kazeniac and Hall 1970). MHN, which derived from lycopene oxidation, was positively correlated with lycopene content. Some correlations were less expected. For example, MNO and X3O contents, derived from different kinds of metabolism, were positively correlated. Some aroma volatiles were also positively correlated to color parameters (BEA, HXA, MHN and PEA) and others (MNO and X3O) negatively. The evolution of aroma contents in relation to fruit ripening could explain such relationships.

## Methods of QTL detection

The composite interval mapping method allowed more than one QTL to be mapped on the same chromosome and increased the precision of the QTL position and the $R^2$ evaluation (Zeng 1994). Most of the QTLs (66%) had higher $R^2$ values in CIM than in IM, while their additive effects were higher in IM. The power of the CIM test is lower than that of IM when only one QTL occurred on a chromosome since it involved conditional tests. Estimation of additive effects by CIM is, however, more accurate. CIM analyses were especially useful on chromosome 2 where several traits were each controlled by two or three QTLs in a region of 36 cM. Figure 2 shows a LOD-score plot for sugar content as revealed by IM and CIM on chromosome 2. IM and CIM each detected two peaks. While the two IM peaks had similar and high LODs, and the LOD between the two peaks was also high, CIM allowed the detection of two well-dissociated peaks with a smaller LOD for the first peak. Despite the advantages of CIM, the localization of QTLs linked within less than 20 cM was still inaccurate. We have undertaken fine mapping studies, which may allow evaluation of the actual QTL number.

## QTL detection

Some QTLs (for fruit weight and diameter, and the aroma volatiles MNO and MYP) explained a large part of the phenotypic variation and could be considered as major genes. By contrast, for some traits like pH and pigment contents, only a small part of the phenotypic variation was explained. High positive correlations were detected between the heritability and the overall percentage of variation explained by QTLs per trait (between 0.7 and 0.8 in IM and CIM). The contents of lycopene, carotene and the aroma volatiles PNA, X3O and MHN, had low $R^2$ and low heritabilities.

Two-way ANOVAs showed significant epistasis for six traits. The percentage of significant epistatic interactions was slightly higher than the percentage expected by chance. In tomato, only minimal evidence of epistasis was found in conventional segregating populations (Paterson et al. 1991; Grandillo and Tanksley 1996) and the frequencies of statistically significant QTL interactions were close to the frequencies expected to occur by chance. A major QTL was detected for the aroma volatile MNO on chromosome 4 (TG287), while there was no significant difference between parental MNO contents. The large effect of this QTL may be a residue of the epistatic effect between CT85 (on chromosome 3) and TG339 (on chromosome 4). Actually, the MNO content of RILs having a Cervil allele at CT85 and a Levovil allele at TG339 is 8-fold higher than those with a Cervil allele at TG339. The same situation was detected for EUG content, and QTLs on chromosomes 2 and 9 may be a residual bias of the epistatic interaction, as the L alleles are necessary at both QTLs to observe a significant difference in EUG content.

## QTL clustering and co-localization of QTLs

QTLs were localized on all the chromosomes except chromosome 5, but they were not evenly dispersed. QTLs for aroma volatiles were mainly localized on chromosomes 4 (eight QTLs), 8 (four QTLs), and 9 (five QTLs), suggesting the involvement of these regions in aroma-volatile metabolisms. Other chemical traits were mainly controlled by three linked regions on chromosome 2 (ten QTLs), and by QTLs on chromosomes 3

(three QTLs), 9 (three QTLs) and 11 (three QTLs). Physical traits were approximately controlled by the same regions on chromosomes 2 (eight QTLs in two regions), 3 (three QTLs), 4 and 9 (five QTLs each). The region characterized by the largest cluster of QTLs was at the lower end of chromosome 2 (a region of 50 cM). The major QTLs for fruit weight, fruit elasticity, brightness (L), dry matter weight, soluble-solids, sugar and EUG contents were localized in this cluster. Furthermore, most of these traits were each represented by more than one peak linked in less than 20 cM (Table 4). Some QTL co-localizations could be due to physiological relationships. Fruit elasticity QTLs were detected on two chromosomes (4 and 9) close to QTLs for L, a and b, suggesting an association between fruit elasticity and color development. Frequent co-localizations were observed between QTLs for dry matter weight and titratable acidity, as expected, since acids are among the major components of dry matter weight. Nevertheless QTLs for sugar content, which composed 50% of the dry matter, were not detected in the same regions. Only one co-localization between these traits was observed on chromosome 2. The negative correlation between fruit weight and sugar content or dry matter weight is well illustrated by the co-localization of QTLs of these traits on chromosomes 2, 3 and 11. Such co-localizations were found in several studies between fruit weight and soluble-solids content (Paterson et al. 1991; Goldman et al. 1995). In such cases, it is difficult to distinguish the pleiotropic effect of a single gene from the effects of tightly linked loci. Since these QTLs are frequently co-localized, one can assume the pleiotropic effect of a single gene. On chromosome 4, in a region of 30 cM, QTLs for lycopene content, color parameters (L, a, b) and seven aroma volatiles (derived from amino acids, fatty acids and lycopene degradation) were detected. Cervil provided favorable alleles for all these traits except for the aroma volatiles MNO and MEO. The co-localization of QTLs for lycopene content and color parameters proved that the evaluation of color is directly related to lycopene content. Two hypotheses could explain the co-localization of aroma volatile, lycopene content and color QTLs. (1) The development of aroma volatiles depends on the ripening stage, which is associated with the fruit color. While the contents of some aroma volatiles decrease with ripening, most of them increase. (2) Some aroma volatiles can derive from carotenoid pigment degradation, such as lycopene and carotene. In the same region, Giovannoni et al. (1999) localized an ethylene-related cDNA (ERT16) showing homology with an ABA stress-related protein. Acting upstream of fruit changes, such a gene could be responsible for the variation in many fruit quality characteristics. Other co-localizations of QTLs for aroma volatiles and carotene content were identified on chromosomes 2 and 8. QTLs of aroma volatiles derived from the same metabolic pathway were often co-localized, as on chromosome 1 for PNA and HXA, both derived from fatty acid metabolism, and on chromosome 9 for EUG and MYP, both phenolic compounds.

## Comparison of QTLs among tomato species

This is the first QTL study in tomato based on a cross between two *L. esculentum* lines. The QTL localizations were compared with those detected in other studies involving crosses between *L. esculentum* and wild tomato species. The QTL localizations of only 11 traits could be compared, since QTLs for fruit elasticity, titratable acidity, carotene content, and aroma-volatile contents were never previously studied. QTLs were considered to be in the same region when they mapped within the same 20-cM region of the high-density tomato map (Tanksley et al. 1992). Since all QTL studies on tomato concerned processing tomato, the most-studied traits were fruit weight, soluble-solids content, and pH. On chromosome 6, only two QTLs for aroma volatiles were detected, whereas other studies on tomato quality traits detected a large number of QTLs on this chromosome (Paterson et al. 1991; Goldman et al. 1995). Actually, the *sp* (*self pruning*) gene, which controls the determinate growth habit, is localized on chromosome 6. Many QTLs detected in its neighborhood, in populations segregating for this gene, could be due to the pleiotropic effects of *sp* (Paterson et al. 1988; Goldman et al. 1995). In the present study, both parent lines were *sp+*. A major QTL for fruit weight (*fw2.2*) mapped to the same position on chromosome 2 (near TG167) in the green-fruited species *Lycopersicon pennellii* and *L. hirsutum*, the orange-fruited species *Lycopersicon cheesmanii*, and the red-fruited species *L. pimpinellifolium* (Paterson et al. 1991; Alpert et al. 1995; Bernacchi et al. 1998). Here, we found that the most-significant QTL for fruit weight also mapped on chromosome 2 between TG492 and TG167. It explained 46% of the phenotypic variation and so could be considered as a major gene. *fw2.2* would then represent an orthologous (derived by speciation) fruit-weight QTL distributed in wild tomato species, and domestication of the cultivated tomato seemed to have involved a macromutation at this locus (Alpert et al. 1995). It would thus also distinguish small vs. large fruits in *L. esculentum*. The other fruit-weight QTLs were localized on chromosome 3 in a common position with those detected in crosses with *L. hirsutum* and *L. pimpinellifolium* (Bernacchi et al. 1998; Chen et al. 1999), on chromosome 11 in the same region as a QTL detected in a cross with *L. pimpinellifolium* (Grandillo and Tanksley 1996), and on chromosome 12 close to a QTL detected in a cross with *Lycopersicon peruvianum* (Fulton et al. 1997).

Soluble-solids content QTLs shared the same positions on chromosome 2 in our study as the QTLs detected in crosses with *L. cheesmanii* (Paterson et al. 1991), *L. pennellii* (Eshed and Zamir 1995), *L. pimpinellifolium* (Tanksley et al. 1996; Chen et al. 1999) and *L. peruvianum* (Fulton et al. 1997). The QTL for soluble-solid content on chromosome 9 also mapped in the same region as a soluble-solids content QTL detected by Fulton et al. (1997). For pH, the QTL on chromosome 12 was localized in the same region as that detected in a cross with *L. hirsutum* (Bernacchi et al. 1998). The fruit-color QTL

on chromosome 4 was localized in the same region as the QTL detected by Bernacchi et al. (1998), where the fruit color was estimated visually from canned paste. The fruit color QTL on chromosome 9 shared the same position as QTLs for external (L, a and b) and internal color (visually scored) detected in a progeny involving *L. peruvianum* (Fulton et al. 1997). Among the two QTLs detected for lycopene content in our study, only *lyc4.2* was close to the QTL detected by Chen et al. (1999) on chromosome 4. QTLs for fruit firmness (evaluated by a penetrometer) on chromosome 4 (*fir4.1*) and chromosome 9 (*fir9.1*) were detected in the same regions as the fruit-firmness (evaluated by hand squeezing) QTLs detected in crosses with *L. pimpinellifolium* (Tanksley et al. 1996) and *L. peruvianum* (Fulton et al. 1997), respectively.

## Conclusion

This is the first study concerning QTLs for organoleptic quality in fresh market tomato. We detected 81 QTLs involved in the major physical and chemical components of organoleptic quality. In a companion paper, QTLs for sensory traits will be presented (Causse et al. 2000). Physical and chemical traits could be an alternative approach to routinely measure quality traits. Tomato breeders need to dispose of such selection criteria both efficient and easy to assess. Recently, the fruit organoleptic quality has seen a surge of interest, and QTLs of this characteristic have been mapped in a few species. For example, the organoleptic quality of peach (Dirlewanger et al. 1999) was studied on traits such as fresh weight, color, pH, titratable acidity, soluble-solids content, acid and sugar contents. The QTLs were mainly localized on two linkage groups. In *Citrus*, molecular markers linked to a gene controlling fruit acidity were detected (Fang et al. 1997). QTLs for chemical (like starch and sucrose content) and sensory (like aroma, sweetness, starchiness, and tenderness) traits were examined in sweet corn (Azanza et al. 1996). Kennard and Havey (1995) studied QTLs for the length, diameter, and color of cucumber. QTLs of aroma volatiles were less well studied. In rice, the concentration of the main compound of rice aroma (2-acetyl-1-pyrroline) is controlled by a major gene and two QTLs (Lorieux et al. 1996). The QTLs found in this study could be used in marker-assisted selection in order to transfer the pleasant flavor characteristic of the Cervil line into elite lines with larger fruits. As few clusters were detected, and some QTLs showed high effects, future genetic progress can be expected. Particular attention must, however, be paid when transferring QTLs with opposite effects, as for fruit weight and dry matter weight. The QTL map should allow the selection of regions where only QTLs for sugar or acid content were detected without fruit weight QTLs.

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