Received: 27 October 2023 | Revised: 30 January 2024 | Accepted: 5 March 2024

DOI: 10.1111/pbr.13168

ORIGINAL ARTICLE

Plant Breeding WILEY

Flavour improvement in early generations of fresh market tomatoes (*Solanum lycopersicum*): I. Identification of QTL for sensory attributes, physicochemical measurements and volatile compounds

Julia Hagenguth[1] | Larissa Kanski[2] | Hannah Kahle[3] | Heiko C. Becker[1] | Bernd Horneburg[4,5]

[1]Division of Plant Breeding Methodology, Department of Crop Sciences, Faculty of Agriculture, University of Goettingen, Goettingen, Germany

[2]Division of Quality of Plant Products, Department of Crop Sciences, Faculty of Agriculture, University of Goettingen, Goettingen, Germany

[3]Department of Horticultural Production, University of Applied Sciences Osnabrueck, Osnabrueck, Germany

[4]Division of Plant Breeding, Section of Genetic Resources and Organic Plant Breeding, Department of Crop Sciences, Faculty of Agriculture, University of Goettingen, Goettingen, Germany

[5]Section of Organic Plant Breeding and Agrobiodiversity, University of Kassel, Witzenhausen, Germany

Correspondence
Julia Hagenguth, Division of Plant Breeding Methodology, Department of Crop Sciences, Faculty of Agriculture, University of Goettingen, Carl-Sprengel-Weg 1, 37075 Goettingen, Germany.
Email: julia.hagenguth@agr.uni-goettingen.de

Present address
Bernd Horneburg, Section of Organic Plant Breeding and Agrobiodiversity, University of Kassel, Witzenhausen, Germany.

Funding information
Ministry for Science and Culture of Lower Saxony, Grant/Award Number: VWZN3255; Software AG Foundation; Open Access Publication Funds of the University of Goettingen

Abstract

Human sensory analysis is the most appropriate method for assessing the flavour of fresh market tomatoes, but it is very labour and time consuming. Therefore, sensory attributes are often neglected in early generations of breeding programmes and genetic studies, although there is a demand for tomatoes with improved flavour. In this study, the recently developed Breeders' Sensory Test was applied to an F_2 mapping population derived from two parents with superior flavour. Sensory attributes, physicochemical measurements, volatiles and fruit weight were assessed in organic low-input and hydroponic cultivation. A linkage map spanning 1070 cM was developed. In total, 71 quantitative trait loci (QTL) were detected for the means of both cultivation systems, 61 for organic and 46 for hydroponic cultivation. A proportion of 27% of the loci were co-localized between both cultivation systems. Nine distinct QTL clusters for flavour-related traits were identified, including a large cluster on chromosome 6 comprising five sensory and nine volatile QTL. The sensory QTL on chromosomes 2, 5, 6, 10 and 11, partly within clusters, are recommended for marker-assisted selection.

KEYWORDS
fruit flavour, QTL mapping, sensory analysis, *Solanum*, tomato, volatiles

We dedicate this study to Prof. Wolfgang Ecke on the occasion of his retirement. For more than 25 years, he supported numerous students and scientists of the Division of Plant Breeding Methodology (former Plant Breeding), including us, in linkage mapping, QTL analyses and other genetic studies.

1 | INTRODUCTION

Tomatoes (*Solanum lycopersicum* L., 2n = 2x = 24) are among the most popular vegetables worldwide, consumed fresh and processed, and are an important source of micronutrients, such as antioxidants and vitamins (Klee, 2010; Piombino et al., 2013). Nevertheless, the loss of flavour in fresh market tomatoes is a major cause of consumer complaints (Causse et al., 2010; Colantonio et al., 2022; Folta & Klee, 2016). Flavour results from the interaction of primary and secondary metabolites, and flavour perception is additionally influenced by texture and external properties, such as colour and size (Causse et al., 2003; Klee, 2010; Piombino et al., 2013). Sugars (glucose and fructose) and acids (citric, malic and glutamic acid) are the most important compounds contributing to taste; both are necessary in sufficient quantities and in an appropriate balance (Klee, 2010; Stevens et al., 1977). Aroma volatiles cause the diversity of flavours (Klee, 2010; Klee & Tieman, 2018). The increasing demand for flavourful tomatoes raises the need for breeding high-yielding cultivars with outstanding flavour (Colantonio et al., 2022; Zörb et al., 2020). Nonetheless, improving flavour remains a challenge due to the difficulties in assessing this complex trait, the lack of clear selection criteria and a negative correlation between quality characteristics and fruit size or yield (Causse et al., 2003; Klee & Tieman, 2013; Klee & Tieman, 2018).

According to Tieman et al. (2017), flavour phenotyping is expensive, limited to a small number of samples and therefore not possible in the first segregating generations of a breeding programme. Sensory analysis by a trained or consumer panel is the best method for evaluating taste and aroma attributes but is not suitable for breeding purposes (Causse et al., 2001; Causse et al., 2010; Piombino et al., 2013). Thus, the Breeders' Sensory Test (Hagenguth et al., 2022) was introduced. Because simple physicochemical measurements are not sufficient to predict flavour, molecular markers for key aroma compounds and sensory attributes can contribute substantially to flavour improvement (Causse et al., 2003; Klee & Tieman, 2018; Tieman et al., 2017). As simultaneous selection for many molecular markers is challenging (Xu & Crouch, 2008), the number of aroma volatiles contributing to tomato flavour and consumer liking needs to be reduced to a smaller set of primary or secondary metabolites, which is possible, as many volatile compounds are metabolically linked (Klee & Tieman, 2018; Martina et al., 2021; Rambla et al., 2014). An alternative is to develop molecular markers directly for sensory attributes that reflect the perceived flavour. Such quantitative trait loci (QTL) are a promising tool for the preselection of seedlings and thus in reducing the loss of valuable genotypes. Several studies have been conducted to identify genetic regions controlling the quantitative variation of fresh tomato flavour, focusing on primary and secondary metabolites (Martina et al., 2021; Tikunov et al., 2020). Sensory attributes, however, are only considered by a few authors (Causse et al., 2001; Tikunov et al., 2020; Zanor et al., 2009). Tikunov et al. (2020) identified several QTL for sensory properties but fewer than for primary metabolites and volatile compounds. One reason for this might be the complexity of flavour perception; many genetically and functionally independent loci are likely to be involved in the variation in sensory attributes (Tikunov et al., 2020). Many studies have worked with genetically distant material, such as crosses between cultivated and wild tomatoes to increase genetic and phenotypic variation. However, studies using modern cultivars are needed for the direct implementation of QTL into practical breeding programmes (Kimbara et al., 2018; Tikunov et al., 2020). In particular, studies using mapping populations developed from a cross between cultivars with superior flavours are missing.

Flavour is not only influenced by genetics but also by the cultivation system and agronomic practices (Beckles, 2012; Causse et al., 2001; Klee, 2010). The majority of greenhouse tomatoes are grown in conventional hydroponic systems, where plants are grown in an inert substrate (Korčok et al., 2021), but the demand for organically produced tomatoes is constantly increasing (Raigón et al., 2022; Willer et al., 2022). QTL might not only be specific for the plant material used but also for the cultivation system. QTL studies are often conducted over several seasons or years (Bauchet et al., 2017; Capel et al., 2015; Zanor et al., 2009) but rarely in different cultivation systems, such as fields and greenhouses, as in Tieman et al. (2006, 2017) and Mathieu et al. (2009). Co-localized QTL detected in contrasting cultivation systems are of special interest for breeding programmes.

To map QTL for superior flavour in organic low-input and hydroponic cultivation, an F_2 mapping population was developed from an intraspecific cross between two high-quality cultivars. The parents are characterized by excellent but contrasting quality attributes and different fruit weights. Sensory attributes, physicochemical measurements (total soluble solids [TSS], pH, titratable acidity [TA], dry matter [DM]), volatile compounds and fruit weight were assessed.

2 | MATERIALS AND METHODS

2.1 | Mapping population

An F_2 population of 188 individuals, originating from a single F_1 plant, was developed from a cross between the two open-pollinated cultivars 'Resi' (Organic Outdoor Tomato Project, released in 2010, Zörb et al., 2020 and CPVO, 2022) and 'Auriga' (Saatzucht Quedlinburg, released in 1980, CPVO, 2022). Resi, a red cocktail tomato, was chosen for its sweetness, tomato and fruity (named banana-melon) aroma. Auriga, an orange salad tomato, has distinctly sour fruit and a characteristic aroma profile (named orange aroma).

2.2 | Cultivation systems

The F_2 mapping population and three plants per parental cultivar were phenotyped in an organic low-input system at Reinshof experimental farm (51°30′17.0″ N, 9°55′14.5″ E), University of Goettingen, Germany, and in hydroponic cultivation at the University of Applied Sciences, Department of Horticultural Production, Osnabrueck, Germany, in 2018. In both cultivation systems, plants were grown in a

randomized complete block design with two replications (blocks) surrounded by border plants.

Seeds were sown in trays in Bio-Traysubstrat (Klasmann-Deilmann, Geeste, Germany) in a greenhouse (22°C day/18°C night, 16/8 h) in Week 13. Seedlings with fully developed cotyledons were transferred 8 days later into QP96 trays (Hermann Meyer, Rellingen, Germany) filled with Bio-Traysubstrat. After another 8 days, the seedlings were potted in 1.1-L pots with Bio-Kräutererde (Klasmann-Deilmann, Geeste, Germany). In Week 19, three side shoots were taken from each individual plant. The largest one was planted into a 1.1-L pot; the two smaller ones were cut to an equal size and planted in QP96 trays filled with Bio-Traysubstrat.

In the organic cultivation system, the original plants were transferred to the field in Week 21 (replication 1) and the largest cuttings 1 week later (replication 2). Plants were grown in silty loam (Hagenguth et al., 2022) under a well-ventilated rain-out shelter (greenhouse film Euro 4, Folien Bernhard, Dreieich, Germany) to minimize major pathogens that are relevant in greenhouses (e.g. *Cladosporium fulvum* Cooke) and the open field (*Phytophthora infestans* [Mont.] de Bary). Plants were spaced 0.5 m apart within and 1 m between rows. Low-input conditions were defined as no application of fertilizer and moderate irrigation. During the entire growing season, 239 L m^{-2} were irrigated with a drip system. Temperature, relative humidity and soil water content are given in Figure S1 and mineral nitrogen in Table S1.

In hydroponic cultivation, the two smaller cuttings were transferred to rockwool cubes (10 × 10 × 6.5 cm, Grodan®, Roermond, The Netherlands) in Week 22. Three weeks later, Grodan cubes were placed on rockwool slabs (100 × 15 × 7.5 cm, Grodan®, Roermond, the Netherlands) in the greenhouse (19°C day/17°C night; single glazed) in double rows (distance 0.5 m) with 0.36 m between plants and 1 m between double rows. The plants were irrigated with a nutrient solution. This nutrient solution was prepared according to De Kreij et al. (2003). The amount and concentration of nutrients were adapted according to solar irradiation and development stage.

2.3 | Evaluation of F_2 plants

In the organic trial, mature fruits were harvested, weighted and counted every second week from week 27 onwards. Ideally, four fruits per plant were weighed in the hydroponic trial at Weeks 37 and 39 to obtain the average fruit weight. Fruits with blossom end rot were discarded. Fully mature fruits were harvested in the organic cultivation system in Week 33 and in hydroponic cultivation in Week 36 for sensory, physicochemical and volatile analyses. Up to 82 samples were evaluated and processed each day.

2.3.1 | Sensory evaluation

For sensory evaluation, the Breeders' Sensory Test (Hagenguth et al., 2022) was applied by a three-person team. Depending on the range of experience, the team members were trained on two to six dates for 4 weeks before the evaluation (5–12 h in total). Sweetness, sourness, total aroma, tomato aroma and the special aroma attributes banana, melon, orange, berry, spicy and green (Table 1) were evaluated on a scale from 1 to 9 (1 = not perceptible, 9 = maximum intensity). The following four standard cultivars were used to define the scale of the assessed attributes: mini plum (origin and cultivar unknown, high score for sweetness), a standard salad tomato purchased at a supermarket (low scores for all sensory attributes) and both parental cultivars. Each evaluation started by tasting these standard cultivars, followed by tasting three to five random samples to calibrate the team on each evaluation day. Samples were double-blind randomized and served on transparent plastic trays (Petri dishes). For neutralization, tap water, herb tea, brown bread and yoghurt were served. Breaks were regularly taken as required by the team, including a 1-h break after about 50% of the daily samples.

TABLE 1 Description of sensory attributes as developed for the Breeders' Sensory Test.

Attribute	Description	Scale[a]
Sweetness[b]	Taste associated with the impression of sweetness	1–9
Sourness[b]	Taste associated with the impression of sourness	1–9
Total aroma[b]	Sum of tomato aroma and additional aroma components including off-taste	1–9
Tomato aroma[b]	Aroma associated with tomato	1–9
Banana [like] aroma[c]	Fruity aroma associated with banana; typical for the parent Resi	1–9
Melon [like] aroma[c]	Fruity aroma associated with honeydew melon; typical for the parent Resi	1–9
Orange [like] aroma	Fruity aroma associated with citrus fruits; typical for the parent Auriga	1–9
Berry [like] aroma	Fruity aroma associated with berry fruits such as gooseberry	1–9
Spicy aroma	Spicy, tangy aroma	1–9
Green aroma	Aroma associated with freshly cut tomato stems, vines or grass and green vegetables	1–9

[a]1 indicates the lowest level of the trait scored (e.g. no sweetness) and 9 the highest level (e.g. extremely sweet).
[b]Hagenguth et al. (2022).
[c]For the final analysis, the sum of banana and melon aroma was used [2–18].

2.3.2 | Physicochemical measurements and volatile analysis

The physicochemical measurement of TSS, TA and DM were performed according to Kanski et al. (2020) at the University of

Goettingen, Division Quality of Plant Products, Germany. The pH value was recorded at the beginning of the TA measurement with a pH electrode (pH titrator Titroline 96, SCHOTT AG, Mainz, Germany). The analysis of volatiles followed the method of Olbricht et al. (2008) with some modifications as described in Kanski et al. (2020). Volatiles were extracted from samples prepared directly on the day of harvest and stored at −20°C by headspace solid-phase-micro-extraction (SPME) with a 100-µm polydimethylsiloxane (PDMS) fibre (PAL System, CTC Analytics, Zwingen, Switzerland). The analysis was conducted with a GC-2010 Plus (Shimadzu Deutschland GmbH, Duisburg, Germany) equipped with a flame ionization detector (FID). A gas chromatograph coupled to a mass spectrometer (GCMS-TQ8040, Shimadzu Deutschland GmbH, Duisburg, Germany) was used to identify the volatile compounds. Eighteen volatile compounds were identified with NIST 14 library (National Institute of Standards and Technology, MD, United States) and confirmed with analytical standards. The relative concentration was expressed in relation to the internal standard 1-octanol in ng mL^{-1} sample according to Zhang et al. (2015).

2.4 | Phenotypic data analysis

The following linear mixed model was applied to physicochemical measurements, agronomic traits and volatile compounds:

$$x_{ijk} = \mu + G_i + R_j : E_k + E_k + GE_{ik} + \varepsilon_{ijk},$$

where x_{ijk} represents the observed phenotypic value, μ the general mean, G_i the effect of the ith genotype, $R_j : E_k$ the effect of the jth replication within the kth environment (cultivation system), E_k the effect of the kth environment, GE_{ik} the effect of the genotype-by-environment interaction and ε_{ijk} the residual effect. For sensory attributes, the model was extended by the factor person:

$$x_{ijkl} = \mu + G_i + R_j : E_k + E_k + P_l + GE_{ik} + GP_{il} + EP_{kl} + GEP_{ikl} + \varepsilon_{ijkl},$$

where x_{ijkl} represents the observed phenotypic value, μ the general mean, G_i the effect of the ith genotype, $R_j : E_k$ the effect of the jth replication within the kth environment (cultivation system), E_k the effect of the kth environment, P_l the effect of the lth person, GE_{ik} the effect of the genotype-by-environment interaction, GP_{il} the effect of the genotype-by-person interaction, EP_{kl} the effect of the environment-by-person interaction, GEP_{ikl} the effect of the genotype-by-environment-by-person interaction and ε_{ijkl} the residual effect. The effect of genotype, replication and person were treated as random and the effect of the environment as fixed. Genotypes that were completely missing in one environment were discarded from the analysis of the corresponding trait. The number of F_2 plants used for the different traits is shown in Table S2. Linear mixed models were used for the calculation of least square means and the analysis of variance. Least squares were also calculated for the mean values of the individual cultivation systems based on linear models without the factor environment and corresponding interactions. These analyses and the estimation of heritability were conducted in Plabstat version 3Bp-rep (Utz, 2014). Heritability was estimated according to Knapp and Bridges (1987). Correlations between all phenotypic traits were estimated by Spearman's correlation coefficients in the R programming environment version 4.0.5 (R Core Team, 2021).

2.5 | Linkage map construction

Leaf samples for DNA extraction were taken from young leaves of the original plants (organic cultivation system) 10 weeks after planting. DNA extraction and genotyping using the Axiom 200K SOLCUC vegetable array (Graner et al., 2017) was conducted by the SGS Institut Fresenius GmbH, TraitGenetics Section (Seeland, Germany). The linkage map was constructed using the R package ASMap version 1.0-4 (Taylor & Butler, 2017). Initially, genotypic data from 188 F_2 plants and 6113 pre-filtered (polymorphic, <10% missing allele scores) SNP markers were available. Preliminary linkage groups were constructed using a threshold of $p = 1 \times 10^{-8}$. Genetic distances were estimated based on the Kosambi mapping function. Subsequently, low-quality markers were dropped according to the following strict filtering protocol to obtain linkage groups with a typical length for tomato: <1% missing allele scores, significant segregation distortion using Bonferroni-adjusted alpha level (0.05/3391), co-located markers and ≥1 double crossover. In addition, genotypes were investigated for high genotyping error rates and double crossovers. Finally, 178 F_2 plants and 738 SNP markers were available for the construction of the linkage map. After fixing the linkage groups, markers were reordered using a less strict threshold of $p = 1 \times 10^{-6}$. Linkage groups were assigned to the particular tomato chromosome and oriented according to the physical map. Finally, a framework map aiming at a distance of 5–10 cM between markers was constructed, resulting in linkage groups with 12–21 markers. To fill the gaps, a few of the discarded markers were reintroduced into the framework map. The final map included 205 markers spanning a total length of 1070.26 cM. The average length of the linkage groups was 89.19 cM, and the average distance between markers was 5.2 cM, with a maximum gap of 14.75 cM. A linkage map, including graphical visualization of QTL positions and intervals, was drawn in MapChart 2.32 (Voorrips, 2002).

2.6 | QTL mapping

QTL analysis was performed with the R package R/qtl version 1.48-1 (Broman et al., 2003) for least square means over both cultivation systems and for each system individually. Logarithm of the odds (LOD) significance thresholds for a type I error rate of $\alpha = .05$ were obtained by running 1000 permutations (*scanone* and *scantwo*) for the respective trait and cultivation system and their mean values. Single QTL mapping was applied using the Haley–Knott regression method (Haley & Knott, 1992), followed by two-dimensional QTL scans. Afterwards, a multiple-QTL model was fitted, including all significant QTL

TABLE 2 Phenotypic variation (Min, minimum; Mean; Max, maximum; SD, standard deviation) of parental cultivars 'Resi' (R; $n = 3$) and 'Auriga' (A; $n = 3$) and their F_2 mapping population ($n \geq 172$) for sensory attributes, physicochemical measurements and fruit weight for two cultivation systems and broad-sense heritability (H^2).

	Organic cultivation						Hydroponic cultivation						
			Resi × Auriga (F_2)						Resi × Auriga (F_2)				
Trait	R	A	Min	Mean	Max	SD	R	A	Min	Mean	Max	SD	H^2
Sweetness [1–9]	4.89[a]	3.59[b]	2.67	3.99	5.67	±0.57	4.39[a]	2.92[b]	2.17	3.63	5.58	±0.68	0.73
Sourness [1–9]	4.00	5.17	2.83	4.43	6.50	±0.69	3.64[b]	5.17[a]	2.36	4.12	6.75	±0.78	0.69
Total aroma [1–9]	5.39	4.88	3.92	5.29	7.00	±0.57	5.50	4.67	3.42	5.05	6.75	±0.67	0.72
Tomato aroma [1–9]	4.19	3.79	2.83	4.00	5.42	±0.49	4.22	3.25	2.42	3.59	5.11	±0.46	0.55
Banana-melon aroma [2–18][†]	3.53[a]	2.30[b]	2.00	3.39	7.92	±1.39	4.03	2.34	2.00	3.38	8.83	±1.52	0.87
Orange aroma [1–9]	1.67	2.50	0.95	2.10	5.05	±0.77	1.00[b]	3.84[a]	0.89	1.72	5.67	±0.78	0.50
Berry aroma [1–9]	1.53	1.84	1.00	1.84	3.95	±0.59	2.67	1.34	0.95	2.08	4.17	±0.76	0.27
Spicy aroma [1–9]	2.67	1.75	1.00	1.82	4.83	±0.70	1.69	1.67	0.93	1.40	2.92	±0.42	0.36
Green aroma [1–9]	1.22	2.58	1.00	1.81	3.08	±0.51	2.11	2.34	0.99	1.77	2.99	±0.43	0.15
TSS [°Brix]	7.32[a]	6.04[b]	6.00	7.04	8.20	±0.41	6.98[a]	5.60[b]	5.40	6.54	7.65	±0.40	0.80
pH	3.94	3.99	3.60	3.96	4.40	±0.15	4.09	4.03	3.59	4.08	4.54	±0.16	0.11
TA [%]	0.49	0.53	0.42	0.52	0.68	±0.05	0.87	0.86	0.77	0.87	0.97	±0.04	0.27
TSS/TA	15.27[a]	11.55[b]	10.69	13.62	16.85	±1.17	10.93[a]	7.65[b]	7.54	10.47	14.36	±1.37	0.64
DM [%]	8.72[a]	7.23[b]	6.86	8.24	10.02	±0.56	8.64[a]	6.37[b]	6.02	7.72	9.42	±0.61	0.84
FW [g]	17.33[b]	74.84[a]	22.01	33.65	56.25	±6.58	15.26[b]	59.80[a]	16.05	28.65	52.69	±7.18	0.93

Note: Small letters indicate significant differences between the parental cultivars within one cultivation system (LSD, $p = .05$); only significant differences are indicated.

Abbreviations: DM, dry matter; FW, fruit weight; TA, titratable acidity; TSS, total soluble solids.

[†]Sum of banana and melon aroma.

and QTL-by-QTL interactions. The model was further explored for the presence of additional QTL and QTL-by-QTL interactions. If there was an indication of a second QTL on a chromosome, *addpair* was used for further investigation. Finally, QTL positions were optimized based on the final multiple-QTL model, which contained all significant QTL and QTL-by-QTL interactions. The overall fit of the full model was tested against the null model using an analysis of variance. In the drop-one analysis, the effect of each single QTL was determined by comparing the full model and the model with the respective term omitted. For each QTL, a 95% Bayesian confidence interval was calculated. Co-localized QTL between the individual cultivation systems and their mean values were defined as QTL with overlapping confidence intervals or peak positions within 15 cM. Regions harbouring QTL associated with two or more traits with overlapping confidence intervals were defined as QTL clusters.

3 | RESULTS

3.1 | Phenotypic analysis and heritability

The 9 sensory attributes, 5 physicochemical traits, 18 volatile compounds and fruit weight displayed continuous distributions (Tables 2 and 3). In the mapping population, transgressive segregation was observed in both directions for most traits and was most clear in the organic cultivation system (Table S3). The parental cultivars differed in most traits, but the differences were only significant for some of them (Tables 2 and 3). Resi was characterized by higher values for sweetness, total, tomato and banana-melon aroma, TSS, TSS/TA and DM compared with Auriga in both cultivation systems, spicy aroma in the organic cultivation and berry aroma in hydroponic cultivation. Most volatiles except ß-damascenone, ß-ionone, Z-3-hexenal, methyl salicylate and benzaldehyde were more abundant in Resi. For benzaldehyde, this was only true for the organic cultivation system.

The effect of the genotype was highly significant ($p = .01$) for all sensory attributes except green aroma, for all physicochemical measurements except pH, for fruit weight and for most volatile compounds (Tables S4 and S5). The effect of the cultivation system (environment) was significant for most physicochemical measurements and the volatile compounds hexanol, Z-3-hexenol and hexanal (Table S5) but not for the sensory attributes (Table S4). Nevertheless, the mean values of the F_2 population were higher in the organic cultivation system for sensory attributes and physicochemical measurements, with the exception of berry aroma and TA (Table 2). Additionally, most aroma volatiles were more abundant in organic cultivation (Table 3). The genotype-by-environment interaction was significant for most sensory attributes, physicochemical measurements, fruit weight and a few volatiles (Tables S4 and S5).

TABLE 3 Phenotypic variation (Min, minimum; Mean; Max, maximum; SD, standard deviation) of parental cultivars 'Resi' (R; $n = 3$) and 'Auriga' (A; $n = 3$) and their F_2 mapping population ($n \geq 163$) for volatile compounds [ng mL^{-1} sample] including their precursor and flavour description for two cultivation systems and broad-sense heritability (H^2).

			Organic cultivation						Hydroponic cultivation						
					Resi × Auriga (F_2)						Resi × Auriga (F_2)				
Trait	Precursor[1]	Flavour[2]	R	A	Min	Mean	Max	SD	R	A	Min	Mean	Max	SD	H^2
6-Methyl-5-hepten-2-one	AC	Green, musty	4.94[a]	1.22[b]	0.00	2.12	8.38	±1.53	6.56[a]	1.42[b]	0.70	4.11	17.75	±2.53	0.82
Neral	AC	Citrus, lemon	0.41	0.16	0.04	0.24	1.11	±0.17	0.72[a]	0.17[b]	0.00	0.42	2.54	±0.29	0.71
Geranial	AC	Citrus, lemon	1.49[a]	0.27[b]	0.01	0.58	2.52	±0.46	1.69[a]	0.44[b]	0.15	1.16	4.26	±0.77	0.83
E-Geranylacetone	AC	Floral, fruity	6.09[a]	1.69[b]	0.38	2.48	8.28	±1.44	3.15	1.57	0.54	2.25	6.40	±1.16	0.72
β-Damascenone	AC	Woody, herbal	1.87	2.35	0.33	1.19	3.74	±0.62	0.98	2.15	0.20	1.05	3.42	±0.64	0.32
β-Ionone	AC	Woody, berry	0.96[b]	3.60[a]	0.24	1.99	6.14	±1.01	0.55[b]	3.56[a]	0.11	2.17	6.83	±1.12	0.79
1-Penten-3-one	FA	Spicy, pungent	0.09	0.04	0.00	0.09	0.28	±0.05	0.02	0.01	0.01	0.02	0.04	±0.01	0.20
Hexanol	FA	Green, fruity	2.69[a]	0.94[b]	0.46	1.73	4.08	±0.68	1.92[a]	0.29[b]	0.14	1.10	5.50	±0.78	0.66
Z-3-Hexenol	FA	Green, fresh	2.35	1.57	0.84	2.42	5.38	±0.76	1.16	0.61	0.29	1.00	3.03	±0.50	0.62
Hexanal	FA	Green, woody	83.35[a]	16.77[b]	11.17	31.09	99.39	±12.81	43.15[a]	6.69[b]	4.19	19.77	56.52	±10.77	0.57
E-2-Hexenal	FA	Green, fruity	6.66	3.71	0.11	5.38	13.53	±2.43	2.00	2.09	0.61	1.86	4.30	±0.81	0.04
Z-3-Hexenal	FA	Green, grassy	1.69	2.15	0.14	1.99	4.47	±0.72	0.67[b]	2.16[a]	0.37	1.28	3.27	±0.59	0.43
E-2-Heptenal	FA	Green, sweet	0.33	0.21	0.01	0.27	0.67	±0.12	0.14	0.07	0.03	0.11	0.22	±0.04	0.13
Phenylacetaldehyde	PHA	Honey, floral	0.19	0.12	0.04	0.20	0.86	±0.10	0.27[a]	0.06[b]	0.06	0.21	0.47	±0.08	0.49
2-Phenylethanol	PHA	Floral, sweet	1.08[a]	0.49[b]	0.25	0.56	1.00	±0.14	0.72	0.60	0.16	0.46	0.84	±0.12	0.53
Methyl salicylate	PHP	Minty, sweet	0.57[b]	3.20[a]	0.00	0.88	7.95	±1.33	0.05[b]	0.20[a]	0.02	0.07	0.40	±0.06	0.78
Benzaldehyde	BA	Fruity, almond	0.28[b]	0.46[a]	0.09	0.32	0.68	±0.10	0.50	0.26	0.13	0.43	1.08	±0.17	0.58
2-Isobutylthiazole	BCA	Green, tomato	1.54[a]	0.45[b]	0.00	0.68	1.72	±0.39	0.67	0.31	0.04	0.47	1.05	±0.21	0.27

Note: Small letters indicate significant differences between the parental cultivars within cultivation systems (LSD, $p = .05$); only significant differences are indicated.

[1]Precursors of volatile compounds (Martina et al., 2021; Rambla et al., 2014; Tikunov et al., 2020): AC = apocarotenoids; FA = fatty acids; phenolic volatiles derived from PHA = phenylalanine, PHP = phenylpropanoid and BA = benzoic acid; BCA = branched chain amino acids.

[2]Flavour description obtained from The Good Scents Company Information System (2021) (http://www.thegoodscentscompany.com/search2.html, 10.01.2021).

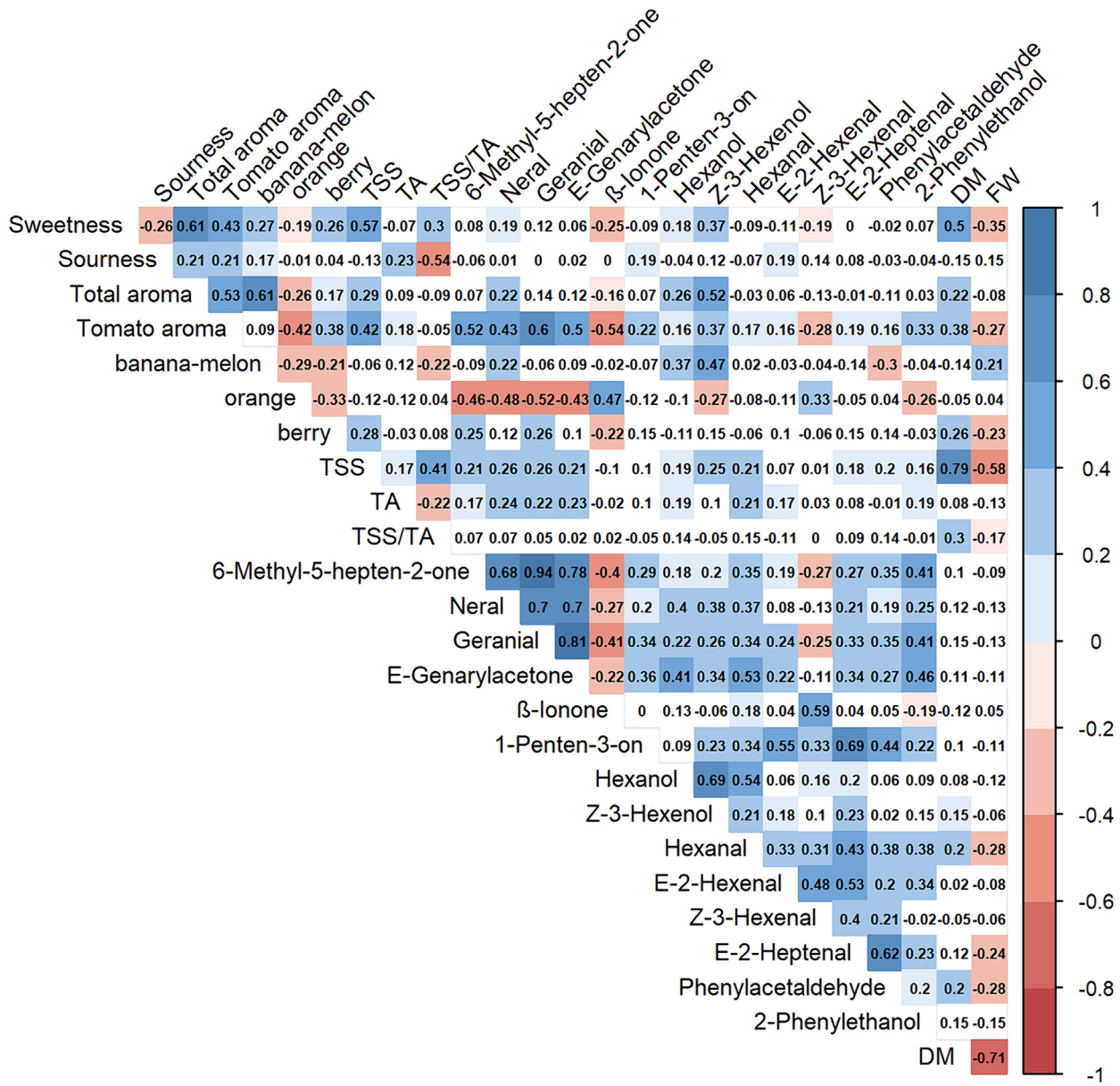

FIGURE 1 Spearman's correlation coefficients (*r*) for selected sensory attributes, physicochemical measurements (TSS = total soluble solids, TA = titratable acidity, DM = dry matter), aroma volatiles and fruit weight analysed in two cultivation systems ($n \geq 163$); significant positive correlations are shown in blue and significant negative correlations in red with $p = .05$. [Color figure can be viewed at wileyonlinelibrary.com]

Among the sensory attributes, heritability was high (≥0.69) for sweetness, sourness and total and banana-melon aroma. For tomato, orange and spicy aroma, the heritability was medium (0.36–0.55) and low (≤0.27) for berry and green aroma (Table 2). Heritability was high (≥0.80) for TSS, DM, and fruit weight, medium (0.64) for TSS/TA, and low (≤0.27) for pH and TA (Table 2). For most volatile compounds, the heritability was medium to high (0.32–0.83) (Table 3).

3.2 | Correlations

Sweetness was significantly correlated with the physicochemical trait TSS ($r = .57$) and sourness with TA ($r = .23$) (Figure 1). Tomato aroma showed significant positive correlations with sweetness, sourness, total and berry aroma, TSS, TA, DM and several aroma volatiles derived from apocarotenoids, fatty acids and phenylalanine, and it was highly negatively correlated with orange aroma, β-ionone, Z-3-hexenal and fruit weight. Total aroma showed highly significant positive correlations with sweetness and, specifically, banana-melon aroma ($r = .61$). Among the volatiles, apocarotenoid-derived volatiles showed the strongest positive correlation with tomato aroma ($r \geq .43$). Banana-melon aroma was positively correlated with the volatiles hexanol and Z-3-hexenol ($r \geq .37$) as well as neral and methyl salicylate ($r \geq .22$) (Figure S2). In contrast to the other sensory attributes, orange aroma showed positive correlations with β-ionone and Z-3-hexenal ($r \geq .33$) and negative correlations with several other volatiles. The

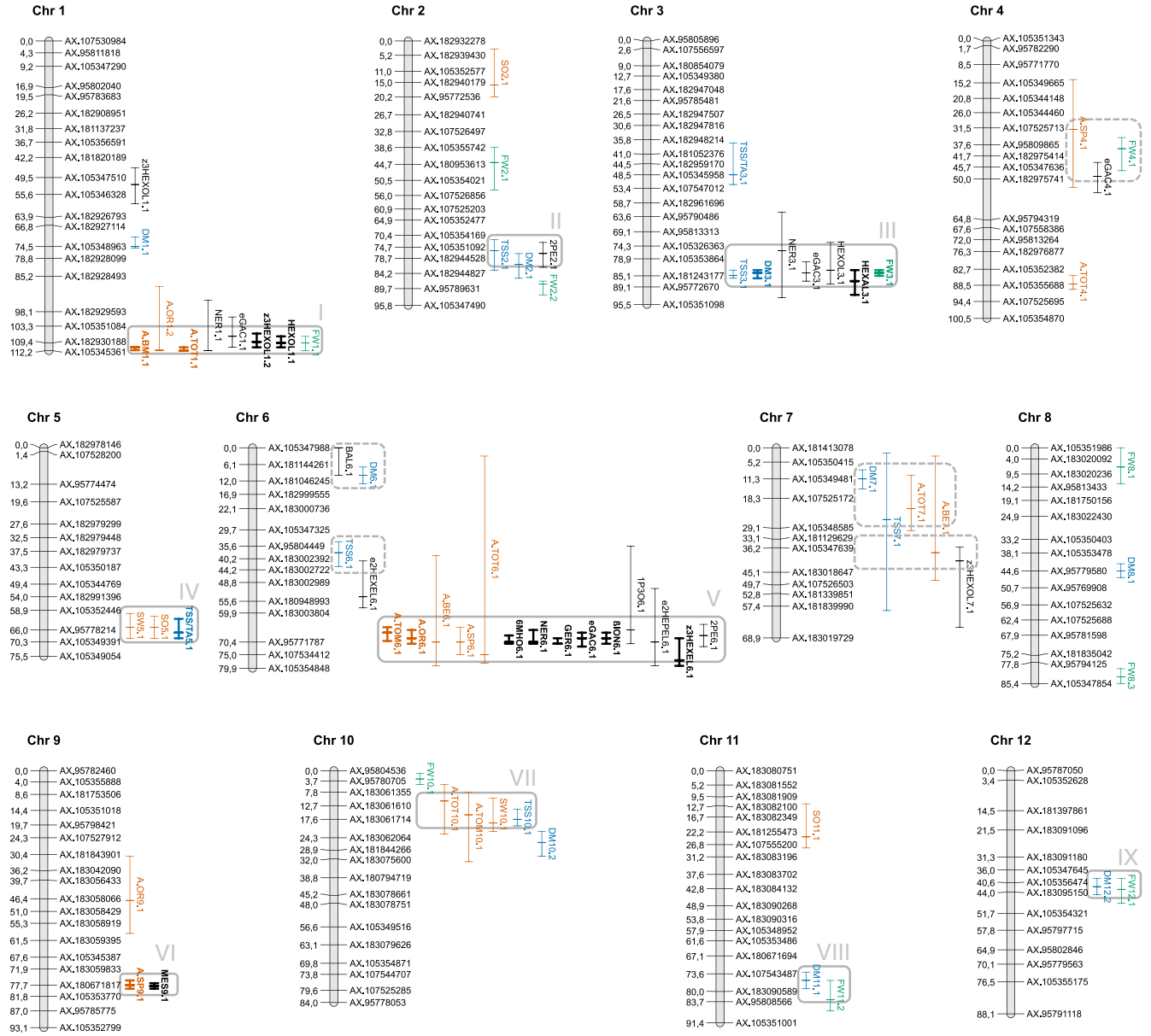

FIGURE 2 Linkage map constructed from 178 F_2 plants of the cross 'Resi' × 'Auriga' using the Axiom 200K SOLCUC vegetable array; quantitative trait loci (QTL; peak position and 95% Bayesian confidence interval) for the sensory attributes (orange), physicochemical measurements (blue), aroma volatiles (black) and fruit weight (green) detected by multiple-QTL mapping for the mean values of two cultivation systems; QTL with an phenotypic variance >20% are marked in bold; QTL enclosed in boxes indicate clusters for co-localized QTL (distinct clusters: solid line; suspected cluster: dashed line). [Color figure can be viewed at wileyonlinelibrary.com]

apocarotenoid-derived volatiles 6-methyl-5-hepten-2-one, neral, geranial and E-geranylacetone were highly significantly and strongly ($r \geq .68$) correlated with each other, whereas these volatiles were negatively correlated with β-ionone. Fruit weight was negatively correlated with sweetness, tomato and berry aroma, a few volatile compounds and DM.

3.3 | QTL detection

QTL were mapped on all chromosomes. For 18 of the 33 traits, QTL with relatively major effects (percentage of phenotypic variation explained by a QTL, PVE > 20%) were identified on chromosomes 1, 3, 5, 6 and 9 (Figure 2, Table 4). Of the total number of 100 significant QTL, 27 were co-localized between both cultivation systems and their mean values (Table S6). A total of 71 QTL (sensory attributes: 21, physicochemical traits: 16, volatiles: 24, fruit weight: 10) and two QTL-by-QTL interactions were detected for the mean values of both cultivation systems (Table 4, Figure 2). A total of 61 QTL (sensory attributes: 15, physicochemical traits: 14, volatiles: 22, fruit weight: 10) were mapped in the organic cultivation system, and 46 QTL (sensory attributes: 12, physicochemical traits: 14, volatiles: 17, fruit weight: 3) were mapped in hydroponic cultivation, each with one QTL-by-QTL interaction (Tables S7 and S8, Figures S3 and S4). QTL

TABLE 4 Location and estimates of QTL for sensory attributes, physicochemical measurements, fruit weight and volatile compounds detected by multiple-QTL mapping in an F_2 population of 'Resi' × 'Auriga' for the mean values of two cultivation systems.

Trait QTL	Chr[1]	CS[2]	Closest marker	Pos[3]	LOD[4]	PVE[5]	PVE_{full}[6]	Add[7]	Dom[8]	Allele[9]
Sweetness										
SW5.1	5	AV, Or	AX-95778214	65.0 (60.0–69.0)	6.30	11.82	33.63	−0.26	0.05	A
SW10.1	10	AV, Or, Hy	AX-183061714	19.0 (10.0–22.0)	8.57	16.57		−0.26	0.17	A
Sourness										
SO2.1	2	AV	AX-182940179	16.0 (3.0–20.2)	5.24	9.39	35.67	−0.22	0.14	A
SO5.1	5	AV, Or	AX-95778214	65.0 (61.0–69.0)	8.38	15.67		0.29	0.13	B
SO11.1	11	AV, Or, Hy	AX-181255473	24.0 (12.0–28.0)	6.68	12.22		0.28	−0.08	B
Total aroma										
A.TOT1.1	1	AV, Or, Hy	AX-105345361	112.2 (111.0–112.2)	15.05	21.46	55.23	−0.33	−0.14	A
A.TOT4.1	4	AV	AX-105355688	88.0 (85.0–90.0)	6.44	8.16		−0.06	0.14	A
A.TOT6.1	6	AV	AX-107534412	75.0 (3.0–78.0)	5.58	6.99		−0.02	−0.13	A
A.TOT7.1	7	AV, Hy	AX-107525172	22.0 (10.0–30.0)	4.63	5.73		0.18	0.03	B
A.TOT10.1	10	AV, Hy	AX-183061610	11.0 (5.0–23.0)	4.63	5.74		−0.18	0.03	A
A.TOT4.1:6.1		AV			4.95	6.16				
Tomato aroma										
A.TOM6.1	6	AV, Or, Hy	AX-95771787	67.0 (65.0–70.0)	23.25	41.08	50.57	−0.38	−0.08	A
A.TOM10.1	10	AV	AX-183061714	16.0 (7.8–33.0)	3.84	5.19		−0.10	0.11	A
Banana-melon aroma										
A.BM1.1	1	AV, Or, Hy	AX-105345361	111.0 (111.0–112.0)	52.37	74.40	74.40	−1.44	−0.81	A
Orange aroma										
A.OR1.2	1	AV	AX-105345361	112.0 (89.0–112.2)	4.35	6.47	46.03	0.21	0.08	B
A.OR6.1	6	AV, Or, Hy	AX-95771787	69.0 (66.0–71.0)	18.18	32.64		0.54	−0.07	B
A.OR9.1	9	AV	AX-183058066	47.0 (31.0–59.0)	3.63	5.35		−0.20	−0.16	A
Berry aroma										
A.BE6.1	6	AV	AX-95771787	70.4 (39.0–79.0)	3.74	8.22	19.64	−0.22	−0.06	A
A.BE7.1	7	AV, or	AX-105347639	38.0 (3.0–48.0)	3.82	8.39		0.21	0.01	B
Spicy aroma										
A.SP4.1	4	AV	AX-107525713	32.0 (14.0–53.0)	3.66	6.11	38.75	−0.15	−0.10	A
A.SP6.1	6	AV, Or	AX-95771787	70.4 (65.0–75.0)	6.08	10.49		−0.21	0.02	A
A.SP9.1	9	AV, Or	AX-180671817	77.7 (76.0–79.0)	12.44	23.41		0.26	−0.19	B
Total soluble solids										
TSS2.1	2	AV, Hy	AX-105351092	76.0 (72.0–83.0)	6.49	8.04	57.38	−0.13	−0.10	A
TSS3.1	3	AV, Or, Hy	AX-181243177	85.0 (83.0–86.0)	12.26	16.46		−0.24	0.10	A
TSS6.1	6	AV, Or, Hy	AX-183002392	38.0 (34.0–43.0)	8.52	10.86		−0.18	0.00	A
TSS7.1	7	AV	AX-105348585	26.0 (2.0–59.0)	4.00	4.79		0.09	−0.10	B
TSS10.1	10	AV, Or, Hy	AX-183061714	17.6 (14.0–20.0)	13.27	18.07		−0.19	0.10	A
TSS/TA										
TSS/TA3.1	3	AV	AX-105345958	48.5 (37.0–52.0)	4.06	7.69	33.06	−0.39	0.30	A
TSS/TA5.1	5	AV, Or, Hy	AX-95778214	67.0 (62.0–69.0)	12.81	27.38		−0.74	−0.05	A
Dry matter										
DM1.1	1	AV, Or	AX-105348963	74.5 (71.0–75.0)	12.52	7.63	80.59	0.18	0.05	B
DM2.1	2	AV, Or, Hy	AX-182944528	81.0 (77.0–86.0)	13.36	8.23		−0.22	−0.04	A
DM3.1	3	AV, Or, Hy	AX-181243177	84.0 (83.0–86.0)	32.83	26.87		−0.44	0.05	A
DM6.1	6	AV, Or	AX-181046245	10.0 (7.0–13.0)	8.57	4.94		−0.17	−0.06	A
DM7.1	7	AV, Hy	AX-105349481	11.3 (8.0–15.0)	5.99	3.33		0.14	0.01	B
DM8.1	8	AV	AX-95779580	44.6 (42.0–47.0)	9.17	5.33		−0.13	−0.09	A

TABLE 4 (Continued)

Trait QTL	Chr[1]	CS[2]	Closest marker	Pos[3]	LOD[4]	PVE[5]	PVE_{full}[6]	Add[7]	Dom[8]	Allele[9]
DM10.2	10	AV, Or	AX-183062064	26.0 (22.0–31.0)	18.91	12.61		−0.27	0.01	A
DM11.1	11	AV, Or	AX-107543487	76.0 (73.0–79.0)	12.34	7.50		−0.17	0.20	A
DM12.2	12	AV	AX-105356474	42.0 (39.0–45.0)	13.37	8.25		−0.22	0.07	A
DM1.1:8.1		AV			4.64	2.54				
Fruit weight										
FW1.1	1	AV	AX-182930188	109.4 (107.0–112.2)	5.82	2.55	84.81	−1.30	0.74	A
FW2.1	2	AV, Or	AX-180953613	44.0 (38.6–54.0)	6.13	2.69		1.60	0.09	B
FW2.2	2	AV, Or, Hy	AX-95789631	88.0 (87.0–92.0)	28.28	17.06		3.90	−2.39	B
FW3.1	3	AV, Or, Hy	AX-181243177	84.0 (83.0–85.1)	38.20	26.80		5.39	0.72	B
FW4.1	4	AV	AX-95809865	39.0 (35.0–47.0)	7.74	3.48		1.87	0.25	B
FW8.1	8	AV	AX-183020236	7.0 (0.0–13.0)	4.52	1.94		1.29	0.58	B
FW8.3	8	AV, Or	AX-105347854	83.0 (80.0–85.4)	8.42	3.82		1.37	2.04	B
FW10.1	10	AV	AX-95780705	3.0 (1.0–5.0)	15.88	7.99		2.88	−0.82	B
FW11.2	11	AV, Or	AX-95808566	83.0 (76.0–87.0)	12.24	5.85		2.32	−0.33	B
FW12.1	12	AV, Or, Hy	AX-183095150	43.0 (39.0–48.0)	9.57	4.41		2.10	0.13	B
6-Methyl-5-hepten-2-one										
6MHO6.1	6	AV, Or, Hy	AX-95771787	70.4 (68.0–71.0)	31.27	58.22	58.22	−2.03	−0.88	A
Neral										
NER1.1	1	AV, Or	AX-105345361	112.2 (94.0–112.2)	5.50	9.46	42.98	−0.07	0.05	A
NER3.1	3	AV	AX-105326363	76.0 (62.0–93.0)	3.81	6.39		−0.08	0.01	A
NER6.1	6	AV, Or, Hy	AX-95771787	70.4 (66.0–71.0)	12.86	24.62		−0.14	−0.07	A
Geranial										
GER6.1	6	AV, Or, Hy	AX-95771787	71.0 (69.0–71.0)	41.82	68.65	68.65	−0.65	−0.36	A
E-Geranylacetone										
eGAC1.1	1	AV, Or	AX-182930188	107.0 (100.0–111.0)	6.34	7.72	60.06	−0.41	0.17	A
eGAC3.1	3	AV, Or, Hy	AX-181243177	84.0 (80.0–87.0)	7.35	9.10		−0.53	0.00	A
eGAC4.1	4	AV	AX-182975741	49.0 (44.0–55.0)	3.66	4.30		−0.13	−0.43	A
eGAC6.1	6	AV, Or, Hy	AX-95771787	69.0 (67.0–72.0)	21.34	32.51		−0.96	−0.14	A
ß-Ionone										
ßION6.1	6	AV, Or, Hy	AX-95771787	69.0 (67.0–71.0)	35.29	62.21	62.21	1.09	0.29	B
1-Penten-3-one										
1P3O6.1	6	AV, Or	AX-95771787	66.0 (35.6–71.0)	4.46	11.64	11.64	−0.01	−0.01	A
Hexanol										
HEXOL1.1	1	AV, Or, Hy	AX-182930188	109.4 (107.0–111.0)	11.85	25.91	34.82	−0.40	−0.10	A
HEXOL3.1	3	AV	AX-181243177	83.0 (73.0–88.0)	5.10	10.11		−0.32	0.08	A
Z-3-Hexenol										
z3HEXOL1.1	1	AV, Or	AX-105347510	52.0 (46.0–59.0)	4.06	7.22	39.81	0.20	0.05	B
z3HEXOL1.2	1	AV, Or, Hy	AX-182930188	109.0 (106.0–111.0)	11.98	23.90		−0.33	0.02	A
z3HEXOL7.1	7	AV, Or	AX-183018647	41.0 (36.0–65.0)	5.13	9.26		0.22	−0.02	B
Hexanal										
HEXAL3.1	3	AV, Or, Hy	AX-181243177	87.0 (83.0–92.0)	10.13	24.37	24.37	−7.36	−0.15	A
E-2-Hexenal										
e2HEXEL6.1	6	AV, Or	AX-180948993	54.0 (41.0–58.0)	4.90	12.72	12.72	−0.33	−0.82	A
Z-3-Hexenal										
z3HEXEL6.1	6	AV, Or, Hy	AX-107534412	77.0 (69.0–79.0)	10.64	25.43	25.43	0.36	−0.10	B
E-2-Heptenal										

(Continues)

TABLE 4 (Continued)

Trait	QTL	Chr[1]	CS[2]	Closest marker	Pos[3]	LOD[4]	PVE[5]	PVE_{full}[6]	Add[7]	Dom[8]	Allele[9]
	e2HEPEL6.1	6	AV	AX-95771787	70.4 (51.0–79.0)	4.00	10.44	10.44	−0.02	−0.03	A
2-Phenylethanol											
	2PE2.1	2	AV, Or, Hy	AX-182944528	77.0 (73.0–82.0)	8.26	16.99	34.00	−0.06	0.00	A
	2PE6.1	6	AV, Hy	AX-95771787	68.0 (64.0–72.0)	8.56	17.70		−0.06	−0.01	A
Methyl salicylate											
	MES9.1	9	AV, Or, Hy	AX-180671817	78.0 (77.0–79.0)	29.21	56.18	56.18	0.58	−0.53	B
Benzaldehyde											
	BAL6.1	6	AV, Or	AX-105347988	0.0 (0.0–10.0)	4.54	11.83	11.83	0.06	−0.01	B

[1]Chr, chromosome.
[2]CS, cultivation system with AV = environmental means, Or = organic cultivation system and Hy = hydroponic cultivation (details for the QTL mapped in Or and Hy are available in Tables S7 and S8).
[3]Pos, peak position with 95% Bayesian confidence interval.
[4]LOD, log of likelihood ratio.
[5]PVE, percentage of phenotypic variation explained by the QTL.
[6]PVE_{full}, percentage of phenotypic variation explained by the multi QTL model.
[7]Add, additive effect (positive effect denote increasing effect of the B allele).
[8]Dom, dominance effects.
[9]Allele, allele increasing the phenotypic value (A from Resi, B from Auriga).

for green aroma were only found in organic cultivation and for pH and TA only in hydroponic cultivation. Hereafter, we focus on the QTL detected for the mean values of both cultivation systems.

A minimum of one QTL (banana-melon aroma, 10 volatile compounds) and a maximum of 10 QTL (fruit weight) were identified per trait (Table 4). The individual contribution of a QTL to the phenotypic variance explained ranged from 1.9% (fruit weight) to 74.4% (banana-melon aroma). For the sensory attributes, we detected two QTL for sweetness (percentage of phenotypic variation explained by the multiple-QTL model, PVE_{full} = 33.63%), three for sourness (PVE_{full} = 35.7%), five and one QTL-by-QTL interaction for total aroma (PVE_{full} = 55.2%) and two for tomato aroma (PVE_{full} = 50.6%). Both QTL for tomato aroma overlapped with QTL for total aroma (Figure 2). The phenotypic variance explained ranged from 19.6% to 74.4% for the special sensory attributes and from 33.1% to 80.6% for the physicochemical measurements. QTL were detected for all aroma volatiles (PVE_{full} from 10.44% to 68.7%) except ß-damascenone, 2-isobutylthiazole and phenylacetaldehyde. Auriga carried most alleles that increased sourness, orange aroma and fruit weight. For most of the other QTL, Resi contributed to increased phenotypic values, with the exception of the QTL mapped on chromosome 7 and some volatile compounds.

A total of nine clusters were identified and five more suspected (Figure 2). The largest cluster was located on chromosome 6, comprising QTL for five sensory attributes, five volatiles derived from apocarotenoids, three from fatty acids and one from phenylalanine. QTL for several sensory attributes were clustered together with QTL for physicochemical measurements on chromosomes 5 and 10 and for aroma volatiles on chromosomes 1, 6 and 9. On chromosomes 2 and 3, QTL for physicochemical measurements and aroma volatiles were co-localized. In addition, QTL for fruit weight were mapped within the cluster on chromosomes 1 and 3 and close to those on chromosomes 2 and 10.

4 | DISCUSSION

4.1 | Phenotyping of the parental cultivars and the effect of the cultivation system

In the present study, the Breeders' Sensory Test (Hagenguth et al., 2022), introduced as a sensory method for small sample sizes from a high number of individual plants, was successfully implemented for QTL mapping. Sensory differences between the parental cultivars Resi and Auriga, characterized by different fruit sizes, colours and sensory and metabolic profiles, were detected for most attributes (Table 2). Resi, a cocktail tomato, had higher scorings for sweetness, tomato, total and banana-melon aroma; higher values for TSS, TSS/TA and DM; and higher concentrations of most volatile compounds in both cultivation systems (Tables 2 and 3). Auriga, a salad tomato, had higher scores for sourness and orange aroma.

Flavour is not only influenced by genetics but also by environmental factors and agronomic handling (Baldwin et al., 2015; Erika et al., 2022; Klee & Tieman, 2018), as also shown by our results (Tables S4 and S5). Most sensory attributes and physicochemical measurements and several volatile compounds showed higher values in organic cultivation (Tables 2 and 3). The differences between the cultivation systems are probably due to higher stress levels, reduced fertilization and a longer time for fruit development in the organic system, which favours higher production of primary and secondary metabolites in organic cultivation (Mitchell et al., 2007; Oliveira

et al., 2013). However, summarizing several studies, no clear trend of tomato quality was identified as favouring a specific cultivation system (Pieper & Barrett, 2009).

4.2 | Correlation of sensory attributes with physicochemical measurements and volatiles

Tomato aroma was significantly ($p \geq .21$) positively correlated with the sensory attributes sweetness, sourness and total and berry aroma (Figure 1). These findings are consistent with the description of tomato flavour as sweet, fruity, green-grassy, ripe and sour (Hongsoongnern & Chambers, 2008). However, tomato aroma was not correlated with banana-melon aroma and negatively correlated with orange aroma ($r = -.42$). Apparently, these two special sensory attributes were not perceived as typical for tomatoes and might be specific to this mapping population. In agreement with Baldwin et al. (2015) and Erika et al. (2022), we found significant correlations between TSS and sweetness ($r = .57$) and between TA and sourness ($r = .23$). Although measuring TSS and TA allows breeders to select for tomato taste (Tandon et al., 2003), Colantonio et al. (2022) emphasized the importance of aroma volatiles for sensory attributes by quantifying the proportion of phenotypic variance explained by sugars, acids and volatile compounds. Volatile compounds explained 68% of flavour intensity and 62% of sweetness assessed by a consumer panel, and sourness was much less affected by volatiles (Colantonio et al., 2022).

Among the sensory attributes, tomato aroma showed the highest number of significant correlations with volatile compounds (Figure 1). The most important contributors to tomato aroma were aroma volatiles derived from apocarotenoids ($r \geq .43$) with the exception of β-damascenone (Figure S2). Consistent with these results, apocarotenoid-derived volatiles, characterized by fruity or floral aroma notes, have been described as important contributors to tomato aroma (Martina et al., 2021; Rambla et al., 2014). However, the importance of specific apocarotenoid-derived volatiles has been questioned by more recent studies (Tieman et al., 2012), as also seen for β-damascenone in the present study. In contrast to earlier descriptions by Baldwin et al. (2000) and Baldwin et al. (2015), β-ionone was negatively correlated with tomato aroma ($r = -.54$), possibly due to the relatively high concentration in the mapping population. Because β-ionone has a very low odour threshold (Baldwin et al., 2000; Rambla et al., 2014), high concentrations might lead to a negative effect on tomato aroma. As described in previous studies (Klee & Tieman, 2018; Piombino et al., 2013; Tikunov et al., 2020), the fatty acid-derived volatile Z-3-hexenol ($r = .37$) and the phenylalanine-derived volatile 2-phenylethanol ($r = .33$) were also important contributors to tomato aroma. In agreement with Tandon et al. (2003), a negative effect of Z-3-hexenal on tomato aroma ($r = -.28$) was observed, and this volatile was positively correlated with orange aroma ($r = .33$) in our study and with fruitiness in their study.

4.3 | QTL for flavour-related traits, including sensory attributes

Despite the difficulty of assessing sensory attributes in large mapping populations, we detected QTL for all sensory attributes, with the exception of green aroma (only in the organic cultivation system) (Figure 2). For the main sensory attributes sweetness, sourness and tomato aroma, the PVE per attribute ranged from about 34% to 51% (Table 4). The QTL for these sensory attributes on chromosomes 2, 5, 6, 10 and 11 are of interest for marker-assisted selection (MAS), as they directly contributed to the perceived taste and aroma. The largest number of QTL per trait mapped in this study was identified for fruit weight with 10 QTL. This was expected because the two parents of the mapping population were characterized by very different fruit weights. All QTL for fruit weight were consistent with previously published genetic regions for this trait (Grandillo et al., 1999; Pereira et al., 2021; Saliba-Colombani et al., 2001). QTL for the special aroma attributes banana-melon, orange, berry and spicy provide novel information, although previous studies have worked with different aroma notes, and naming is not standardized. Therefore, the QTL for the spicy aroma on chromosome 9 might overlap with the smoky QTL detected by Tikunov et al. (2020). The QTL for methyl salicylate co-localized with the QTL for spicy aroma corresponds to the *SlSAMT* gene identified by Tieman et al. (2010), involved in the synthesis of this aroma volatile. Working with an F_2 mapping population enabled the estimation of additive and dominance effects. For most QTL, the additive effect was larger than the dominance effect, whereas for some QTL, the effect was similar, and for the three QTL A.TOT4.1, A.TOT6.1 and FW8.3, the dominance effect was larger (Table 4). In addition to the 27 robust QTL detected in each of the two cultivation systems and their mean values, QTL specific to organic or hydroponic cultivation or their mean values were found (Table S6). For the QTL detected only for the mean values, we assume that they were weakly present in both trials. Because the environment significantly influenced several flavour-related traits (Table S5), it was expected to find also specific QTL for the different cultivation systems.

Several QTL formed clusters resulting from either physiological relationships or genetically linked genes (Bauchet et al., 2017; Zanor et al., 2009). Such clusters are of great interest because they provide the opportunity to identify genetic loci associated with large sets of metabolic changes affecting tomato flavour (Folta & Klee, 2016). Genetic regions altering the concentration of several volatiles with a common biological origin have been reported by several authors (Bauchet et al., 2017; Rambla et al., 2017; Zhang et al., 2015), but QTL studies combining physicochemical measurements or primary metabolites and volatile compounds with sensory attributes are rare (Causse et al., 2002; Tikunov et al., 2020; Zanor et al., 2009). As expected from the correlations, most of the sensory QTL were co-localized with QTL for either other sensory attributes, physicochemical measurements, aroma volatiles or fruit weight (Figure 2).

In the largest identified cluster on chromosome 6, the major QTL for tomato aroma were co-localized with QTL for orange, berry, spicy and total aroma; five apocarotenoid-volatiles; three fatty acid-derived volatiles; and the phenylalanine-derived volatile 2-phenylethanol (Figure 2). Tikunov et al. (2020) detected QTL for aroma intensity, sour taste and TSS on the same linkage group, confirming that this genetic region may be important for improving sensory attributes in tomato. Within this cluster and the clusters on chromosomes 1 and 3, the co-localization of QTL for volatiles derived from apocarotenoids and fatty acids is striking. Similar to this observation, the apocarotenoids 6-methyl-5-hepten-2-one and geranylacetone clustered together with C_6 volatiles (fatty acids) in the construction of a metabolic tree by Mathieu et al. (2009), and a metabolic dependency was proposed (Mathieu et al., 2009). Most of the volatile QTL from our study could be roughly classified into the QTL genomic regions summarized by Martina et al. (2021) and, in some cases, complement the volatile groups; for example, E-geranylacetone, neral and hexanol complement the cluster of apocarotenoid- and fatty acid-derived QTL towards the end of chromosome 1.

The QTL for sweetness and sourness on chromosome 5 (PVE ≥ 11.8%) and for sweetness, total and tomato aroma on chromosome 10 (PVE ≥ 5.2%) were mapped for the first time. In a similar region of chromosome 5, Causse et al. (2001) and Tikunov et al. (2020) mapped QTL for texture-related traits but reported no sensory QTL. The QTL cluster on chromosome 5 is likely to influence the perceived sweet–sour taste, as indicated by the presence of a QTL for TSS/TA (PVE = 27.4%). Both QTL clusters provide interesting candidates for MAS to improve the sweet and sour taste of tomatoes. In addition, QTL for physicochemical measurements and aroma volatiles were co-localized on chromosomes 2 and 3 in similar regions, where Causse et al. (2001), Causse et al. (2002) and Tikunov et al. (2020) also identified QTL clusters for flavour-related traits. The genetic region towards the end on chromosome 2 is well studied due to the presence of *fw2.2*, a gene largely involved in increased fruit size during domestication (Frary et al., 2000), but antagonistic effects for flavour-related traits were observed, most likely due to a dilution effect (Causse et al., 2002; Lecomte et al., 2004).

5 | CONCLUSIONS

QTL mapping based on an F_2 population derived from two tomato cultivars with superior quality but different fruit weights revealed many insights into the relationship between sensory attributes, physicochemical measurements, aroma volatiles and fruit weight and their inheritance. Phenotyping conducted in two contrasting cultivation systems, organic low-input and hydroponic, enabled the identification of robust QTL. This study highlights QTL for sensory attributes, including novel ones on chromosomes 5 and 10, which are partially co-localized with QTL for physicochemical measurements, aroma volatiles and fruit weight. QTL for sourness on chromosomes 2 and 11 and genetic regions harbouring QTL for multiple flavour-related traits, including sweetness and tomato aroma, on chromosomes 5, 6 and 10 are recommended for MAS to improve the flavour of fresh market tomatoes. The application of molecular markers for sensory attributes that directly reflect human flavour perception to seedlings enables breeders to consider sensory attributes in the first segregating generations and reduce the risk of losing genotypes with favourable attributes. However, QTL may partly be specific to the mapping population and the environments of this experiment. Therefore, we verified the applicability of the identified QTL for MAS in the following year for both the mapping population and a second independent population and compared it with the response to phenotypic selection (Hagenguth et al., 2024).

AUTHOR CONTRIBUTIONS

HB and BH were responsible for funding acquisition. JH, HB and BH planned and designed the experiment. JH performed the experiment in the organic and HK in the hydroponic cultivation system. LK conducted all physicochemical measurements and the aroma volatile analysis. JH analysed the data, wrote the original draft and was supervised by HB and BH. All authors reviewed, edited and approved the manuscript.

ACKNOWLEDGEMENTS

We thank Moritz Halekotte (Culinaris–Quality seed for Wholesome Food), Magdalena Kircher, Theo Steffens and Heidi Inderwies for supporting the Breeders' Sensory Test. Prof. Andreas Ulbricht (Department of Horticultural Production, University of Applied Sciences Osnabrueck) made the trial in the hydroponic cultivation system possible. We acknowledge the technicians of the Division of Plant Breeding (Robin Koebel) and Division of Quality of Plant Products (Arne Gull, Gunda Jansen and Evelyn Krüger) for supporting the organic field trial and analytical measurements, respectively. The study was part of the PETRA^{q+n} project that was financially supported by the Ministry for Science and Culture of Lower Saxony (grant number VWZN3255). The Software AG Foundation supported the Section of Genetic Resources and Organic Plant Breeding. We acknowledge support by the Open Access Publication Funds of the University of Goettingen. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Julia Hagenguth https://orcid.org/0000-0001-9159-9327

REFERENCES

Baldwin, E. A., Scott, J. W., & Bai, J. (2015). Sensory and chemical flavor analyses of tomato genotypes grown in Florida during three different growing seasons in multiple years. *Journal of the American Society for*

Horticultural Science, *140*(5), 490–503. https://doi.org/10.21273/JASHS.140.5.490

Baldwin, E. A., Scott, J. W., Shewmaker, C. K., & Schuch, W. (2000). Flavor trivia and tomato aroma: Biochemistry and possible mechanisms for control of important aroma components. *HortScience*, *35*(6), 1013–1022. https://doi.org/10.21273/HORTSCI.35.6.1013

Bauchet, G., Grenier, S., Samson, N., Segura, V., Kende, A., Beekwilder, J., Cankar, K., Gallois, J.-L., Gricourt, J., Bonnet, J., Baxter, C., Grivet, L., & Causse, M. (2017). Identification of major loci and genomic regions controlling acid and volatile content in tomato fruit: Implications for flavor improvement. *New Phytologist*, *215*(2), 624–641. https://doi.org/10.1111/nph.14615

Beckles, D. M. (2012). Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biology and Technology*, *63*(1), 129–140. https://doi.org/10.1016/j.postharvbio.2011.05.016

Broman, K. W., Wu, H., Sen, S., & Churchill, G. A. (2003). R/QTL: QTL mapping in experimental crosses. *Bioinformatics*, *19*(7), 889–890. https://doi.org/10.1093/bioinformatics/btg112

Capel, C., Fernández del Carmen, A., Alba, J. M., Lima-Silva, V., Hernández-Gras, F., Salinas, M., Boronat, A., Angosto, T., Botella, M. A., Fernández-Muñoz, R., Granell, A., Capel, J., & Lozano, R. (2015). Wide-genome QTL mapping of fruit quality traits in a tomato RIL population derived from the wild-relative species *Solanum pimpinellifolium* L. *Theoretical and Applied Genetics*, *128*(10), 2019–2035. https://doi.org/10.1007/s00122-015-2563-4

Causse, M., Buret, M., Robini, K., & Verschave, P. (2003). Inheritance of nutritional and sensory quality traits in fresh market tomato and relation to consumer preferences. *Journal of Food Science*, *68*(7), 2342–2350. https://doi.org/10.1111/j.1365-2621.2003.tb05770.x

Causse, M., Friguet, C., Coiret, C., Lépicier, M., Navez, B., Lee, M., Holthuysen, N., Sinesio, F., Moneta, E., & Grandillo, S. (2010). Consumer preferences for fresh tomato at the European scale: A common segmentation on taste and firmness. *Journal of Food Science*, *75*(9), S531–S541. https://doi.org/10.1111/j.1750-3841.2010.01841.x

Causse, M., Saliba-Colombani, V., Lecomte, L., Duffé, P., Rousselle, P., & Buret, M. (2002). QTL analysis of fruit quality in fresh market tomato: A few chromosome regions control the variation of sensory and instrumental traits. *Journal of Experimental Botany*, *53*(377), 2089–2098. https://doi.org/10.1093/jxb/erf058

Causse, M., Saliba-Colombani, V., Lesschaeve, I., & Buret, M. (2001). Genetic analysis of organoleptic quality in fresh market tomato. 2. Mapping QTLs for sensory attributes. *Theoretical and Applied Genetics*, *102*(2–3), 273–283. https://doi.org/10.1007/s001220051644

Colantonio, V., Ferrão, L. F. V., Tieman, D. M., Bliznyuk, N., Sims, C., Klee, H. J., Munoz, P., & Resende, M. F. R. (2022). Metabolomic selection for enhanced fruit flavor. *Proceedings of the National Academy of Sciences*, *119*(7), e2115865119. https://doi.org/10.1073/pnas.2115865119

CPVO. (2022). Community Plant Variety Office. CPVO Variety Finder. https://vf.plantvarieties.eu/varieties

De Kreij, C., de Voogt, W., & Baas, R. (2003). Nutrient solutions and water quality for soilless cultures. (Brochure/Applied Plant Research, Division Glasshouse; No. 191). Applied Plant Research, Division Glasshouse. https://edepot.wur.nl/456342

Erika, C., Ulrich, D., Naumann, M., Smit, I., Horneburg, B., & Pawelzik, E. (2022). Flavor and other quality traits of tomato cultivars bred for diverse production systems as revealed in organic low-input management. *Frontiers in Nutrition*, *9*, 916642. https://doi.org/10.3389/fnut.2022.916642

Folta, K. M., & Klee, H. J. (2016). Sensory sacrifices when we mass-produce mass produce. *Horticulture Research*, *3*(1), 16032. https://doi.org/10.1038/hortres.2016.32

Frary, A., Nesbitt, T. C., Frary, A., Grandillo, S., van der Knaap, E., Cong, B., Liu, J., Meller, J., Elber, R., Alpert, K. B., & Tanksley, S. D. (2000). *fw2.2*: A quantitative trait locus key to the evolution of tomato fruit size. *Science*, *289*(5476), 85–88. https://doi.org/10.1126/science.289.5476.85

Grandillo, S., Ku, H. M., & Tanksley, S. D. (1999). Identifying the loci responsible for natural variation in fruit size and shape in tomato. *Theoretical and Applied Genetics*, *99*(6), 978–987. https://doi.org/10.1007/s001220051405

Graner, E. M., Plieske, J., Polley, A., & Ganal, M. W. (2017). Towards the development of a SOLCUC Affymetrix genotyping array. XIV Solanaceae and 3rd Cucurbitaceae Joint Conference, 81.

Hagenguth, J., Kanski, L., Kahle, H., Becker, H. C., & Horneburg, B. (2024). Marker-assisted selection for flavour improvement in early flavour improvement in early generations of fresh market tomatoes (*Solanum lycopersicum* L.): II. Response to breeders' sensory and marker-assisted selection. Submitted Manuscript.

Hagenguth, J., Kanski, L., Kahle, H., Naumann, M., Pawelzik, E., Becker, H. C., & Horneburg, B. (2022). Breeders' sensory test: A new tool for early selection in breeding for tomato (*Solanum lycopersicum*) flavour. *Plant Breeding*, *141*(1), 96–107. https://doi.org/10.1111/pbr.12994

Haley, C. S., & Knott, S. A. (1992). A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. *Heredity*, *69*(4), 315–324. https://doi.org/10.1038/hdy.1992.131

Hongsoongnern, P., & Chambers, E. (2008). A lexicon for texture and flavor characteristics of fresh and processed tomatoes. *Journal of Sensory Studies*, *23*(5), 583–599. https://doi.org/10.1111/j.1745-459X.2008.00174.x

Kanski, L., Naumann, M., & Pawelzik, E. (2020). Flavor-related quality attributes of ripe tomatoes are not significantly affected under two common household conditions. *Frontiers in Plant Science*, *11*, 472. https://doi.org/10.3389/fpls.2020.00472

Kimbara, J., Ohyama, A., Chikano, H., Ito, H., Hosoi, K., Negoro, S., Miyatake, K., Yamaguchi, H., Nunome, T., Fukuoka, H., & Hayashi, T. (2018). QTL mapping of fruit nutritional and flavor components in tomato (*Solanum lycopersicum*) using genome-wide SSR markers and recombinant inbred lines (RILs) from an intra-specific cross. *Euphytica*, *214*(11), 210. https://doi.org/10.1007/s10681-018-2295-z

Klee, H. J. (2010). Improving the flavor of fresh fruits: Genomics, biochemistry, and biotechnology. *New Phytologist*, *187*(1), 44–56. https://doi.org/10.1111/j.1469-8137.2010.03281.x

Klee, H. J., & Tieman, D. M. (2013). Genetic challenges of flavor improvement in tomato. *Trends in Genetics*, *29*(4), 257–262. https://doi.org/10.1016/j.tig.2012.12.003

Klee, H. J., & Tieman, D. M. (2018). The genetics of fruit flavour preferences. *Nature Reviews Genetics*, *19*(6), 347–356. https://doi.org/10.1038/s41576-018-0002-5

Knapp, S. J., & Bridges, W. C. (1987). Confidence interval estimators for heritability for several mating and experiment designs. *Theoretical and Applied Genetics*, *73*(5), 759–763. https://doi.org/10.1007/BF00260787

Korčok, M., Vietorisová, N., Martišová, P., Štefániková, J., Mravcová, A., & Vietoris, V. (2021). Aromatic profile of hydroponically and conventionally grown tomatoes. *Applied Sciences*, *11*(17), 8012. https://doi.org/10.3390/app11178012

Lecomte, L., Saliba-Colombani, V., Gautier, A., Gomez-Jimenez, M. C., Duffé, P., Buret, M., & Causse, M. (2004). Fine mapping of QTLs of chromosome 2 affecting the fruit architecture and composition of

tomato. *Molecular Breeding*, *13*(1), 1–14. https://doi.org/10.1023/B:MOLB.0000012325.77844.0c

Martina, M., Tikunov, Y., Portis, E., & Bovy, A. G. (2021). The genetic basis of tomato aroma. *Genes*, *12*(2), 226. https://doi.org/10.3390/genes12020226

Mathieu, S., Cin, V. D., Fei, Z., Li, H., Bliss, P., Taylor, M. G., Klee, H. J., & Tieman, D. M. (2009). Flavour compounds in tomato fruits: Identification of loci and potential pathways affecting volatile composition. *Journal of Experimental Botany*, *60*(1), 325–337. https://doi.org/10.1093/jxb/ern294

Mitchell, A. E., Hong, Y.-J., Koh, E., Barrett, D. M., Bryant, D. E., Denison, R. F., & Kaffka, S. (2007). Ten-year comparison of the influence of organic and conventional crop management practices on the content of flavonoids in tomatoes. *Journal of Agricultural and Food Chemistry*, *55*(15), 6154–6159. https://doi.org/10.1021/jf070344+

Olbricht, K., Grafe, C., Weiss, K., & Ulrich, D. (2008). Inheritance of aroma compounds in a model population of *Fragaria* × *ananassa* Duch. *Plant Breeding*, *127*(1), 87–93. https://doi.org/10.1111/j.1439-0523.2007.01422.x

Oliveira, A. B., Moura, C. F. H., Gomes-Filho, E., Marco, C. A., Urban, L., & Miranda, M. R. A. (2013). The impact of organic farming on quality of tomatoes is associated to increased oxidative stress during fruit development. *PLoS ONE*, *8*(2), e56354. https://doi.org/10.1371/journal.pone.0056354

Pereira, L., Zhang, L., Sapkota, M., Ramos, A., Razifard, H., Caicedo, A. L., & van der Knaap, E. (2021). Unraveling the genetics of tomato fruit weight during crop domestication and diversification. *Theoretical and Applied Genetics*, *134*(10), 3363–3378. https://doi.org/10.1007/s00122-021-03902-2

Pieper, J. R., & Barrett, D. M. (2009). Effects of organic and conventional production systems on quality and nutritional parameters of processing tomatoes. *Journal of the Science of Food and Agriculture*, *89*(2), 177–194. https://doi.org/10.1002/jsfa.3437

Piombino, P., Sinesio, F., Moneta, E., Cammareri, M., Genovese, A., Lisanti, M. T., Mogno, M. R., Peparaio, M., Termolino, P., Moio, L., & Grandillo, S. (2013). Investigating physicochemical, volatile and sensory parameters playing a positive or a negative role on tomato liking. *Food Research International*, *50*(1), 409–419. https://doi.org/10.1016/j.foodres.2012.10.033

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing *(4.0.5)*. https://www.R-project.org/

Raigón, M. D., García-Martínez, M. D., & Chiriac, O. P. (2022). Nutritional characterization of a traditional cultivar of tomato grown under organic conditions—Cv. "Malacara". *Frontiers in Nutrition*, *8*, 810812. https://doi.org/10.3389/fnut.2021.810812

Rambla, J. L., Medina, A., Fernández-del-Carmen, A., Barrantes, W., Grandillo, S., Cammareri, M., López-Casado, G., Rodrigo, G., Alonso, A., García-Martínez, S., Primo, J., Ruiz, J. J., Fernández-Muñoz, R., Monforte, A. J., & Granell, A. (2017). Identification, introgression, and validation of fruit volatile QTLs from a red-fruited wild tomato species. *Journal of Experimental Botany*, *68*(3), 429–442. https://doi.org/10.1093/jxb/erw455

Rambla, J. L., Tikunov, Y. M., Monforte, A. J., Bovy, A. G., & Granell, A. (2014). The expanded tomato fruit volatile landscape. *Journal of Experimental Botany*, *65*(16), 4613–4623. https://doi.org/10.1093/jxb/eru128

Saliba-Colombani, V., Causse, M., Langlois, D., Philouze, J., & Buret, M. (2001). Genetic analysis of organoleptic quality in fresh market tomato. 1. Mapping QTLs for physical and chemical traits. *Theoretical and Applied Genetics*, *102*(2–3), 259–272. https://doi.org/10.1007/s001220051643

Stevens, M. A., Kader, A. A., Albright-Holton, M., & Algazi, M. (1977). Genotypic variation for flavor and composition in fresh market tomatoes. *Journal of the American Society for Horticultural Science*, *102*(5), 680–689. https://doi.org/10.21273/JASHS.102.5.680

Tandon, K. S., Baldwin, E. A., Scott, J. W., & Shewfelt, R. L. (2003). Linking sensory descriptors to volatile and nonvolatile components of fresh tomato flavor. *Journal of Food Science*, *68*(7), 2366–2371. https://doi.org/10.1111/j.1365-2621.2003.tb05774.x

Taylor, J., & Butler, D. (2017). R package ASMap: Efficient genetic linkage map construction and diagnosis. *Journal of Statistical Software*, *79*(6), 1–29. https://doi.org/10.18637/jss.v079.i06

The Good Scents Company Information System - Information for the Flavor, Fragrance, Food and Cosmetic Industries. (2021). Retrieved 10 January 2021, from http://www.thegoodscentscompany.com/search2.html

Tieman, D., Bliss, P., McIntyre, L. M., Blandon-Ubeda, A., Bies, D., Odabasi, A. Z., Rodríguez, G. R., van der Knaap, E., Taylor, M. G., Goulet, C., Mageroy, M. H., Snyder, D. J., Colquhoun, T., Moskowitz, H., Clark, D. G., Sims, C., Bartoshuk, L., & Klee, H. J. (2012). The chemical interactions underlying tomato flavor preferences. *Current Biology*, *22*(11), 1035–1039. https://doi.org/10.1016/j.cub.2012.04.016

Tieman, D., Zeigler, M., Schmelz, E., Taylor, M. G., Rushing, S., Jones, J. B., & Klee, H. J. (2010). Functional analysis of a tomato salicylic acid methyl transferase and its role in synthesis of the flavor volatile methyl salicylate. *The Plant Journal*, *62*(1), 113–123. https://doi.org/10.1111/j.1365-313X.2010.04128.x

Tieman, D., Zhu, G., Resende, M. F. R., Lin, T., Nguyen, C., Bies, D., Rambla, J. L., Beltran, K. S. O., Taylor, M., Zhang, B., Ikeda, H., Liu, Z., Fisher, J., Zemach, I., Monforte, A., Zamir, D., Granell, A., Kirst, M., Huang, S., & Klee, H. (2017). A chemical genetic roadmap to improved tomato flavor. *Science*, *355*(6323), 391–394. https://doi.org/10.1126/science.aal1556

Tieman, D. M., Zeigler, M., Schmelz, E. A., Taylor, M. G., Bliss, P., Kirst, M., & Klee, H. J. (2006). Identification of loci affecting flavour volatile emissions in tomato fruits. *Journal of Experimental Botany*, *57*(4), 887–896. https://doi.org/10.1093/jxb/erj074

Tikunov, Y. M., Roohanitaziani, R., Meijer-Dekens, F., Molthoff, J., Paulo, J., Finkers, R., Capel, I., Carvajal Moreno, F., Maliepaard, C., Nijenhuis-de Vries, M., Labrie, C. W., Verkerke, W., van Heusden, A. W., van Eeuwijk, F., Visser, R. G. F., & Bovy, A. G. (2020). The genetic and functional analysis of flavor in commercial tomato: The *FLORAL4* gene underlies a QTL for floral aroma volatiles in tomato fruit. *The Plant Journal*, *103*(3), 1189–1204. https://doi.org/10.1111/tpj.14795

Utz, H. F. (2014). Plabstat. A computer program for statistical analysis of plant breeding experiments. University of Hohenheim, Stuttgart, Germany. https://plant-breeding.uni-hohenheim.de/en/83113

Voorrips, R. E. (2002). MapChart: Software for the graphical presentation of linkage maps and QTLs. *Journal of Heredity*, *93*(1), 77–78. https://doi.org/10.1093/jhered/93.1.77

Willer, H., Meier, C., Schlatter, B., Dietermann, L., Kemper, L., & Trávníček, J. (2022). The World of Organic Agriculture 2022—Summary. In H. Willer, J. Trávníček, C. Meier, & B. Schlatter (Eds.), *The world of organic agriculture statistics and emerging trends 2022* (pp. 20–30). Research Institute of Organic Agriculture FiBL, Frick, and IFOAM – Organics International.

Xu, Y., & Crouch, J. H. (2008). Marker-assisted selection in plant breeding: From publications to practice. *Crop Science*, *48*(2), 391–407. https://doi.org/10.2135/cropsci2007.04.0191

Zanor, M. I., Rambla, J.-L., Chaïb, J., Steppa, A., Medina, A., Granell, A., Fernie, A. R., & Causse, M. (2009). Metabolic characterization of loci affecting sensory attributes in tomato allows an assessment of the influence of the levels of primary metabolites and volatile organic contents. *Journal of Experimental Botany*, *60*(7), 2139–2154. https://doi.org/10.1093/jxb/erp086

Zhang, J., Zhao, J., Xu, Y., Liang, J., Chang, P., Yan, F., Li, M., Liang, Y., & Zou, Z. (2015). Genome-wide association mapping for tomato volatiles positively contributing to tomato flavor. *Frontiers in Plant Science*, *6*, 1042. https://doi.org/10.3389/fpls.2015.01042

Zörb, C., Piepho, H.-P., Zikeli, S., & Horneburg, B. (2020). Heritability and variability of quality parameters of tomatoes in outdoor production. *Research*, *2020*(1-9), 6707529. https://doi.org/10.34133/2020/6707529

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hagenguth, J., Kanski, L., Kahle, H., Becker, H. C., & Horneburg, B. (2024). Flavour improvement in early generations of fresh market tomatoes (*Solanum lycopersicum*): I. Identification of QTL for sensory attributes, physicochemical measurements and volatile compounds. *Plant Breeding*, *143*(3), 334–349. https://doi.org/10.1111/pbr.13168

Supplementary Materials for

Flavour Improvement in Early Generations of Fresh Market Tomatoes *(Solanum lycopersicum* L.): I. Identification of QTL for Sensory Attributes, Physicochemical Measurements and Volatile Compounds

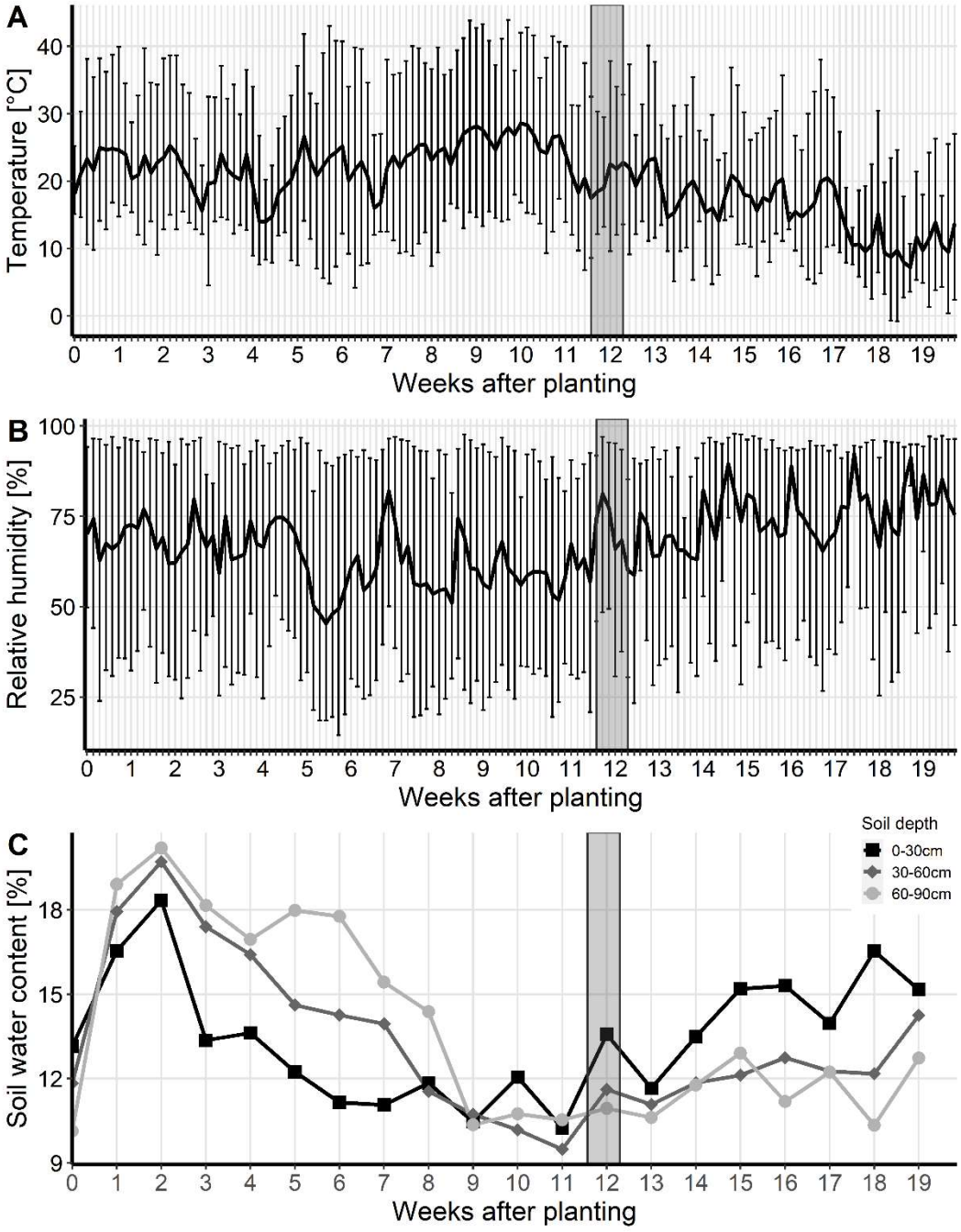

Figure S1. (A) Mean, minimum and maximum temperature per day, (B) mean relative humidity with minimum and maximum per day, and (C) soil water content in the organic cultivation system. The harvest period for the sensory assessment and analytical analyses is marked in grey.
Temperature and humidity data were recorded every 15 min in about 0.5 m above soil surface using an EBI 20-TH Data Logger (ebro Electronic GmbH & Co. KG, Ingolstadt, Germany); soil water content is expressed as gravimetric moisture content

Table S1. Mineral nitrogen in the organic low-input cultivation system

Soil sample	Soil depth (cm)	Mineral nitrogen[1] (N_{min}) [kg/ha]
23.05.2018 start of experiment	0–30	73.57
	30–60	94.33
31.07.2018	0–30	15.23
	30–60	52.84
09.10.2018 end of experiment	0–30	10.90
	30–60	7.40

[1]analysed by University of Goettingen, Division of Agronomy, Goettingen, Germany

Table S2. Number of F_2 genotypes used for the estimation of least square means and QTL analysis

Trait	n
Sweetness	177
Sourness	177
Total aroma	177
Tomato aroma	177
Banana-melon aroma	177
Orange aroma	177
Berry aroma	177
Spicy aroma	177
Green aroma	177
TSS	173
pH	174
TA	173
TSS/TA	172
DM	174
FW	176
6-Methyl-5-hepten-2-one	165
Neral	165
Geranial	166
E-Geranylacetone	165
ß-Damascenone	166
ß-Ionone	167
1-Penten-3-one	166
Hexanol	163
Z-3-Hexenol	165
Hexanal	167
E-2-Hexenal	166
Z-3-Hexenal	167
E-2-Heptenal	167
Phenylacetaldehyde	166
2-Phenylethanol	166
Methyl salicylate	163
Benzaldehyde	166
2-Isobutylthiazole	166

Abbreviation: TSS, total soluble solids; TA, titratable acidity; DM, dry matter; FW, fruit weight

Table S3. Minimum (Min) and maximum (Max) of the parental cultivars 'Resi' (R, n = 3) and 'Auriga' (A, n = 3) and their F_2 mapping population (n ≥ 163) for sensory attributes, physicochemical measurements, fruit weight and volatile compounds [ng mL^{-1} sample] for two cultivation systems

Trait	Organic cultivation						Hydroponic cultivation					
	Resi		Auriga		F_2		Resi		Auriga		F_2	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Sweetness [1–9]	4.25	5.42	2.92	4.25	2.67	5.67	4.17	4.67	2.71	3.12	2.17	5.58
Sourness [1–9]	3.58	4.58	4.08	6.25	2.83	6.50	3.25	3.92	4.19	6.14	2.36	6.75
Total aroma [1–9]	5.17	5.67	4.67	5.08	3.92	7.00	5.33	5.83	4.25	5.08	3.42	6.75
Tomato aroma [1–9]	4.00	4.33	3.75	3.83	2.83	5.42	4.08	4.42	3.06	3.44	2.42	5.11
Banana-melon aroma [2–18] ‡	2.88	4.67	2.17	2.42	2.00	7.92	3.00	5.42	2.00	2.67	2.00	8.83
Orange aroma [1–9]	1.00	2.17	2.33	2.67	0.95	5.05	1.00	1.00	2.45	5.22	0.89	5.67
Berry aroma [1–9]	1.00	2.25	1.67	2.00	1.00	3.95	1.67	3.33	1.05	1.62	0.95	4.17
Spicy aroma [1–9]	2.17	3.17	1.17	2.33	1.00	4.83	1.50	1.83	0.93	2.40	0.93	2.92
Green aroma [1–9]	1.00	1.33	1.83	3.33	1.00	3.08	1.67	2.50	2.33	2.34	0.99	2.99
TSS [°Brix]	7.20	7.45	5.80	6.27	6.00	8.20	6.95	7.05	5.01	6.19	5.40	7.65
pH	3.75	4.03	3.95	4.03	3.60	4.40	3.84	4.24	3.74	4.32	3.59	4.54
TA [%]	0.44	0.52	0.52	0.54	0.42	0.68	0.82	0.90	0.80	0.92	0.77	0.97
TSS/TA	14.36	16.66	11.23	11.86	10.69	16.85	9.76	11.87	6.02	9.27	7.54	14.36
DM [%]	8.67	8.79	6.85	7.60	6.86	10.02	8.28	9.08	5.75	6.99	6.02	9.42
FW [g]	16.93	17.68	74.84 †		22.01	56.25	15.04	15.44	59.80 †		16.05	52.69
6-Methyl-5-hepten-2-one	3.90	6.49	1.20	1.23	0.00	8.38	2.76	10.41	0.69	2.15	0.70	17.75
Neral	0.34	0.51	0.13	0.19	0.04	1.11	0.37	1.00	0.00	0.42	0.00	2.54
Geranial	1.26	1.93	0.24	0.29	0.01	2.52	0.67	2.41	0.19	0.69	0.15	4.26
E-Geranylacetone	5.40	7.23	1.45	1.93	0.38	8.28	1.41	4.70	1.07	2.06	0.54	6.40
ß-Damascenone	1.15	2.56	1.72	2.97	0.33	3.74	0.75	1.32	0.81	3.49	0.20	3.42
ß-Ionone	0.80	1.22	3.17	4.03	0.24	6.14	0.45	0.65	2.82	4.29	0.11	6.83
1-Penten-3-one	0.07	0.11	0.04 †		0.00	0.28	0.01	0.02	0.01 †		0.01	0.04
Hexanol	1.87	4.20	0.70	1.17	0.46	4.08	1.27	3.07	0.08	0.49	0.14	5.50
Z-3-Hexenol	1.91	2.98	1.47	1.66	0.84	5.38	0.82	1.45	0.39	0.83	0.29	3.03
Hexanal	66.50	93.41	15.36	18.18	11.17	99.39	26.91	61.61	5.88	7.50	4.19	56.52
E-2-Hexenal	4.40	8.18	1.86	5.55	0.11	13.53	1.56	2.23	1.91	2.27	0.61	4.30
Z-3-Hexenal	0.83	2.92	1.73	2.56	0.14	4.47	0.51	0.83	1.11	3.20	0.37	3.27

Continued next page.

Table S3. Continued.

Trait	Organic cultivation						Hydroponic cultivation					
	Resi		Auriga		F_2		Resi		Auriga		F_2	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
E-2-Heptenal	0.24	0.41	0.12	0.30	0.01	0.67	0.07	0.25	0.05	0.09	0.03	0.22
Phenylacetaldehyde	0.13	0.25	0.10	0.14	0.04	0.86	0.13	0.45	0.05	0.06	0.06	0.47
2-Phenylethanol	0.82	1.28	0.38	0.59	0.25	1.00	0.68	0.80	0.56	0.63	0.16	0.84
Methyl salicylate	0.42	0.81	2.95	3.44	0.00	7.95	0.04	0.06	0.12	0.28	0.02	0.40
Benzaldehyde	0.27	0.30	0.41	0.50	0.09	0.68	0.34	0.64	0.26	0.26	0.13	1.08
2-Isobutylthiazole	1.32	1.66	0.32	0.57	0.00	1.72	0.62	0.77	0.18	0.43	0.04	1.05

Abbreviation: TSS, total soluble solids; TA, titratable acidity; DM, dry matter; FW, fruit weight

† Data only available for one of the three parental plants; ‡sum of banana and melon aroma

Table S4. Mean values and standard deviation (SD) of sensory attributes and variance components for the effects of genotype (V_G), person (V_P), replication within environment ($V_{R:E}$), environment (V_E), genotype-by-person interaction (V_{GP}), genotype-by-environment interaction (V_{GE}), person-by-environment interaction (V_{PE}), genotype-by-person-by-environment interaction (V_{GPE}) and residuals (V_ε) of the F_2 mapping population 'Resi' × 'Auriga' (n = 177) in two cultivation systems

Trait	Mean	SD	V_G	V_P	$V_{R:E}$	V_E†	V_{GP}	V_{GE}	V_{PE}	V_{GPE}	V_ε
Sweetness [1–9]	3.81	±0.51	0.192**	0.093**	0.044**	0.001	0.000	0.136**	0.125**	0.000	0.987
Sourness [1–9]	4.28	±0.53	0.196**	0.128**	0.045**	0.022	0.000	0.350**	0.005	0.000	1.147
Total aroma [1–9]	5.17	±0.51	0.187**	0.018**	0.013**	0.018	0.000	0.114**	0.010**	0.000	0.930
Tomato aroma [1–9]	3.80	±0.40	0.086**	0.018**	0.010**	0.048	0.066**	0.038**	0.081**	0.005	0.581
Banana–melon aroma [2–18]‡	3.38	±1.30	1.482**	0.272**	0.040**	0.000	0.098*	0.404**	0.059**	0.000	2.240
Orange aroma [1–9]	1.91	±0.63	0.200**	0.002	0.012*	0.053	0.096*	0.102*	0.028**	0.000	2.021
Berry aroma [1–9]	1.96	±0.52	0.072**	0.018**	0.002	0.019	0.130**	0.044	0.018*	0.111	1.855
Spicy aroma [1–9]	1.61	±0.45	0.072**	0.139**	0.004	0.072	0.071**	0.069*	0.033**	0.000	1.257
Green aroma [1–9]	1.79	±0.36	0.019	0.844**	0.000	0.000	0.021	0.000	0.002	0.060	1.234

*, ** significant at 0.05 and 0.01 level, respectively

†cultivation system; ‡sum of banana and melon aroma

Table S5. Mean values and standard deviation (SD) of physicochemical measurements, fruit weight and volatile compounds [ng mL^{-1} sample] and variance components for the effects of genotype (V_G), replication within environment ($V_{R:E}$), environment (V_E), genotype-by-environment interaction (V_{GE}) and residuals (V_ε) of the mapping population 'Resi' × 'Auriga' (n ≥ 163) in two cultivation systems

Trait	Mean	SD	V_G	$V_{R:E}$	V_E[†]	V_{GE}	V_ε
TSS [°Brix]	6.79	±0.36	0.1012**	0.0000	0.1243**	0.0272**	0.1004
pH	4.02	±0.11	0.0013	0.0000	0.0062**	0.0039	0.0438
TA [%]	0.70	±0.03	0.0002**	0.0002**	0.0600**	0.0005**	0.0024
TSS/TA	12.05	±0.99	0.6246**	0.1187**	4.9102**	0.5846**	1.4054
DM [%]	7.98	±0.52	0.2240**	0.0196**	0.1216	0.0699**	0.1707
FW [g]	31.15	±6.48	39.6614**	1.2613**	11.2666*	5.2358**	12.2807
6-Methyl-5-hepten-2-one	3.11	±1.87	2.8689**	0.5318**	1.7142	0.5240**	2.4908
Neral	0.33	±0.20	0.0278**	0.0539**	0.0000	0.0130**	0.0445
Geranial	0.87	±0.56	0.2597**	0.0440**	0.1434	0.0652**	0.2106
E-Geranylacetone	2.37	±1.10	0.8752**	0.0485**	0.0000	0.2920**	1.3765
ß-Damascenone	1.12	±0.44	0.0632**	0.0273**	0.0000	0.1263**	0.5338
ß-Ionone	2.08	±0.94	0.7030**	0.0470**	0.0000	0.1352*	0.7310
1-Penten-3-one	0.06	±0.03	0.0001	0.0012**	0.0017	0.0003	0.0024
Hexanol	1.42	±0.60	0.2353**	0.0180**	0.1924*	0.1215**	0.4880
Z-3-Hexenol	1.71	±0.52	0.1704**	0.0048	1.0034**	0.0716*	0.4126
Hexanal	25.43	±9.62	52.6905**	1.8817	62.4638**	15.2686	159.4186
E-2-Hexenal	3.62	±1.27	0.0675	12.3140**	0.0251	0.2726	6.1584
Z-3-Hexenal	1.64	±0.50	0.1100**	0.5230**	0.0000	0.0715	0.5783
E-2-Heptenal	0.19	±0.06	0.0005	0.0101**	0.0076	0.0001	0.0139
Phenylacetaldehyde	0.20	±0.07	0.0025**	0.0015**	0.0000	0.0013	0.0104
2-Phenylethanol	0.51	±0.10	0.0054**	0.0157**	0.0000	0.0028*	0.0193
Methyl salicylate	0.48	±0.68	0.3582**	0.1048**	0.2653	0.6477**	0.4100
Benzaldehyde	0.37	±0.11	0.0065**	0.0030**	0.0036	0.0056**	0.0191
2-Isobutylthiazole	0.58	±0.24	0.0153*	0.1144**	0.0000	0.0000	0.1684

*, ** significant at 0.05 and 0.01 level, respectively

Abbreviation: TSS, total soluble solids; TA, titratable acidity; DM = dry matter; FW = fruit weight

[†]cultivation system

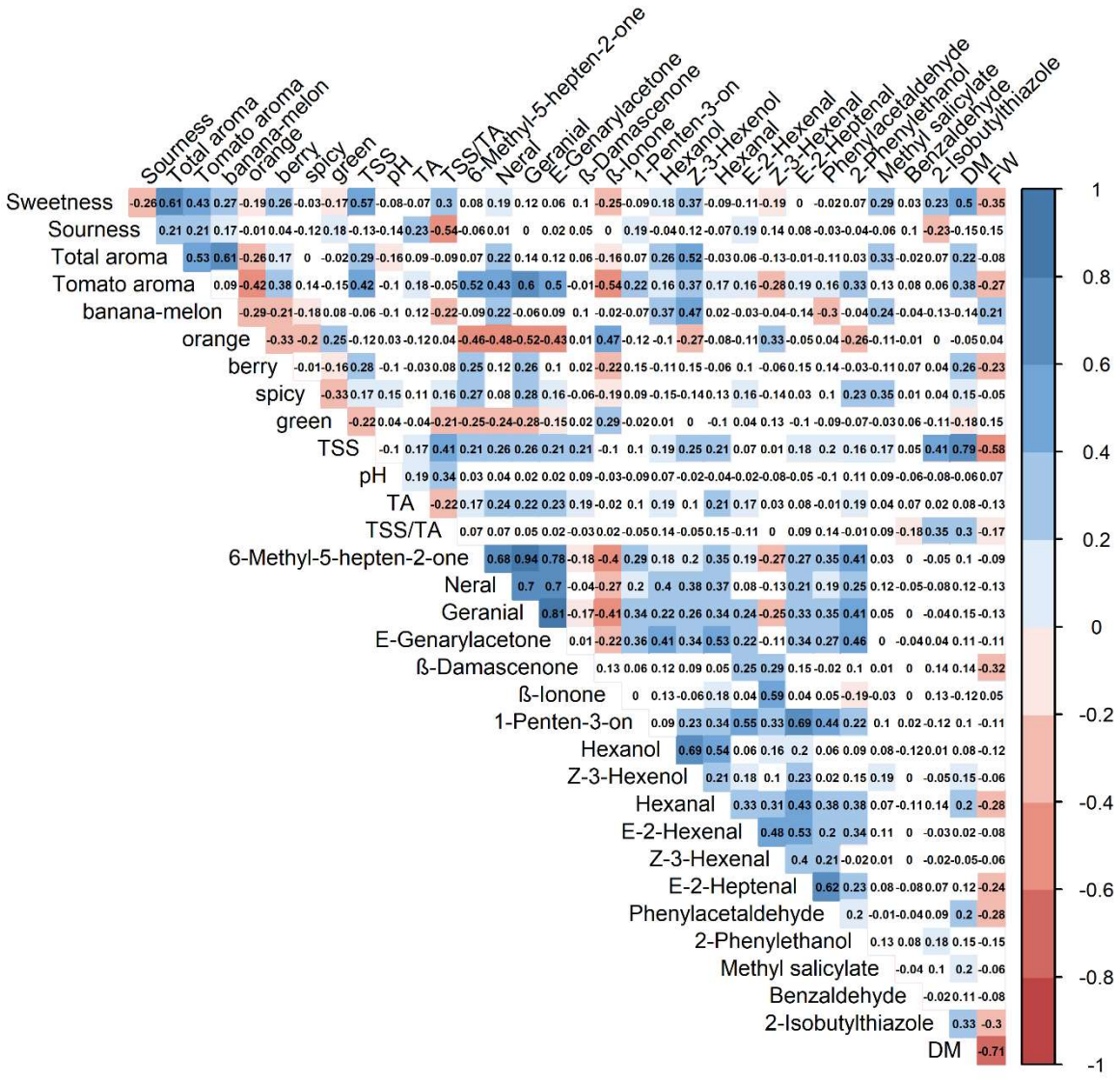

Figure S2. Spearman's correlation coefficients (r) for all sensory attributes, physicochemical measurements (TSS, total soluble solids; TA, titratable acidity; DM, dry matter), volatile compounds and fruit weight (FW) analysed in two cultivation systems (n ≥ 163); significant positive correlations are shown in blue and significant negative correlations in red with p = 0.05

Table S6. Comparison of QTL detected for the environmental means (AV), the organic cultivation system (Or) and the hydroponic cultivation systems (Hy) with their peak position and 95% Bayesian confidence interval; classification into co-localised QTL between the different environments

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
	Frequency				27	19	5	20	15	14	
	Percentage [%]				27	19	5	20	15	14	
Sweetness											
1	SW2.1			86 (76–94)						x	
2	SW5.1	65 (60–69)	65 (58.9–72)	-		x					
3	SW10.1	19 (10–22)	21 (9–27)	11 (6–20)	x						
Sourness											
4	SO2.1	16 (3–20.2)	-	-				x			
5	SO3.1	-	-	85.1 (82–87)						x	
6	SO5.1	65 (61–69)	68 (58.9–75.5)	-		x					
7	SO11.1	24 (12–28)	12.7 (8–33)	24 (15–34)	x						
Total aroma											
8	A.TOT1.1	112.2 (111–112.2)	112 (106–112.2)	112.2 (111–112.2)	x						
9	A.TOT4.1	88 (85–90)	-	-				x			
10	A.TOT6.1	75 (3–78)	-	-				x			
11	A.TOT7.1	22 (10–30)	-	9 (4–51)			x				
12	A.TOT10.1	11 (5–23)	-	10 (5–32)			x				
Int[†]	A.TOT4.1:6.1	x	-	-							
Tomato aroma											
13	A.TOM2.1	-	-	87 (70–95.8)						x	
14	A.TOM6.1	67 (65–70)	67 (64–70)	69 (65–72)	x						
15	A.TOM10.1	16 (7.8–33)	-	-				x			
Banana-melon aroma											
16	A.BM1.1	111 (111–112)	111 (111–112)	111 (110–112)	x						
17	A.BM5.1	-	14 (8–18)	-					x		

Continued next page.

Table S6. Continued.

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
18	A.BM6.1	-	68 (59–74)	-					x		
19	A.BM8.1	-	71 (48–76)	-					x		
Int[†]	A.BM5.1:8.1	-	x	-							
Orange aroma											
20	A.OR1.1	-	-	83 (77–92)						x	close
21	A.OR1.2	112 (89–112.2)	-	-				x			
22	A.OR6.1	69 (66–71)	70.4 (67–72)	67 (64–71)	x						
23	A.OR9.1	47 (31–59)	-	-				x			
Berry aroma											
24	A.BE6.1	70.4 (39–79)	-	-				x			
25	A.BE7.1	38 (3–48)	36.2 (12–43)	-		x					
Spicy aroma											
26	A.SP4.1	32 (14–53)	-	-				x			
27	A.SP6.1	70.4 (65–75)	70.4 (65–75)	-		x					
28	A.SP9.1	77.7 (76–79)	77.7 (76–79)	-		x					
Green aroma											
29	A.GR6.1	-	75 (64–78)	-					x		
Total soluble solids (TSS)											
30	TSS2.1	76 (72–83)	-	74.7 (71–77)			x				
31	TSS3.1	85 (83–86)	84 (82–86)	85.1 (82–91)	x						
32	TSS6.1	38 (34–43)	42 (38–45)	37 (32–58)	x						
33	TSS7.1	26 (2–59)	-	-				x			
34	TSS10.1	17.6 (14–20)	20 (16–23)	17 (6–22)	x						
35	TSS11.1	-	-	68 (65–77)						x	
36	TSS12.1	-	30 (19–42)	-					x		
Titratable acidity (TA)											
37	TA7.1	-	-	36.2 (24–46)						x	

Continued next page.

Table S6. Continued.

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
pH											
38	pH7.1	-	-	36.2 (26–47)						x	
TSS/TA											
39	TSS/TA3.1	48.5 (37–52)	-	-				x			
40	TSS/TA3.2	-	-	85.1 (37–91)						x	
41	TSS/TA5.1	67 (62–69)	64 (51–72)	66 (61–72)	x						
42	TSS/TA6.1	-	11 (5–15)	-					x		
43	TSS/TA10.1	-	10 (5–26)	-					x		
Dry matter											
44	DM1.1	74.5 (71–75)	75 (70–91)	-		x					
45	DM2.1	81 (77–86)	81 (76–87)	80 (76–87)	x						
46	DM3.1	84 (83–86)	85 (83–86)	82 (78.9–84)	x						
47	DM6.1	10 (7–13)	12 (5–24)	-		x					
48	DM7.1	11.3 (8–15)	-	8 (4–12)			x				
49	DM8.1	44.6 (42–47)	-	-				x			
50	DM8.2	-	-	75.2 (46–81)						x	
51	DM10.1	-	-	14 (9–18)						x	
52	DM10.2	26 (22–31)	32 (22–34)	-		x					close
53	DM11.1	76 (73–79)	84 (76–87)	-		x					
54	DM12.1	-	26 (20–30)	-					x		
55	DM12.2	42 (39–45)	-	-				x			close
Int[†]	DM1.1:8.1	x	-	-							
Int[†]	DM3.1:7.1	-	-	x							
Fruit weight											
56	FW1.1	109.4 (107–112.2)	-	-				x			
57	FW2.1	44 (38.6–54)	46 (43–49)	-		x					

Continued next page.

Table S6. Continued.

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
58	FW2.2	88 (87–92)	89 (86–92)	83 (81–86)	x						
59	FW3.1	84 (83–85.1)	84 (83–85.1)	77 (76–83)	x						
60	FW4.1	39 (35–47)	-	-				x			close
61	FW4.2	-	58 (47–66)	-					x		
62	FW8.1	7 (0–13)	-	-				x			
63	FW8.2	-	38.1 (36–42)	-					x		
64	FW8.3	83 (80–85.4)	83 (76–85.4)	-		x					
65	FW10.1	3 (1–5)	-	-				x			close
66	FW10.2	-	17.6 (15–20)	-					x		
67	FW11.1	-	12.7 (11–15)	-					x		
68	FW11.2	83 (76–87)	88 (85–91.4)	-		x					
69	FW12.1	43 (39–48)	56 (48–62)	43 (20–61)	x						
6-Methyl-5-hepten-2-one											
70	6MHO6.1	70.4 (68–71)	70 (68–71)	70.4 (69–72)	x						
71	6MHO9.1	-	-	0 (0–43)						x	
Neral											
72	NER1.1	112.2 (94–112.2)	111 (102–112.2)	-		x					
73	NER3.1	76 (62–93)	-	-				x			
74	NER6.1	70.4 (66–71)	67 (64–71)	70.4 (66–72)	x						
Geranial											
75	GER6.1	71 (69–71)	70 (68–71)	71 (69–72)	x						
E-Geranylacetone											
76	eGAC1.1	107 (100–111)	103 (98–111)	-		x					
77	eGAC3.1	84 (80–87)	84 (40–93)	85.1 (76–91)	x						
78	eGAC4.1	49 (44–55)	-	-				x			
79	eGAC6.1	69 (67–72)	68 (65–70.4)	72 (67–77)	x						

Continued next page.

Table S6. Continued.

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
ß-Ionone											
80	ßION6.1	69 (67–71)	69 (67–72)	69 (67–72)	x						
1-Penten-3-one											
81	1P3O1.1	-	-	107 (105–112)						x	
82	1P3O6.1	66 (35.6–71)	39 (35–71)	-		x					
Hexanol											
83	HEXOL1.1	109.4 (107–111)	108 (105–112)	109.4 (98–112.2)	x						
84	HEXOL3.1	83 (73–88)	-	-				x			
Z-3-Hexenol											
85	z3HEXOL1.1	52 (46–59)	55.6 (15–62)	-		x					
86	z3HEXOL1.2	109 (106–111)	111 (106–112.2)	109.4 (107–112)	x						
87	z3HEXOL4.1	-	-	17 (4–25)						x	
88	z3HEXOL7.1	41 (36–65)	41 (35–65)	-		x					
89	z3HEXOL10.1	-	10 (5–21)	-					x		
Hexanal											
90	HEXAL3.1	87 (83–92)	86 (71–94)	87 (83–92)	x						
E-2-Hexenal											
91	e2HEXEL6.1	54 (41–58)	53 (39–58)	-		x					
Z-3-Hexenal											
92	z3HEXEL6.1	77 (69–79)	78 (42–79.9)	68 (65–72)	x						
E-2-Heptenal											
93	e2HEPEL6.1	70.4 (51–79)	-	-				x			
2-Phenylethanol											
94	2PE1.1	-	-	112 (106–112.2)						x	
95	2PE2.1	77 (73–82)	67 (42–87)	82 (74.7–87)	x						
96	2PE6.1	68 (64–72)	-	70.4 (66–72)			x				

Continued next page.

Table S6. Continued.

#	Name	AV	Or	Hy	All	AV/Or	AV/Hy	AV	Or	Hy	Note
Methyl salicylate											
97	MES9.1	78 (77–79)	78 (77–79)	80 (77–85)	x						
Benzaldehyde											
98	BAL4.1	-	73 (70–84)	-					x		
99	BAL6.1	0 (0–10)	18 (3–31)	-		x					
100	BAL10.1	-	12 (9–49)	-					x		

[†]QTL-by-QTL interaction

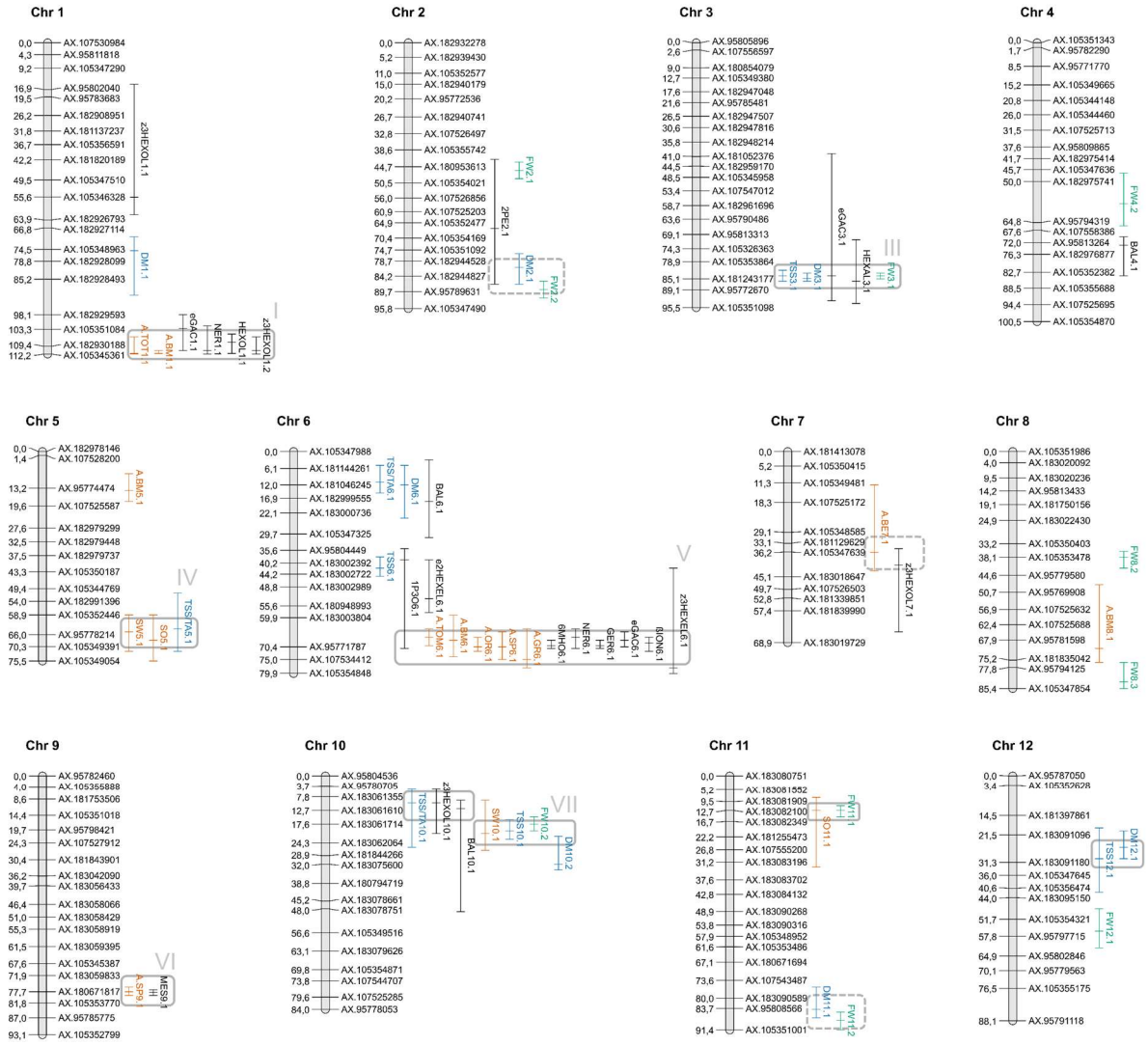

Figure S3. Organic cultivation: QTL (peak position and 95% Bayesian confidence interval) for the sensory attributes (orange), physicochemical measurements (blue), volatile compounds (black) and fruit weight (green) on the linkage map of 'Resi' × 'Auriga' detected by multiple-QTL mapping; QTL enclosed in boxes indicate clusters for co-localised QTL (distinct clusters: solid line; suspected clusters: dashed line), numbering according to QTL clusters identified for mean values of both cultivation systems

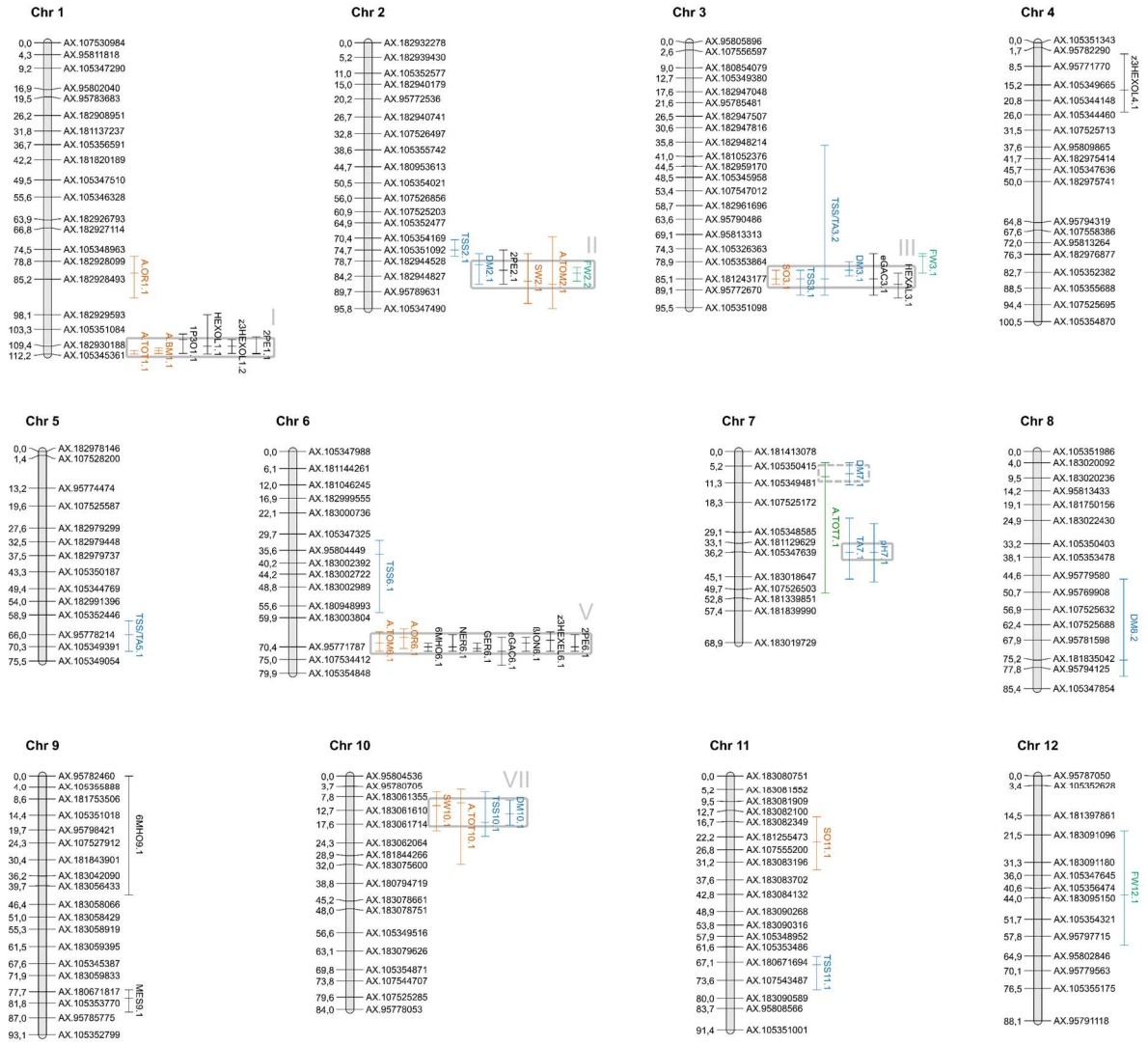

Figure S4. Hydroponic cultivation: QTL (peak position and 95% Bayesian confidence interval) for sensory attributes (orange), physicochemical measurements (blue), volatile compounds (black) and fruit weight (green) on the linkage map of 'Resi' × 'Auriga' detected by multiple-QTL mapping; QTL enclosed in boxes indicate clusters for co-localised QTL (distinct clusters: solid line; suspected clusters: dashed line), numbering according to QTL clusters identified for mean values of both cultivation systems

Table S7. Organic cultivation: Location and estimates of QTL for sensory attributes, physicochemical measurements, fruit weight and volatile compounds detected by multiple-QTL mapping in an F_2 population of 'Resi' × 'Auriga'

Trait	QTL	Chr[1]	Closest marker	Pos[2]	LOD[3]	PVE[4]	PVE$_{full}$[5]	Add[6]	Dom[7]	Allel[8]
Sweetness										
	SW5.1	5	AX-95778214	65.0 (58.9–72.0)	4.59	9.94	21.62	−0.26	0.04	A
	SW10.1	10	AX-183062064	21.0 (9.0–27.0)	3.82	8.19		−0.21	0.13	A
Sourness										
	SO5.1	5	AX-95778214	68.0 (58.9–75.5)	4.57	10.29	18.40	0.32	0.01	B
	SO11.1	11	AX-183082100	12.7 (8.0–33.0)	3.67	8.17		0.28	−0.17	B
Total aroma										
	A.TOT1.1	1	AX-105345361	112.0 (106.0–112.2)	8.29	19.39	19.39	−0.32	−0.13	A
Tomato aroma										
	A.TOM6.1	6	AX-95771787	67.0 (64.0–70.0)	19.66	40.04	40.04	−0.46	−0.13	A
Banana-melon aroma										
	A.BM1.1	1	AX-105345361	111.0 (111.0–112.0)	42.44	50.50		−1.38	−0.52	A
	A.BM5.1	5	AX-95774474	14.0 (8.0–18.0)	9.63	7.13		−0.001	−0.41	A
	A.BM6.1	6	AX-95771787	68.0 (59.0–74.0)	4.92	3.42	74.95	0.37	0.26	B
	A.BM8.1	8	AX-95781598	71.0 (48.0–76.0)	9.02	6.63		−0.26	−0.15	A
	A.BM5.1:8.1				7.35	5.28				
Orange aroma										
	A.OR6.1	6	AX-95771787	70.4 (67.0–72.0)	8.63	20.12	20.12	0.48	0.24	B
Berry aroma										
	A.BE7.1	7	AX-105347639	36.2 (12.0–43.0)	4.02	9.92	9.92	0.24	−0.10	B
Spicy aroma										
	A.SP6.1	6	AX-95771787	70.4 (65.0–75.0)	5.91	11.70	29.68	−0.35	−0.01	A
	A.SP9.1	9	AX-180671817	77.7 (76.0–79.0)	10.22	21.41		0.38	−0.31	B
Green aroma										
	A.GR6.1	6	AX-107534412	75.0 (64.0–78.0)	4.05	10.00	10.00	0.23	0.06	B
Total soluble solids (TSS)										
	TSS3.1	3	AX-181243177	84.0 (82.0–86.0)	10.97	15.96		−0.27	0.09	A
	TSS6.1	6	AX-183002392	42.0 (38.0–45.0)	8.55	12.02	52.97	−0.22	0.05	A
	TSS10.1	10	AX-183061714	20.0 (16.0–23.0)	11.46	16.77		−0.22	0.13	A
	TSS12.1	12	AX-183091180	30.0 (19.0–42.0)	5.07	6.80		−0.15	−0.06	A
TSS/TA										
	TSS/TA5.1	5	AX-95778214	64.0 (51.0–72.0)	5.97	11.79		−0.59	0.12	A
	TSS/TA6.1	6	AX-181046245	11.0 (5.0–15.0)	5.37	10.54	31.92	−0.54	0.40	A
	TSS/TA10.1	10	AX-183061355	10.0 (5.0–26.0)	3.93	7.56		−0.36	0.42	A
Dry matter										
	DM1.1	1	AX-105348963	75.0 (70.0–91.0)	5.25	5.10		0.18	0.14	B
	DM2.1	2	AX-182944528	81.0 (76.0–87.0)	5.59	5.46		−0.18	−0.08	A
	DM3.1	3	AX-181243177	85.0 (83.0–86.0)	22.13	27.25		−0.44	−0.08	A
	DM6.1	6	AX-181046245	12.0 (5.0–24.0)	4.72	4.56	65.77	−0.19	0.07	A
	DM10.2	10	AX-183075600	32.0 (22.0–34.0)	10.59	11.07		−0.28	−0.01	A
	DM11.1	11	AX-95808566	84.0 (76.0–87.0)	8.95	9.15		−0.23	0.14	A
	DM12.1	12	AX-183091096	26.0 (20.0–30.0)	10.82	11.35		−0.27	0.02	A
Fruit weight										
	FW2.1	2	AX-180953613	46.0 (43.0–49.0)	10.46	5.03		2.24	−0.55	B

Continued next page.

Table S7. Continued.

Trait	QTL	Chr[1]	Closest marker	Pos[2]	LOD[3]	PVE[4]	PVE_{full}[5]	Add[6]	Dom[7]	Allel[8]
	FW2.2	2	AX-95789631	89.0 (86.0–92.0)	14.18	7.18		2.59	−1.31	B
	FW3.1	3	AX-181243177	84.0 (83.0–85.1)	37.12	26.40		5.37	0.63	B
	FW4.2	4	AX-95794319	58.0 (47.0–66.0)	5.95	2.69		1.69	−1.18	B
	FW8.2	8	AX-105353478	38.1 (36.0–42.0)	3.91	1.72		0.67	−1.65	B
	FW8.3	8	AX-105347854	83.0 (76.0–85.4)	3.80	1.67	84.34	1.18	0.85	B
	FW10.2	10	AX-183061714	17.6 (15.0–20.0)	20.09	11.07		3.06	−0.92	B
	FW11.1	11	AX-183082100	12.7 (11.0–15.0)	7.62	3.52		1.95	−0.62	B
	FW11.2	11	AX-105351001	88.0 (85.0–91.4)	11.75	5.75		2.23	−1.25	B
	FW12.1	12	AX-95797715	56.0 (48.0–62.0)	9.82	4.68		1.90	−1.27	B
6-Methyl-5-hepten-2-one										
	6MHO6.1	6	AX-95771787	70.0 (68.0–71.0)	34.84	62.18	62.18	−1.72	−0.81	A
Neral										
	NER1.1	1	AX-105345361	111.0 (102.0–112.2)	6.11	11.78	36.62	−0.07	0.03	A
	NER6.1	6	AX-95771787	67.0 (64.0–71.0)	10.39	21.32		−0.11	−0.07	A
Geranial										
	GER6.1	6	AX-95771787	70.0 (68.0–71.0)	33.46	60.47	60.47	−0.49	−0.28	A
E-Geranylacetone										
	eGAC1.1	1	AX-105351084	103.0 (98.0–111.0)	4.95	6.84		−0.46	0.34	A
	eGAC3.1	3	AX-181243177	84.0 (40.0–93.0)	3.74	5.08	53.83	−0.48	−0.15	A
	eGAC6.1	6	AX-95771787	68.0 (65.0–70.4)	22.46	40.26		−1.37	−0.30	A
ß-Ionone										
	ßION6.1	6	AX-95771787	69.0 (67.0–72.0)	24.76	49.47	49.47	1.05	0.23	B
1-Penten-3-one										
	1P3O6.1	6	AX-183002392	39.0 (35.0–71.0)	3.89	10.24	10.24	−0.02	−0.02	A
Hexanol										
	HEXOL1.1	1	AX-182930188	108.0 (105.0–112.0)	8.00	20.24	20.24	−0.41	−0.03	A
Z-3-Hexenol										
	z3HEXOL1.1	1	AX-105346328	55.6 (15.0–62.0)	3.66	6.24		0.26	0.10	B
	z3HEXOL1.2	1	AX-105345361	111.0 (106.0–112.2)	8.65	15.84	41.98	−0.37	0.21	A
	z3HEXOL7.1	7	AX-183018647	41.0 (35.0–65.0)	6.80	12.12		0.37	−0.02	B
	z3HEXOL10.1	10	AX-183061355	10.0 (5.0–21.0)	4.82	8.35		−0.29	0.20	A
Hexanal										
	HEXAL3.1	3	AX-181243177	86.0 (71.0–94.0)	4.05	10.56	10.56	−6.28	−0.88	A
E-2-Hexenal										
	e2HEXEL6.1	6	AX-180948993	53.0 (39.0–58.0)	3.98	10.46	10.46	−0.56	−1.48	A
Z-3-Hexenal										
	z3HEXEL6.1	6	AX-105354848	78.0 (42.0–79.9)	3.72	9.75	9.75	0.29	−0.21	B
2-Phenylethanol										
	2PE2.1	2	AX-105352477	67.0 (42.0–87.0)	3.78	9.97	9.97	−0.06	0.03	A
Methyl salicylate										
	MES9.1	9	AX-180671817	78.0 (77.0–79.0)	28.44	55.23	55.23	1.13	−1.03	B
Benzaldehyde										
	BAL4.1	4	AX-95813264	73.0 (70.0–84.0)	4.31	8.72		0.04	0.02	B
	BAL6.1	6	AX-182999555	18.0 (3.0–31.0)	5.03	10.28	31.35	0.05	−0.01	B
	BAL10.1	10	AX-183061610	12.0 (9.0–49.0)	5.10	10.44		−0.03	0.04	A

[1]Chr, chromosome; [2]Pos, peak position with 95% Bayesian confidence interval; [3]LOD, log of likelihood ratio; [4]PVE, percentage of phenotypic variation explained by the QTL; [5]PVE_{full}, percentage of phenotypic variation explained by the multiple-QTL model; [6]Add, additive effect (positive effect denote increasing effect of the B allele); [7]Dom. dominance; [8]Allele, allele increasing the phenotypic value (A from Resi, B from Auriga)

Table S8. Hydroponic cultivation: Location and estimates of QTL for sensory attributes, physicochemical measurements, fruit weight and volatile compounds detected by multiple-QTL mapping in an F_2 population of 'Resi' × 'Auriga'

Trait	QTL	Chr[1]	Closest marker	Pos[2]	LOD[3]	PVE[4]	PVE_{full}[5]	Add[6]	Dom[7]	Allel[8]
Sweetness										
	SW2.1	2	AX-182944827	86.0 (76.0–94.0)	3.75	7.58	25.95	−0.26	0.00	A
	SW10.1	10	AX-183061610	11.0 (6.0–20.0)	8.63	18.64		−0.43	0.08	A
Sourness										
	SO3.1	3	AX-181243177	85.1 (82.0–87.0)	9.04	19.61	26.04	0.52	−0.41	B
	SO11.1	11	AX-181255473	24.0 (15.0–34.0)	4.13	8.40		0.34	−0.03	B
Total aroma										
	A.TOT1.1	1	AX-105345361	112.2 (111.0–112.2)	12.00	22.70		−0.40	−0.24	A
	A.TOT7.1	7	AX-105349481	9.0 (4.0–51.0)	3.64	6.15	38.07	0.24	−0.03	B
	A.TOT10.1	10	AX-183061355	10.0 (5.0–32.0)	5.09	8.77		−0.29	0.01	A
Tomato aroma										
	A.TOM2.1	2	AX-95789631	87.0 (70.0–95.8)	3.96	7.41	31.66	−0.17	0.09	A
	A.TOM6.1	6	AX-95771787	69.0 (65.0–72.0)	11.82	24.60		−0.34	−0.06	A
Banana-melon aroma										
	A.BM1.1	1	AX-105345361	111.0 (110.0–112.0)	34.92	59.69	59.69	−1.47	−0.98	A
Orange aroma										
	A.OR1.1	1	AX-182928493	83.0 (77.0–92.0)	4.86	8.13	39.66	0.32	0.10	B
	A.OR6.1	6	AX-95771787	67.0 (64.0–71.0)	16.67	32.77		0.63	−0.32	B
Total soluble solids (TSS)										
	TSS2.1	2	AX-105351092	74.7 (71.0–77.0)	6.76	10.67		−0.16	−0.12	A
	TSS3.1	3	AX-181243177	85.1 (82.0–91.0)	7.23	11.49		−0.22	0.15	A
	TSS6.1	6	AX-95804449	37.0 (32.0–58.0)	4.59	7.03	45.87	−0.15	−0.06	A
	TSS10.1	10	AX-183061714	17.0 (6.0–22.0)	6.00	9.38		−0.17	0.05	A
	TSS11.1	11	AX-180671694	68.0 (65.0–77.0)	5.09	7.86		−0.11	0.17	A
Titratable acidity (TA)										
	TA7.1	7	AX-105347639	36.2 (24.0–46.0)	3.65	9.25	9.25	−0.01	0.00	A
pH										
	pH7.1	7	AX-105347639	36.2 (26.0–47.0)	3.66	9.23	9.23	−0.07	0.00	A
TSS/TA										
	TSS/TA3.2	3	AX-181243177	85.1 (37.0–91.0)	5.44	11.51	26.57	−0.69	0.58	A
	TSS/TA5.1	5	AX-95778214	66.0 (61.0–72.0)	5.93	12.64		−0.69	−0.04	A
Dry matter										
	DM2.1	2	AX-182944528	80.0 (76.0–87.0)	11.87	15.53		−0.35	−0.04	A
	DM3.1	3	AX-105353864	82.0 (78.9–84.0)	16.21	22.54		−0.39	0.09	A
	DM7.1	7	AX-105350415	8.0 (4.0–12.0)	9.99	12.73	57.93	0.17	−0.01	B
	DM8.2	8	AX-181835042	75.2 (46.0–81.0)	3.76	4.41		−0.17	−0.05	A
	DM10.1	10	AX-183061610	14.0 (9.0–18.0)	9.35	11.80		−0.31	0.02	A
	DM3.1:7.1				6.26	7.58				
Fruit weight										
	FW2.2	2	AX-182944827	83.0 (81.0–86.0)	17.32	25.51		4.94	−2.99	B
	FW3.1	3	AX-105353864	77.0 (76.0–83.0)	19.86	30.33	56.46	5.74	2.19	B
	FW12.1	12	AX-183095150	43.0 (20.0–61.0)	4.36	5.35		2.48	1.03	B

Continued next page.

Table S8. Continued.

Trait	QTL	Chr[1]	Closest marker	Pos[2]	LOD[3]	PVE[4]	PVE_{full}[5]	Add[6]	Dom[7]	Allel[8]
6-Methyl-5-hepten-2-one										
	6MHO6.1	6	AX-95771787	70.4 (69.0–72.0)	21.21	42.20	47.75	−2.33	−1.07	A
	6MHO9.1	9	AX-95782460	0.0 (0.0–43.0)	3.65	5.60		−0.66	−0.72	A
Neral										
	NER6.1	6	AX-95771787	70.4 (66.0–72.0)	7.85	19.68	19.68	−0.18	−0.10	A
Geranial										
	GER6.1	6	AX-95771787	71.0 (69.0–72.0)	29.36	55.72	55.72	−0.80	−0.43	A
E-Geranylacetone										
	eGAC3.1	3	AX-181243177	85.1 (76.0–91.0)	4.79	10.45	26.95	−0.59	0.11	A
	eGAC6.1	6	AX-95771787	72.0 (67.0–77.0)	7.15	16.13		−0.69	−0.14	A
ß-Ionone										
	ßION6.1	6	AX-95771787	69.0 (67.0–72.0)	23.71	48.00	48.00	1.14	0.35	B
1-Penten-3-one										
	1P3O1.1	1	AX-182930188	107.0 (105.0–112.0)	5.95	15.23	15.23	0.001	0.01	B
Hexanol										
	HEXOL1.1	1	AX-182930188	109.4 (98.0–112.2)	5.22	13.71	13.71	−0.37	−0.14	A
Z-3-Hexenol										
	z3HEXOL1.2	1	AX-182930188	109.4 (107.0–112.0)	7.79	17.20	29.22	−0.27	−0.07	A
	z3HEXOL4.1	4	AX-105349665	17.0 (4.0–25.0)	3.70	7.69		−0.13	−0.22	A
Hexanal										
	HEXAL3.1	3	AX-181243177	87.0 (83.0–92.0)	10.42	24.98	24.98	−8.47	0.63	A
Z-3-Hexenal										
	z3HEXEL6.1	6	AX-95771787	68.0 (65.0–72.0)	14.78	33.47	33.47	0.51	−0.05	B
2-Phenylethanol										
	2PE1.1	1	AX-105345361	112.0 (106.0–112.2)	6.12	10.59		−0.05	0.03	A
	2PE2.1	2	AX-182944827	82.0 (74.7–87.0)	8.11	14.42	42.83	−0.06	−0.01	A
	2PE6.1	6	AX-95771787	70.4 (66.0–72.0)	9.22	16.67		−0.07	−0.02	A
Methyl salicylate										
	MES9.1	9	AX-105353770	80.0 (77.0–85.0)	8.60	21.58	21.58	0.04	−0.03	B

[1]Chr, chromosome; [2]Pos, peak position with 95% Bayesian confidence interval; [3]LOD, log of likelihood ratio; [4]PVE, percentage of phenotypic variation explained by the QTL; [5]PVE_{full}, percentage of phenotypic variation explained by the multiple-QTL model; [6]Add, additive effect (positive effect denote increasing effect of the B allele); [7]Dom. dominance; [8]Allele, allele increasing the phenotypic value (A from Resi, B from Auriga)