Theor Appl Genet (2001) 102:1016–1028 © Springer-Verlag 2001

A. Ben Chaim · I. Paran · R.C. Grube · M. Jahn
R. van Wijk · J. Peleman

QTL mapping of fruit-related traits in pepper (*Capsicum annuum*)

Received: 28 February 2000 / Accepted: 3 July 2000

Abstract QTL analysis of pepper fruit characters was performed in an F_3 population derived from a cross between two *Capsicum annuum* genotypes, the bell-type cultivar Maor and the Indian small-fruited line Perennial. RFLP, AFLP®[1], RAPD and morphological markers (a total of 177) were used to construct a comparative pepper-tomato genetic map for this cross, and 14 quantitatively inherited traits were evaluated in 180 F_3 families. A total of 55 QTL were identified by interval analysis using LOD 3.0 as the threshold for QTL detection. QTL for several traits including fruit diameter and weight, pericarp thickness and pedicel diameter were often located in similar chromosomal regions, thus reflecting high genetic correlations among these traits. A major QTL that accounts for more than 60% of the phenotypic variation for fruit shape (ratio of fruit length to fruit diameter) was detected in chromosome 3. This chromosome also contained QTL for most of the traits scored in the population. Markers in linkage groups 2, 3, 8 and 10 were associated with QTL for multiple traits, thereby suggesting their importance as loci that control developmental processes in pepper. Several QTL in pepper appeared to correspond to positions in tomato for loci controlling the same traits, suggesting the hypothesis that these QTL may be orthologous in the two species.

Keywords *Capsicum* · Quantitative traits · Fruit development · Molecular markers · Comparative mapping

Introduction

Yield parameters and growth habits of crop plants often exhibit continuous (quantitative) variation and are thought to be controlled by multiple genes whose expression is affected by environmental factors. Before genetic maps of crop plants became available, quantitative traits were analyzed using biometrical models. A biometrical approach, although descriptive of inheritance, does not explain the effects of individual quantitative trait loci (QTL) affecting a trait. Construction of a high-density genetic map comprising molecular markers, in conjunction with quantitative phenotypic analysis, allows the identification of individual QTL controlling a quantitative trait.

Pepper (*Capsicum* spp.) has been the subject of many genetic studies on fruit characters and growth habit (Deshpande 1933; Khambanonda 1950; Legg and Lippert 1966; McArdle and Bouwkamp 1983; Peterson 1959; Thakur et al. 1980). These studies employed classical biometrical approaches for the study of quantitative traits and, therefore, knowledge of the numbers and genomic locations of QTL controlling these traits were not obtained.

In recent years, several genetic maps of pepper have been published (Kim at al. 1998; Lefebvre et al. 1995; Livingstone et al. 1999; Prince et al. 1993; Tanksley et al. 1988). The map of Livingstone et al. (1999) is the most detailed, and currently consists of over 1000 markers covering 1245 cM. In that study, use of restriction fragment length polymorphism (RFLP) markers common to both tomato and pepper allowed determination of the comparative genome organization of both species.

Communicated by J. Dvorak

A. Ben Chaim · I. Paran (✉)
Department of Plant Genetics and Breeding,
Agricultural Research Organization, The Volcani Center,
P.O. Box 6, Bet Dagan, 50250 Israel
e-mail: vcparan@netvision.net.il
Fax: +972-3-9669642

R.C. Grube · M. Jahn
Department of Plant Breeding, Cornell Universiy, Ithaca,
NY 14853, USA

R. van Wijk · J. Peleman
Keygene, N.V., 6700 AE Wageningen, the Netherlands

Present address:
R.C. Grube, USDA-ARS, 1636 E. Alisal St., Salinas,
CA 93901, USA

---

[1] AFLP® is a registered trademark of Keygene N.V.

Despite the existence of these maps for *Capsicum*, mapping agriculturally important genes has been restricted primarily to genes controlling resistance to pathogens such as cucumber mosaic virus (CMV; Ben Chaim et al. unpublished; Caranta et al. 1997a), *Phytophthora* (Lefebvre and Palloix 1996) tomato spotted wilt virus (Jahn et al. 2000) and potyviruses (Caranta et al. 1997b; Murphy et al. 1998). Additional genes of economic importance that have been mapped are *up* (erect fruit), *C* (pungency, Lefebvre et al. 1995) and QTL affecting the number of flowers per node (Prince et al. 1993).

The objective of the study reported here, was to identify QTL for the major components of fruit yield and quality in the most important cultivated pepper species, *C. annuum*. A second objective of this study was to determine whether there is any evidence of possible orthology between QTL in pepper and tomato that affect the same morphological traits. We analyzed fruit-related quantitative traits in an intra-specific *C. annuum* cross between the sweet bell-type pepper Maor and the pungent small-fruited Indian accession Perennial. The biometrical analysis for several of these traits has been published (Ben Chaim and Paran 2000).

Materials and methods

Plant material

An intra-specific F_2 population was constructed from the two inbred pepper lines Maor and Perennial. Seeds of Maor were obtained from Dr. C. Shifriss, The Volcani Center, Israel, and those of Perennial were obtained from Dr. A. Palloix, INRA, France. Two hundred and thirty F_2 plants originating from a single (Maor×Perennial) F_1 were grown in the greenhouse in 1995 and self-pollinated to obtain F_3 seeds. A subset of 180 randomly chosen F_2 plants and their F_3 progenies were used for QTL analysis.

Trait evaluation

The two parents, their F_1 and 180 F_3 families were grown in the field in Qiryat Gat, Israel, during the summers of 1996, 1997 and 1998. Individual plants were spaced 30 cm apart in rows spaced 100 cm apart. The experiments were arranged in a randomized complete block design with four replications. Each replication consisted of 5 plants from each F_3 family, the parents and F_1. The populations were planted in April of each year, and three fruits from each plant were harvested 90 days after planting. All traits were measured in both 1996 and 1997. The third planting, in 1998, was used to measure fruit color and firmness. All measurements were taken on individual plants and averaged within each F_3 family.

The following traits were evaluated for each plant: (1) ripening date – the number of days from sowing to the first ripened fruit; records were taken every 3 days for 4 weeks starting 70 days after planting; (2) plant height – the distance (in centimeters) from the base of the plant to its top, taken 45 days after planting; (3) fresh fruit weight (in grams); (4) total soluble solids concentration – expressed as Brix and measured with a refractometer on a drop of fresh juice extracted with a garlic crusher; (5) fruit length – the distance (in millimeters) from the pedicel attachment to its apex; (6) fruit diameter – measured at the maximum width (in millimeters); (7) fruit shape – the ratio of fruit length to fruit diameter; (8) pedicel length – the distance (in millimeters) between the points of the attachment to the stem and to the fruit; (9); pedicel diameter – measured at the maximum width (in millimeters); (10) pericarp thickness – measured at its maximum width (in millimeters); (11) seed weight – weight (in grams) of a bulk of 30 F_3 seeds; (12) fruit firmness – measured by hand squeezing and giving a numerical rating of 1 (firm) to 3 (soft); (13); degree of green (pre-mature) fruit color – measured by a Minolta chromameter (model CR-200), quantifying L (lightness), C (chroma) and H (hue) parameters: (14) degree of red (mature) fruit color – measured by a Minolta chromameter as described above. All plants were also measured for two qualitative traits, presence of pungency and erect fruits. Pungency was sampled by tasting randomly sampled fruit from F_3 plants and families were subsequently sorted into three categories: non-pungent, pungent and segregating. All fruit and pedicel dimensions were measured with a digital caliper. Narrow-sense heritability was estimated as described by Ben Chaim and Paran (2000). Correlations between traits were estimated by the QGENE program, v. 2.3 (Nelson 1997).

Marker analysis and map construction

Tomato and pepper cDNA and genomic clones were chosen for RFLP analysis to allow complete genome coverage based on the map of Livingstone et al. (1999). The clones were radiolabelled and used to probe survey filters containing DNA of the two parents digested with 12 restriction enzymes as described by Livingstone et al. (1999). Mapping filters were prepared using DNA from F_2 or bulked F_3 DNA (from a minimum of 30 plants) extracted according to Prince et al. (1997).

Decamers for random amplified polymorphic DNA (RAPD) analysis were purchased from Operon Technologies, and amplification reactions were performed following the procedure of Paran et al. (1998). AFLP markers were generated as described by Vos et al. (1995). Both *Eco*RI (E)/*Mse*I (M) and *Pst*I(P)/*Mse*I primer combinations were used. The selective nucleotides for the AFLP primers used in this study were: E32-AAC, E33-AAG, E35-ACA, E38-ACT, E41-AGG, E48-CAC, E49-CAG, P11-AA, P13-AG, P14-AT, M47-CAA, M48-CAC, M49-CAG, M50-CAT, M51-CCA, M54-CCT, M59-CTA, M60-CTC, M61-CTG, M62-CTT. AFLP markers were scored as codominant markers by the proprietary AFLP Image Analysis Software developed by Keygene N.V. (Wageningen, the Netherlands).

Mapping was performed using the MAPMAKER/EXP v 2.0 program (Lander et al. 1987). Markers were grouped at LOD 4.0 and a maximum recombination fraction of 30 cM. A framework of markers was generated at a LOD score of 3.0, and additional markers were added at LOD score of 2.0. Map distances were calculated using the Kosambi function.

QTL mapping was performed by interval analysis using a LOD score of 3.0 as a minimum significance level for QTL detection. Estimates of percentage phenotypic variation explained by individual QTL (R^2), additive (a) and dominance (d) effects were determined by single-marker analysis for markers with the highest *F* value within a given QTL region. Dominance estimates were multiplied by two to account for the twofold reduction in heterozygosity in the F_3 generation. Multiple regression was used to determine the proportion of the total phenotypic variance explained by all QTL affecting a given trait. Individual QTL with non-significant ($P>0.05$) coefficients in the multiple regression model were dropped and are not reported in the Results section. All marker analyses were performed using QGENE v.2.3 (Nelson 1997). Two-way ANOVA procedures were performed using the command PROC GLM of SAS statistical software (SAS Institute 1989), and were used to detect digenic interactions between all codominant markers. Significant interactions in both years ($P<0.001$ in 1 year and $P<0.002$ in the 2nd year) were furthered partitioned to four types: additive x additive (AA), additive x dominance (AD), dominance x additive (DA) and dominance x dominance (DD) using JMP v.3.0 statistical software for Macintosh as described by Yu et al. (1997). Only those interactions for which a minimum of 5 individuals were found in each of the nine marker classes were included in the analysis.

Results

Linkage map construction

Seventy-two RFLP, 5 RAPD and 352 amplified fragment length polymorphism (AFLP) markers were used to construct the genetic map. A subset of 108 AFLP markers that evenly cover all 12 linkage groups (LGs) were selected for QTL analysis and are shown on Fig. 1. In addition to the molecular markers, the *C* and *u p* genes that control pungency and erect fruit type, respectively, were placed on the map. The map contains a total of 177 markers distributed across 12 linkage groups with a total length of 1740 cM. Ten markers remained unlinked. The order of the RFLP markers was in good agreement with the map of Livingstone et al. (1999). RFLP markers common to both maps allowed linkage group numbers to be assigned to the intra-specific map. One discrepancy in linkage order between the two maps was identified; CD74 in linkage group 5 (LG5) was mapped to LG7 by Livingstone et al. (1999). The position of CD74 in the current map is in agreement with its position in chromosome 5 of tomato (Tanksley et al. 1992).

Linkage group 1 in Livingstone et al. (1999) represented two pepper chromosomes because of a chromosome interchange between the parents of the mapping population (*C. annuum* and *C. chinense*) and was split into the expected linkage groups in the present map (LG1 and LG8). LG8 in the present study included the RFLP marker TG176 that was assigned to the unlinked group A in the map of Livingstone et al. (1999). For some linkage groups (e.g. LG2, LG3, LG4, LG5 and LG7), the most distal markers in the map of Livingstone et a l. (1999) were not included in the present map due to a lack of polymorphism. For all linkage groups except LG7, the unrepresented portions of the map did not exceed 20 cM and, therefore, QTL detection in these uncovered parts of the genome should not be affected significantly.

Markers in two genomic regions exhibited significant ($P<0.01$) segregation distortion (deviation from the expected 1:2:1 segregation for codominant markers or 3:1 for dominant markers). The most severe distortion ($P<0.00001$) occurred in the middle of linkage group 1 between TG83L and P14/M47–222 where markers were skewed in favor of Perennial alleles. The second distorted region occurred in linkage group 3 between the markers OH2 and E41/M49–89, where markers were skewed in favor of Maor alleles. Both genomic regions were also distorted in the *C. annuum*×*C. chinense* map constructed by Livingstone et al. (1999).

Phenotypic variation and trait correlations

Mean phenotypic values, standard errors and narrow-sense heritability estimates for the quantitative traits are presented in Table 1. Correlations between all traits are presented in Table 2. Data for 6 traits, fruit weight, fruit length, fruit diameter, fruit shape, pedicel length and pericarp thickness, were log-transformed because of a lack of variance homogeneity. The fruits of Maor ripened earlier, were softer, heavier and larger (both in length and diameter) and had lower soluble solids contents and thicker pericarps than those of Perennial. Perennial plants were taller than Maor plants, and although the pedicels were of similar length in the two genotypes, those of Maor were wider than those of Perennial. Perennial fruits are thin and tapered, with a large length to width ratio, whereas Maor fruits are blocky bell-type fruits that produce heavier (larger) seeds. Perennial fruits had greater green and red chroma values, but no difference or only a very small difference was observed between the parents for the red lightness and red hue values of fruits.

A more detailed biometrical analysis of most of the quantitative traits is presented elsewhere (Ben Chaim and Paran 2000); therefore, only significant points related to traits that were not analyzed in the earlier study will be highlighted. Heritability was moderate for firmness, red chroma, red hue and red lightness (0.46, 0.58, 0.45, and 0.55, respectively) and was high for green chroma (0.86). The green and red chroma values were moderately positively correlated ($r=0.42$). While estimates for red chroma and lightness were highly correlated ($r=0.81$), red chroma and red hue values were only moderately correlated ($r=0.42$). Seed weight was positively correlated with fruit weight ($r=0.42$). The three green chromameter measurements (chroma, hue and lightness) were highly correlated ($r=0.9$), therefore, only the chroma measurement is presented.

QTL identification

A total of 55 QTL were identified in this study, ranging from 2 to 6 QTL per trait (Fig. 1 and Table 3). Due to significant genotype×year interaction, the data for each year were analyzed separately. QTL were named such that the first two letters indicate the trait affected, the following two digits represent the linkage group on which the QTL was identified and the chronological order in which the QTL were identified.

Ripening date

A QTL located on LG3 (*rd3.1*) had the largest effect in both years, explaining 21% and 14% of the total phenotypic variation for this trait in 1996 and 1997, respectively. In both years, the Maor allele at *rd3.1* was associated with earlier ripening. Two additional QTL were identified on LG8 (*rd8.1*, *rd8.2*) in 1996 only, and *rd2.1* and *rd7.1* were identified in 1997. The genomic region containing *rd7.1* was also detected in 1996, but its significance level was slightly below the threshold (LOD 2.8). Maor alleles at *rd8.1* and *rd8.2* contributed to earlier ripening, and alleles from Perennial at *rd2.1* and *rd7.1* con-

Table 1 Means, standard errors (SE) and heritabilities of quantitative traits in the parental, F_1 and F_3 generations

Trait	Year	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Heritability
		Maor		Perennial		F_1		F_3		
Ripening date (days)	1996	136.0	0.8	143.0	1.4	127.0	0.0	135.0	0.1	0.40
	1997	133.0	0.6	146.0	0.9	128.0	0.5	136.0	0.1	0.27
Plant height (cm)	1996	32.5	1.1	43.4	1.0	64.1	1.4	48.5	0.1	0.60
	1997	29.2	0.6	38.0	1.1	55.9	0.9	42.6	0.2	0.43
Fruit weight (g)	1996	155.6	8.1	0.7	0.2	9.1	0.6	11.4	0.3	1.00
	1997	130.0	3.1	1.6	0.1	10.2	0.3	11.4	0.2	0.79
Fruit diameter (mm)	1996	77.1	1.6	6.8	0.1	17.7	0.2	20.5	0.1	0.95
	1997	77.1	1.5	6.8	0.1	17.0	0.2	21.0	0.2	0.92
Fruit length (mm)	1996	77.0	1.8	32.0	0.1	67.0	0.8	61.0	0.2	0.76
	1997	73.0	1.3	31.0	0.5	65.0	0.9	59.0	0.4	0.68
Fruit shape	1996	1.0	–	4.7	–	3.7	–	3.2	0.1	1.00
	1997	0.95	–	4.5	–	4.1	–	3.0	0.03	0.87
Pericarp thickness (mm)	1996	4.8	0.1	0.8	0.02	1.9	0.03	2.1	0.01	0.78
	1997	4.7	0.04	0.9	0.02	2.1	0.02	2.2	0.04	0.70
Soluble solids concent. (%)	1996	8.1	0.5	10.9	0.3	10.1	0.2	9.8	0.03	0.54
	1997	7.8	0.3	11.3	0.4	10.0	0.3	9.6	0.04	0.24
Pedicel diameter (mm)	1996	9.0	0.4	1.2	0.0	2.7	0.1	2.5	0.01	0.66
	1997	9.4	0.2	1.3	0.0	3.0	0.01	3.0	0.02	0.63
Pedicel length (mm)	1996	30.0	0.9	26.0	0.4	30.0	0.5	32.0	0.1	0.50
	1997	27.0	0.6	27.0	0.5	36.0	0.5	35.0	0.2	0.68
Seed weight (g)		0.23	0.006	0.1	0.0009	0.13	0.007	0.17	0.001	–
Firmness	1998	1.7	0.06	1.0	0.0	1.9	0.07	1.7	0.01	0.46
Green color (chroma)	1998	26.1	0.5	42.0	0.6	44.5	0.2	41.4	0.1	0.86
Red color (chroma)	1998	30.2	0.4	44.0	0.8	41.1	0.3	42.2	0.07	0.58
Red color (hue)	1998	25.8	0.2	27.4	0.6	22.1	0.2	23.6	0.03	0.45
Red color (lightness)	1998	32.0	0.3	32.9	0.5	32.9	0.1	35.4	0.04	0.55

tributed to earlier ripening. Multiple regression revealed that all QTL detected for each year explained 29% and 27% of the total phenotypic variance in 1996 and 1997, respectively.

Plant height

The 3 QTL detected in 1997 were also detected in 1996, however, 2 additional QTL were identified in 1996. *ph3.1* had the largest effect, with an R^2 value of 0.15 in 1996 and 0.12 in 1997. For all QTL, the alleles originating from the taller parent, Perennial, were associated with increased height. Taken together, the 5 QTL in 1996 and the 3 QTL identified in 1997 accounted for 39% and 29% of the total phenotypic variation in 1996 and 1997, respectively.

Fruit weight

The same 5 QTL were detected in 1996 and 1997. *fw3.2* had the largest effect in both years (R^2=0.15 and 0.12 in 1996 and 1997, respectively). For all QTL, the alleles from the large-fruited parent, Maor, increased fruit weight. All QTL identified accounted for 35% and 38% of the total phenotypic variation in fruit weight in 1996 and 1997, respectively.

Fruit diameter

The same 4 QTL were detected in both years. *fd3.1* had the largest effect on fruit diameter in both years (R^2=0.42 and 0.37 in 1996 and 1997, respectively). For all QTL, the Maor allele was associated with increased fruit diam-

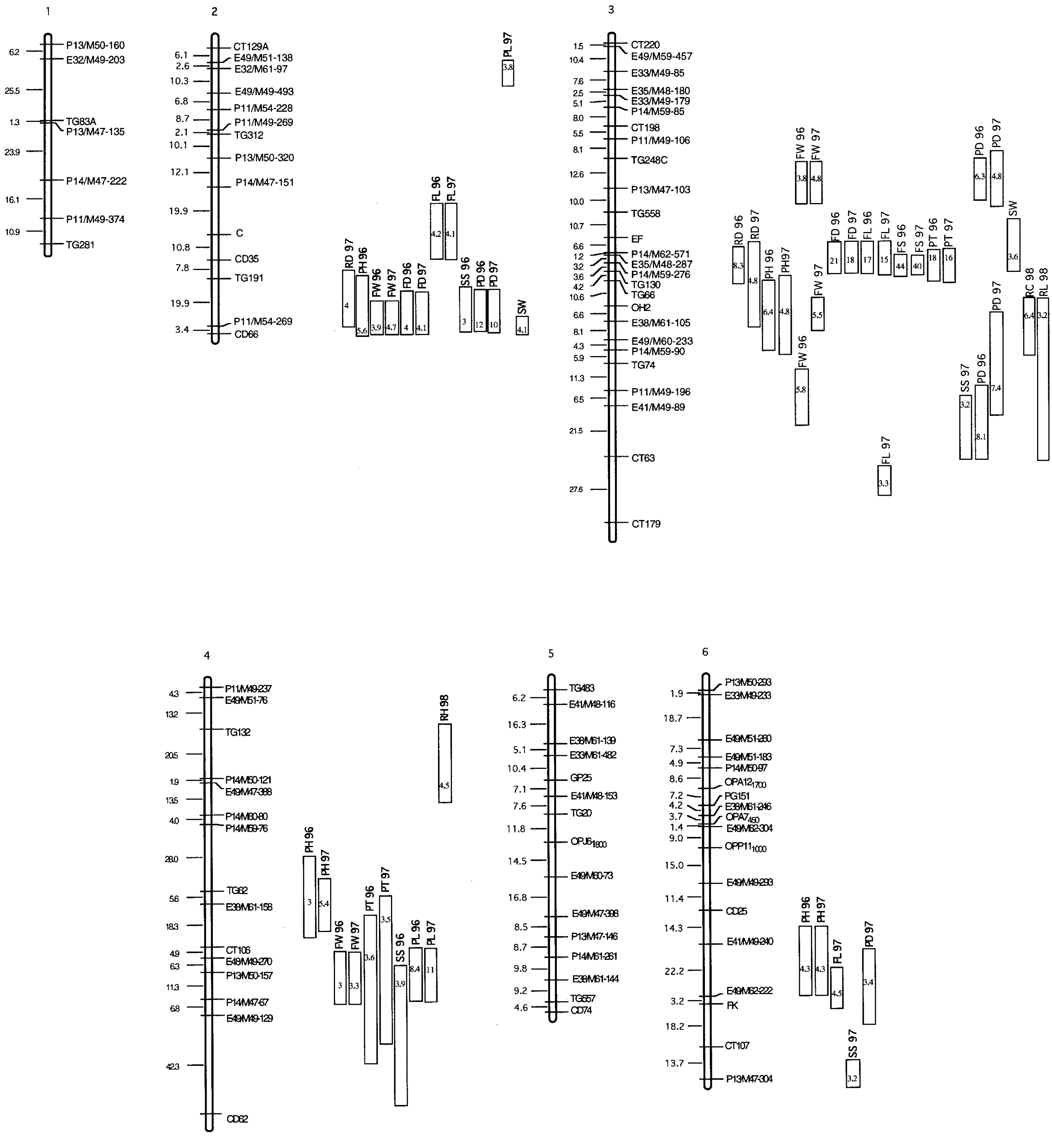

Fig. 1 QTL mapping in *C. annuum*. Marker types are tomato RFLP clones (*TG, CT* and *CD*), pepper RFLP clones (*PG*), and potato RFLP clones (*GP*). AFLP markers are presented as the primer combination followed by the size of the mapped fragment. RAPD markers are presented as *OP* followed by the primer name and band size. Morphological markers are *C* (pungency) and *u p* (erect fruit type). *EF* and *B2* are pepper RFLPs obtained from Dr. U. Bonas (Martin Luther University, Germany). *pN18C* is a tobacco gene provided by B. Baker (USDA, Albany, Calif.). *OH2* is a tomato beta-carotene hydroxylase cDNA obtained from Dr. J. Hirschberg, the Hebrew University of Jerusalem. *FK* is potato fructokinase cDNA obtained from Dr. D. Granot, The Volcani Institute, Israel. Distances in centiMorgans are to the *left* of each linkage group. QTL are presented as *bars* to the *right* of the linkage group with the *number* in each *bar* being the LOD peak value and the *length* of the *bar* representing a 1-LOD support interval from the peak LOD of the QTL. Trait abbreviations are: ripening date (*RD*), plant height (*PH*), fruit weight (*FW*), fruit diameter (*FD*), fruit length (*FL*), fruit shape (*FS*), pericarp thickness (*PT*), soluble solids concentration (*SS*), pedicel diameter (*PD*), pedicel length (*PL*), seed weight (*SW*), firmness (*FI*), green chroma (*GR*), red hue (*RH*), red chroma (*RC*) and red lightness (*RL*). The year of detection is appended

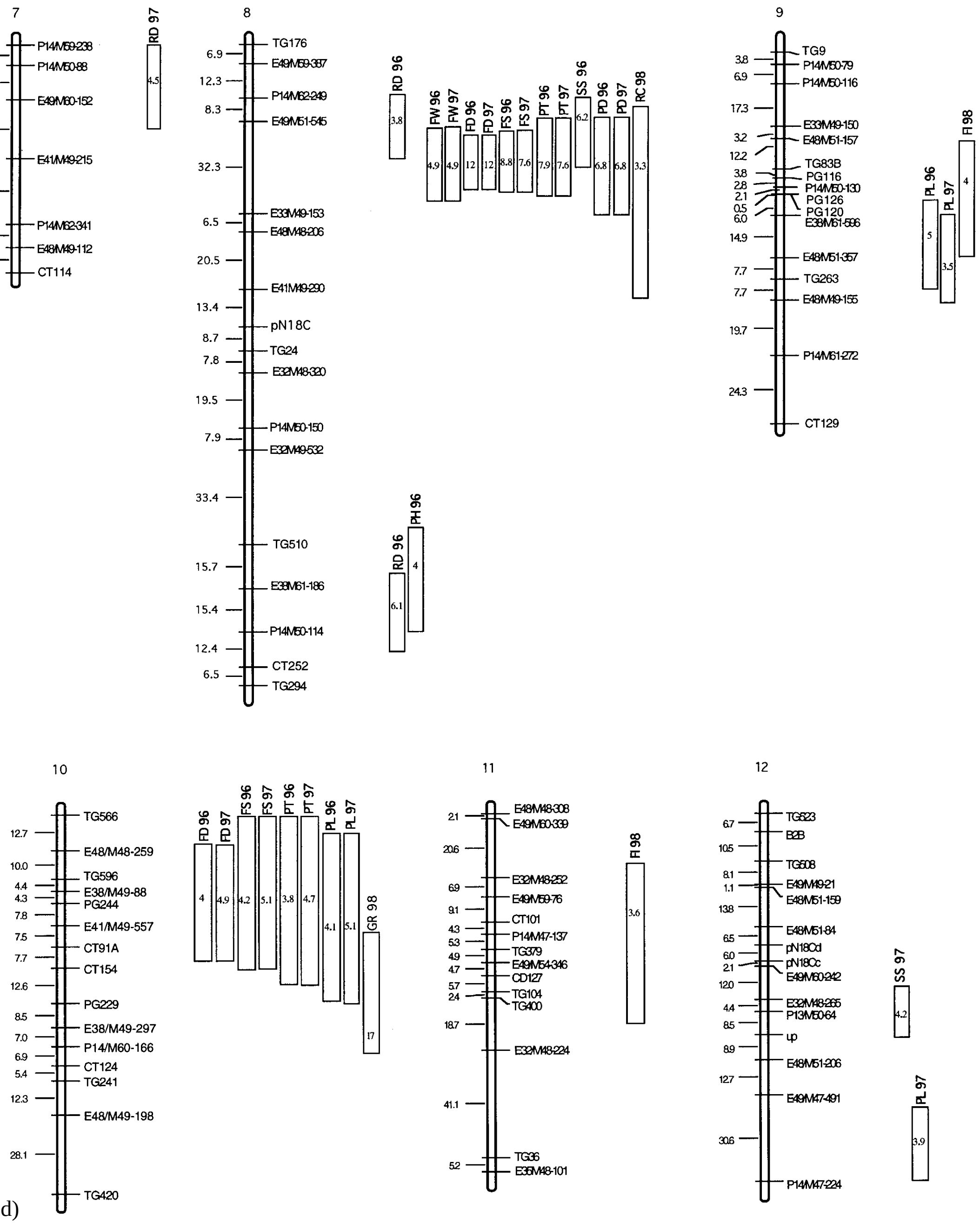

Fig. 1 (continued)

eter. All 4 QTL explained 61% and 58% of the total phenotypic variation in 1996 and 1997, respectively.

Fruit length

The 2 QTL detected in 1996, *fl2.1* and *fl3.1*, were also detected in 1997. Two additional QTL detected in 1997, *fl3.2* and *fl6.1*, had an effect on fruit length in both years, but their significance levels were slightly below the threshold in 1996 (LOD 2.9 for both markers). *fl3.1* had the largest effect in both years (R^2=0.34 and 0.32 in 1996 and 1997, respectively). Both parents contributed alleles for increased fruit length; the Perennial allele at *fl3.1* and the Maor alleles at all other loci were associated with increased fruit length. All QTL identified in 1996 and 1997 explained 45% and 52% of the total phenotypic variability, respectively.

Fruit shape

The same 3 QTL were detected in both years. At all loci, alleles from Perennial were associated with an elongated fruit shape. *fs3.1* had a very large effect on this trait, explaining 67% and 63% of the total phenotypic variation in 1996 and 1997, respectively. The 1996 phenotypic means of the plants homozygous for Perennial alleles,

Table 2 Pearson correlation coefficients (r^a) between traits within years and between years for the same trait measured in the F_3 progeny

Trait	rd	ss	pt	fl	fd	pl	pd	he	sw	fw	gc	rc	rh	rl	fi	fs
Ripening date (rd) 97	0.62															
Soluble solids (ss) 96	–0.07															
Soluble solids 97	–0.03	0.53														
Pericarp thickness (pt) 96	0.23	–0.14														
Pericarp thickness 97	0.13	–0.34	0.89													
Fruit length (fl) 96	–0.27	–0.07	–0.15													
Fruit length 97	–0.33	–0.07	–0.03	0.94												
Fruit diameter (fd) 96	0.31	–0.02	0.87	–0.13												
Fruit diameter 97	0.12	–0.23	0.86	–0.07	0.95											
Pedicel length (pl) 96	0.17	0.09	0.17	0.29	0.10											
Pedicel length 97	0.03	0.01	0.16	0.29	0.10	0.84										
Pedicel diameter (pd) 96	0.14	–0.08	0.75	0.25	0.79	0.10										
Pedicel diameter 97	0.02	–0.29	0.76	0.27	0.80	0.07	0.87									
Height (he) 96	–0.49	0.06	–0.40	–0.04	–0.46	–0.16	–0.46									
Height 97	–0.48	0.23	–0.38	–0.04	–0.37	–0.23	–0.43	0.76								
Seed weight (sw)	0.07	–0.05	0.33	–0.03	0.29	–0.05	0.32	–0.24								
Fruit weight (fw) 96	0.16	–0.06	0.62	0.25	0.65	0.31	–0.68	–0.33	0.42							
Fruit weight 97	0.05	–0.21	0.62	0.26	0.64	0.23	0.60	–0.35	0.42	0.90						
Green C[b] (gc)	0.01	–0.05	–0.16	0.04	–0.18	0.08	–0.10	–0.05	–0.03	–0.21						
Red C (rc)	–0.05	0.16	–0.35	0.06	–0.34	–0.10	–0.27	0.15	–0.16	–0.46	0.42					
Red H[c] (rh)	0.10	0.01	–0.06	0.19	0.05	0.02	0.04	–0.08	–0.20	0.09	0.16	0.42				
Red L[d] (rl)	–0.11	0.12	–0.19	0.04	–0.14	–0.07	–0.11	0.13	–0.06	–0.22	0.38	0.81	0.43			
Firmness (fi)	0.06	0.09	–0.06	0.16	0.15	0.02	0.13	–0.02	0.11	0.28	–0.10	–0.07	0.13	0.00		
Fruit shape 96[e] (fs)	–0.35	0.00	–0.72	0.66	–0.81	0.07	–0.44	0.32	–0.22	–0.32	0.12	0.27	0.06	0.11	–0.01	
Fruit shape 97	–0.27	0.14	–0.66	0.64	–0.79	0.07	–0.43	0.25	–0.20	–0.32	0.16	0.27	0.08	0.12	–0.04	0.96

[a] r Values of 0.18 were significant at $P=0.01$; r values of 0.25 were significant at $P=0.001$

[b] Chroma

[c] Hue

[d] Lightness

[e] Ratio of fruit length to fruit diameter

Table 3 List of QTL detected in the F_3 progeny

Trait	QTL	Marker	LG	Direction[a]	*F*	Variation explained		*P* value	Effect[b]		
						Locus	Trait		Additive	Dominance	D/A
Ripening date 96	*rd3.1*	P14/M62–571	3	Maor	22.0	0.21		0	0.6	–0.3	–0.5
	rd8.1	E49/M51–545	8	Maor	9.8	0.10		0.0001	0.42	–0.1	–0.2
	rd8.2	P14/M50–114	8	Maor	14.0	0.14	0.29	0	0.48	–0.52	–1.1
Ripening date 97	*rd2.1*	*C*	2	Perennial	15.7	0.08		0.0001	–0.42	0	0.0
	rd3.1	OH2	3	Maor	12.1	0.14		0	0.34	–0.52	–1.5
	rd7.1	P14/M50–88	7	Perennial	9.8	0.10	0.27	0.0001	–0.4	–0.16	0.4
Plant height 96	*ph2.1*	CD66	2	Perennial	13.4	0.13		0	–2.48	–2.96	1.2
	ph3.1	E38/M61–105	3	Perennial	13.8	0.15		0	–2.85	–0.42	0.1
	ph4.1	E38/M61–158	4	Perennial	6.9	0.08		0.001	–2	–0.38	0.2
	ph6.1	E41/M49–240	6	Perennial	7.7	0.09		0.0007	–2.19	0.7	–0.3
	ph8.1	E38/M61–186	8	Perennial	9.9	0.11	0.39	0.0001	–2.55	2.12	–0.8
Plant height 97	*ph3.1*	E38/M61–105	3	Perennial	11.1	0.12		0	–2.63	0.82	–0.3
	ph4.1	E38/M61–158	4	Perennial	11.8	0.13		0	–2.61	0.1	0.0
	ph6.1	E49/M62–222	6	Perennial	8.2	0.09	0.29	0.0004	–2.07	2.3	–1.1
Fruit weight 96	*fw2.1*	P11/M54–269	2	Maor	9.6	0.10		0.0001	0.08	0	0.0
	fw3.1	P13/M47–103	3	Maor	8.7	0.09		0.0002	0.07	0	0.0
	fw3.2	E41/M49–89	3	Maor	14.4	0.15		0	0.1	0	0.0
	fw4.1	P14/M47–67	4	Maor	6.0	0.06		0.003	0.06	–0.04	–0.7
	fw8.1	E33/M49–153	8	Maor	9.6	0.10	0.35	0.0001	0.07	0.08	1.1
Fruit weight 97	*fw2.1*	P11/M54–269	2	Maor	11.6	0.12		0	0.08	0.04	0.5
	fw3.1	P13/M47–103	3	Maor	11.3	0.11		0	0.08	0.04	0.5
	fw3.2	E38/M61–105	3	Maor	11.4	0.12		0	0.08	–0.02	–0.3
	fw4.1	P14/M47–67	4	Maor	6.7	0.07		0.001	0.06	–0.02	–0.3
	fw8.1	E33/M49–153	8	Maor	8.3	0.09	0.38	0.0004	0.07	0.02	0.3
Fruit diameter 96	*fd2.1*	P11/M54–269	2	Maor	9.6	0.10		0.0001	0.05	0.02	0.4
	fd3.1	P14/M59–276	3	Maor	63.1	0.42		0	0.1	0.02	0.2
	fd8.1	E49/M51–545	8	Maor	26.1	0.24		0	0.07	–0.04	–0.6
	fd10.1	E38/M49–88	10	Maor	8.8	0.09	0.61	0.0002	0.04	0	0.0
Fruit diameter 97	*fd2.1*	P11/M54–269	2	Maor	9.7	0.10		0.0001	0.04	0.04	1.0
	fd3.1	P14/M59–276	3	Maor	50.7	0.37		0	0.09	0.02	0.2
	fd8.1	E49/M51–545	8	Maor	26.7	0.24		0	0.07	–0.04	–0.6
	fd10.1	E38/M49–88	10	Maor	10.5	0.11	0.58	0	0.05	–0.02	–0.4
Fruit length 96	*fl2.1*	*C*	2	Maor	12.6	0.07		0.0005	0.04	0	0.0
	fl3.1	P14/M59–276	3	Perennial	44.3	0.34	0.45	0	–0.07	0	0.0
Fruit length 97	*fl2.1*	*C*	2	Maor	15.4	0.08		0.0001	0.04	0	0.0
	fl3.1	P14/M59–276	3	Perennial	39.8	0.32		0	–0.06	0	0.0
	fl3.2	CT179	3	Maor	6.5	0.08		0.002	0.03	0	0.0
	fl6.1	E49/M62–222	6	Maor	11.5	0.11	0.52	0	0.03	0.04	1.3
Fruit shape 96	*fs3.1*	P14/M59–276	3	Perennial	172.3	0.67		0	–1.28	–0.5	0.4
	fs8.1	E49/M51–545	8	Perennial	19.2	0.19		0	–0.67	0.14	–0.2
	fs10.1	E38/M49–88	10	Perennial	8.0	0.09	0.75	0.0005	–0.44	0.52	–1.2
Fruit shape 97	*fs3.1*	P14/M59–276	3	Perennial	147.5	0.63		0	–1.05	–0.38	0.4
	fs8.1	E49/M51–545	8	Perennial	18.6	0.18		0	–0.55	0.26	–0.5
	fs10.1	E38/M49–88	10	Perennial	10.3	0.11	0.73	0.0001	–0.42	0.42	–1.0
Pericarp thickness 96	*pt3.1*	P14/M59–276	3	Maor	52.4	0.37		0	0.06	0	0.0
	pt4.1	E49/M49–129	4	Maor	7.5	0.08		0.0008	0.02	0	0.0
	pt8.1	E49/M51–545	8	Maor	17.3	0.17		0	0.04	0	0.0
	pt10.1	E38/M49–88	10	Maor	8.5	0.09	0.53	0.0003	0.02	0	0.0
Pericarp thickness 97	*pt3.1*	P14/M59–276	3	Maor	44.7	0.34		0	0.05	0	0.0
	pt4.1	E49/M49–129	4	Maor	8.1	0.08		0.0004	0.13	–0.2	–1.5
	pt8.1	E49/M51–545	8	Maor	18.0	0.18		0	0.03	–0.02	–0.7
	pt10.1	E38/M49–88	10	Maor	10.8	0.11	0.52	0	0.03	0	0.0
Soluble solids concentration 96	*ss2.1*	P11/M54–269	2	Maor	6.7	0.07		0.001	0.25	0.32	1.3
	ss4.1	P14/M47–67	4	Maor	9.1	0.09		0.0002	0.3	0	0.0
	ss8.1	E49/M51–545	8	Perennial	11.9	0.12	0.27	0	–0.35	–0.14	0.4
Soluble solids concentration 97	*ss3.1*	P11/M49–196	3	Perennial	5.4	0.06		0.005	–0.33	–0.24	0.7
	ss6.1	P13/M47–304	6	Perennial	8.0	0.08		0.0005	–0.37	0.12	–0.3
	ss12.1	P13/M50–64	12	Perennial	8.7	0.09	0.14	0.0003	–0.3	–0.84	2.8

Table 3 (continued)

Trait	QTL	Marker	LG	Direction[a]	F	Variation explained		P value	Effect[b]		
						Locus	Trait		Additive	Dominance	D/A
Pedicel diameter 96	*pd2.1*	P11/M54–269	2	Maor	31.8	0.27		0	0.4	0.02	0.1
	pd3.1	P13/M47–103	3	Maor	15.4	0.15		0	0.27	0.14	0.5
	pd3.2	E41/M49–89	3	Maor	21.3	0.21		0	0.33	–0.1	–0.3
	pd8.1	E49/M51–545	8	Maor	14.2	0.14	0.53	0	0.27	–0.18	–0.7
Pedicel diameter 97	*pd2.1*	P11/M54–269	2	Maor	25.4	0.22		0	0.36	0.12	0.3
	pd3.1	P13/M47–103	3	Maor	11.5	0.12		0	0.24	0.18	0.8
	pd3.2	E49/M60–233	3	Maor	16.4	0.16		0	0.35	0.06	0.2
	pd6.1	E49/M62–222	6	Maor	7.3	0.08		0.0009	0.19	–0.24	–1.3
	pd8.1	E49/M51–545	8	Maor	14.7	0.15	0.54	0	0.28	–0.22	–0.8
Pedicel length 96	*pl4.1*	P13/M50–157	4	Maor	18.1	0.18		0	0.03	–0.02	–0.7
	pl9.1	PG116	9	Perennial	16.0	0.10		0.0001	–0.03	0	0.0
	pl10.1	E48/M48–259	10	Perennial	9.3	0.10	0.31	0.0002	–0.02	0	0.0
Pedicel length 97	*pl2.1*	E32/M61–97	2	Perennial	8.8	0.09		0.0002	–0.02	0.02	–1.0
	pl4.1	P13/M50–157	4	Maor	24.7	0.22		0	0.04	–0.02	–0.5
	pl9.1	E48/M51–357	9	Perennial	9.1	0.10		0.0002	–0.02	0.02	–1.0
	pl10.1	E48/M48–259	10	Perennial	11.8	0.12		0	–0.02	0	0.0
	pl12.1	P14/M47–224	12	Maor	6.8	0.07	0.43	0.001	0.01	0.04	4.0
Seed weight	*sw2.1*	CD66	2	Maor	9.7	0.10		0.0001	0	0	0.0
	sw3.1	P14/M59–276	3	Maor	13.3	0.13	0.21	0	0.01	0	0.0
Firmness 98	*fi9.1*	TG83B	9	Perennial	10.1	0.12		0.0001	–0.2	0.08	–0.4
	fi11.1	E49/M59–76	11	Perennial	8.9	0.10	0.14	0.0002	–0.17	0.1	–0.6
Green chroma 98	*gr10.1*	P14/M60–166	10	Perennial	41.2	0.33		0	–3.43	2.04	–0.6
Red hue 98	*rh4.1*	E49/M47–388	4	Perennial	11.7	0.12		0	–0.62	–0.28	0.5
Red chroma 98	*rc3.1*	P14/M59–90	3	Perennial	13.0	0.13		0	–1.38	1.1	–0.8
	rc8.1	E48/M48–206	8	Perennial	6.8	0.07	0.16	0.001	–1.04	–1.04	1.0
Red lightness 98	*rl3.1*	TG74	3	Perennial	11.4	0.16		0	–0.67	1.24	–1.9

[a] Indicates the parent which contibutes to the increase in the numeric value of the trait

[b] A positive sign of the additive effect indicates that the allele originated from Maor increases the numeric value of the trait; a negative sign of the additive effect indicates that the allele originated from Maor decreases the numeric value of the trait

heterozygous, and homozygous for Maor alleles at *fs3.1* were 4.65±0.1, 3.1±0.08, and 2.09±0.07, respectively, with an additive effect of –1.28 and a dominance deviation of –0.5. The combined R^2 for all QTL was 0.75 and 0.73 in 1996 and 1997, respectively.

Pericarp thickness

The same 4 QTL were detected in both years. For all QTL, alleles from Maor were associated with greater pericarp thickness. *pt3.1* had the largest effect in both years (R^2=0.38 and 0.34 in 1996 and 1997, respectively). The 4 QTL identified in 1996 and 1997 explained, 56% and 52% of the total phenotypic variation, respectively.

Soluble solids concentration

Three QTL were identified in each year, however, none were significantly associated with soluble solids concentration in both years. For 1 QTL in 1996 (*ss8.1*) and 2 QTL in 1997 (*ss6.1* and *ss12.1*), effects slightly below the threshold were detected in the other year (LOD scores of 2.9, 2.9 and 2.8 for *ss8.1*, *ss6.1* and *ss12.1*, respectively). For 2 of the QTL detected in 1996 (*ss2.1* and *ss4.1*), alleles originating from the parent with low soluble solids content (Maor), were associated with greater soluble solids concentration. At all other loci, Perennial alleles were associated with greater soluble solids concentration. The QTL with the largest effect was *ss8.1* (R^2=0.12), while the combined R^2 for all QTL was only 0.27 and 0.14 in 1996 and 1997, respectively.

Pedicel diameter

Four QTL were detected in both years, and an additional QTL (*pd6.1*) was detected in 1996 only. For all QTL, the alleles originating from Maor were associated with increased pedicel diameter. *pd2.1* had the greatest effect in both years, explaining 27% and 22% of the total phenotypic variance observed in 1996 and 1997, respectively. The combined R^2 for all QTL was 0.53 and 0.54 in 1996 and 1997, respectively.

Table 4 Two-locus interactions detected in the F_3 progeny

Trait	Marker 1	LG	Marker 2	LG	Type[a]	1996		1997	
						P[b]	R^2[c]	*P*	R^2
Plant height	P14/M59–85	3	E49/M54–346	11	AA	0.0007	0.2	0.0003	0.22
	CD66[d]	2	TG510	8	AA	0.001	0.24	0.003	0.18
Fruit weight	P14/M59–238	7	E33/M49–85	3	AD	0.0003	0.12	0.0001	0.15
Fruit diameter	E49/M51–260	6	TG510	8	DD	0.01	0.19	0.002	0.22
Fruit length	P14/M50–121	4	E49/M49–121	12	DD	0.001	0.16	0.0002	0.22
	E38/M61–144	5	E48/M48–308	11	AD	0.0002	0.14	0.0002	0.17
	P13/M47–146	5	P14/M50–88	7	DD	0.0002	0.13	0.0002	0.16
	E38/M61–139	5	TG379	11	AA	0.001	0.19	0.002	0.17
Fruit shape	P13/M47–146	5	CT198	3	AD	0.0004	0.31	0.0005	0.3
Pericarp thickness	E49/M51–260	6	TG510	8	DD	0.01	0.13	0.001	0.2
	E32/M61–97	2	E32/M48–265	12	DD	0.0001	0.23	0.001	0.22
					DA	0.0005		0.001	
Pedicel length	P14/M61–272	9	P14/M62–341	7	DD	0.0001	0.26	0.0001	0.25
	E38/M61–105	3	E38/M61–186	8	DA	0.0001	0.24	0.0001	0.24

[a] Interaction types: AA, additive×additive, AD, additive×dominance; DA, dominance×additive; DD, dominance×dominance

[b] Probability for the interaction type derived from parameter estimates in the Fit Model function in JMP

[c] Variance explained by the interaction

[d] Marker had a main QTL effect

Pedicel length

Three QTL (*pl4.1*, *pl9.1* and *pl10.1*) were detected in both years. Two additional QTL were detected in 1997; for both of these loci, an effect slightly below the threshold was also detected in 1996 (LODs 2.7 and 2.9 for *pl2.1* and *pl12.1*, respectively). Although both parents had similar pedicel lengths (Table 1), transgressive segregation was observed in the F_3 generation. Alleles from both parents were found to increase pedicel length. *pl4.1* had the largest effect in both years (R^2=0.18 and 0.22 in 1996 and 1997, respectively). The combined R^2 for all QTL was 0.31 and 0.43 in 1996 and 1997, respectively.

Seed weight

Two QTL were detected with a combined R^2 of 0.21. The QTL with the largest effect was *sw3.1* (R^2=0.13). For both QTL, alleles from the large seeded parent, Maor, were associated with increased seed weight.

Firmess

Two QTL, *fi9.1* and *fi11.1*, were detected. Together, they explained only 14% of the total phenotypic variation. The QTL with the largest effect was *fi9.1* (R^2=0.12). For both QTL, alleles from Perennial were associated with increased firmness.

Green color

A single QTL that explained 33% of the phenotypic variation for this trait was detected on LG10. For this QTL, the Perennial allele was associated with increased color intensity. Several loci that control green color intensity may be present on LG10 because markers across the entire linkage group displayed significant LOD scores.

Red color

A single region of LG3 was associated with increases in both red chroma and red lightness (R^2=0.13 and 0.16 for chroma and lightness, respectively). An additional QTL on LG 8 (R^2=0.07) was detected for the degree of chroma, and a distinct QTL in LG 4 (R^2=0.12) was detected for the hue parameter. For all QTL, alleles from Perennial were associated with increased color intensity.

Using two-way ANOVA tests for all markers, we obtained on average 20 significant interactions ($P<0.001$) per trait in each year. A similar number of interactions are expected by chance alone, given the number of tests performed at the stated significance level (19±4 out of 17000 tests). In order to reduce the probability of making type-I errors, we present only those interactions that were detected in both years. A total of 14 digenic interactions involving 7 traits we detected in both years (Table 4). With the exception of 1 interaction for plant height that involved a QTL with main effect, all other interactions were between markers with no main effect on the trait. A single interaction between E49/M51–260 and

TG510 was detected for the 2 highly correlated traits fruit diameter and pericarp thickness.

Discussion

To our knowledge, this is the first report identifying QTL of fruit-related traits in pepper. Most of the QTL identified were clustered in a few chromosomal regions on LGs 2, 3, 4, 8 and 10. Linkage group 3 contained the largest number of QTL: for 11 out of 14 traits analyzed, QTL were detected in this linkage group. The co-localization of QTL for different traits often reflected the level of correlation between the various traits. For example, three common positions were detected in the analyses of fruit diameter and pericarp thickness (r=0.86, 0.87). Additionally, a common digenic interaction was detected for both traits. Similarly, a single region of LG3 was significantly associated with both red chroma and red lightness values, which are highly correlated (r=0.81). Identification of QTL affecting different traits in the same genomic region can result from pleiotropy or linkage. However, the distinction between the two possibilities requires high-resolution QTL mapping (Eshed and Zamir 1995). A clear physiological relationship between traits, such as that which exists for fruit diameter and pericarp thickness, increases the likelihood that the co-localization of QTL for these traits is a result of pleiotropy.

Three markers had a statistically significant association with several traits. E49/M51–545 (LG8) was associated with 6 traits: ripening date, fruit diameter, fruit shape, pericarp thickness, soluble solids concentration and pedicel diameter. P11/M54–269 (LG2) was associated with 4 traits: fruit weight, fruit diameter, soluble solids concentration and pedicel diameter. P14/M59–276 (LG3) was associated with 5 traits: fruit diameter, fruit length, fruit shape, pericarp thickness and seed weight. All of these traits are dependent upon complex physiological processes involved in fruit development. Our results suggest that each of these three genomic regions contains either a single pleiotropic locus that affects many aspects of pepper fruit development or, alternatively, several linked QTL, each with more limited effects on developmental processes. These QTL will be targeted in further studies for high-resolution mapping in order to distinguish between these possibilities and to determine the feasibility of positional cloning.

Overall, 29 out of 47 QTL identified for traits measured in 1996 and 1997 were identified in both years. The level of QTL consistency between years was related to the estimated heritability of each trait. For low-heritability traits, such as ripening date (h^2=0.27, 0.40) and soluble solids concentration (h^2=0.24, 0.54), different QTL were detected in each year. In contrast, for high-heritability traits such as fruit shape (h^2=0.87, 1.0) and fruit weight (h^2=0.79, 1.0), the same QTL were detected in both years.

For 4 traits (ripening date, fruit length, soluble solids concentration and pedicel length) alleles associated with an increase in the trait value originated from both parents. The identification of alleles with effects opposite to those predicted based on the parental phenotype is consistent with observations made for other crop species (Tanksley and McCouch 1997) and can explain the transgressive segregation observed for these traits in the F_3 generation.

Most of the QTL identified in this study had relatively small effects, controlling less than 20% of the total phenotypic variation. However, for 7 traits (ripening date, fruit diameter, fruit length, fruit shape, pericarp thickness, pedicel diameter and pedicel length), at least 1 locus controlled over 20% of the phenotypic variation. The total amount of phenotypic variation explained by all QTL ranged from less than 30% (for red and green color attributes, firmness, seed weight, soluble solids and ripening date) to over 50% (for fruit diameter, fruit shape, pericarp thickness and pedicel diameter). For all traits, the joint R^2 explained by all QTL was lower than the sum of R^2 for individual QTL. This indicates that the effects of the QTL are not entirely additive.

The locus *fs3.1* had the largest effect of all QTL identified in this study, explaining 60% of the total phenotypic variation in fruit shape. Other QTL with such large effects are those associated with domestication in maize, sorghum and rice (Doebley and Stec 1991; Lin et al. 1995; Xiong et al. 1999). The detection of the major fruit shape QTL in the present study is in close agreement with early studies on the inheritance of this trait in *C. annuum* and *C. frutescens*. In *C. annuum* and *C. frutescens* crosses between elongated and oblate-fruited parents, fruit shape was controlled by a single gene with incomplete dominance of oblate type (Kaiser 1935; Khambanonda 1950). In another *C. annuum* cross between oblate and elongated-fruited parents, fruit shape was inherited as a single gene (*O*) with complete dominance of the oblate type (Peterson 1959). Because neither Maor nor Perennial had oblate fruits, the relationship between the *O* gene and the QTL *fs3.1* remains unclear. The segregation of *fs3.1* in a cross of oblate and elongated–fruited peppers is currently under investigation.

There is increasing evidence that orthologous major genes or QTL in related crop species can exhibit similar phenotypic effects. For example, genes affecting physiologically related traits such as plant height, dwarfing, giberellin insensitivity and yield have been identified in similar positions of different grain genera (Gale and Devos 1998, Lee 1996, Van Deynze et al. 1995). Such a comparison has not been made for fruit-related traits, primarily because the combination of well-developed comparative maps and detailed QTL analyses in multiple genera has not yet been achieved in a fruiting crop family. Many QTL controlling fruit-related traits have been identified in tomato (Bernacchi et al. 1998; Grandillo et al. 1999). Although precise comparative QTL mapping between the two species could not be performed because of the lack of a sufficient number of shared markers, comparison of fruit shape QTL positions in pepper and tomato indicated possible corresponding positions for loci controlling the same trait in the two genera. The tomato fruit shape QTL *fs3.1* mapped in the interval between TG585 and CT171 (Bernacchi et al. 1998) and could correspond to pepper *fs3.1* as both loci are in the vicinity of TG130 (Livingstone et al. 1999; Tanksley et al. 1992). Similarly, the pepper fruit shape QTL *fs8.1* could correspond to tomato *fs8.1* (Grandillo et al. 1996), as both loci are linked to TG176 at the end of chromosome 8. In both pepper and tomato, *fs8.1* was also linked to QTL affecting fruit color. The pepper fruit shape QTL *fs10.1* could correspond to tomato *fs10.1* (Grandillo et al. 1999; Ku et al. 1999), as both loci are closely linked to TG596 (Livingstone et al. 1999; Tanksley et al. 1992).

Additional candidates for orthologous QTL in pepper and tomato are the fruit weight QTL in chromosomes 2 and 3 in both species. On chromosome 2, the RFLP marker CD66 is tightly linked to both *fw2.1* in pepper and *fw2.2* in tomato (Alpert and Tanksley 1996). Similarly, TG74 is linked to *fw3.2* in pepper and to *fw3.1* in tomato (Grandillo et al. 1999). Both *fw2.2* and *fw3.1* were considered major fruit weight QTL in tomato (Grandillo et al. 1999), and the corresponding pepper loci were the major fruit weight loci in the present study. Finally, the tomato plant height QTL *ht3* is linked to TG66 (deVicente and Tanksley 1993) and could correspond to the pepper QTL *ph3.1,* which was identified in the vicinity of the same marker.

We are currently performing additional QTL mapping studies with populations involving different *Capsicum* species. Further accumulation of QTL data in pepper will allow genetic and molecular characterization of the morphological diversity present in the genus. Additionally, more detailed comparative QTL mapping in the Solanaceae will allow determination of the extent of QTL conservation in this family. In conjunction with high-resolution mapping of selected QTL, this information will shed light on the genetic organization and degree of conservation of agriculturally important genes involved in fruit development.

Acknowledgments We thank L. Landry and V. Lackney for technical assistance, K. Livingstone for useful comments on the manuscript, A. Gnizi for help in statistical analyses and S. Ben Harush for assistance in field production. This research was supported by research grant no. IS-2389–94 from BARD, The United States-Israel Binational Agricultural Research and Development Fund and USDA NRI Award no. 94–37300–0333. RCG was supported by a DOE/NSF/USDA interagency Research Training Group grant.

References

Alpert KB, Tanksley SD (1996) High-resolution mapping and isolation of a yeast artificial chromosome contig containing *fw2.2*: a major fruit weight quantitative trait locus in tomato. Proc Natl Acad Sci USA 93:15503–15507

Ben Chaim A, Paran I (2000) Genetic analysis of quantitative traits in pepper (*Capsicum annuum*). Proc Am Soc Hortic Sci 125:66–70

Bernacchi D, Beck-Bunn T, Eshed Y, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley SD (1998) Advanced backcross QTL analysis in tomato. I. Identification of QTL for traits of agronomic importance from *Lycopersicon hirsutum*. Theor Appl Genet 97:381–397

Caranta CA, Palloix A, Lefebvre V (1997a) QTL for a component of partial resistance to cucumber mosaic virus in pepper: restriction of virus installation in host-cell. Theor Appl Genet 94:431–438

Caranta CA, Lefebvre V Palloix A (1997b) Polygenic resistance of pepper to potyviruses consists of a combination of isolate-specific and broad-spectrum quantitative trait loci. Mol Plant Microbe Interact 10:872–878

Deshpande RB (1933) Studies in Indian chillies. 3. The inheritance of some characters in *Capsicum annuum* L. Indian J Agri Sci 3:219–300

DeVicente MC, Tanksley SD (1993) QTL analysis of transgressive segregation in an interspecific tomato cross. Genetics 134: 585–596

Doebley J, Stec A (1991) Genetic analysis of the morphological difference s between Maize and Teosinte. Genetics 129:285–295

Eshed Y, Zamir D (1995) An introgression line population of *Lycopersicon pennelli*i in the cultivated tomato enables the identification and fine mapping of yield-associated QTL. Genetics 141:1147–1162

Gale MD, Devos KM (1998) Comparative genetics in the grasses. Proc Natl Acad Sci USA 95:1971–1974

Grandillo S, Ku HM, Tanksley SD (1996) Characterization of *fs8.1*, a major QTL influencing fruit shape in tomato. Mol Breed 2:251–260

Grandillo S, Ku HM, Tanksley SD (1999) Identifying the loci responsible for natural variation in fruit size and shape in tomato. Theor Appl Genet 99:978–987

Jahn KM, Paran I, Hoffmann K, Radwanski ER, Livingstone KD, Grube RC, Aftergoot E, Lapidot M, Moyer J (2000) Genetic mappin g of the *Tsw* locus for resistance to tomato spotted wilt virus in *Capsicum* and its relationship to the *Sw-5* allele for resistance to the same pathogen in tomato. Mol Plant Microbe Interact 13:673–682

Kaiser S (1935) The factors governing shape and size in *Capsicum* fruits: a genetic and developmental analysis. Torrey Bot Club Bull 62:433–454

Khambanonda I (1950) Quantitative inheritance of fruit size in red pepper (*Capsicum frutescens* L.) Genetics 35:322–343

Kim BD, Kang BC, Nahm SH, Huh JH, Yoo SH, Kwon JK (1998) Construction of molecular linkage map and development of fluorescence *in situ* hybridization technique in hot pepper. In: Palloix A, Daunay MC (eds) 10th Meet Genet Breed Capsicum Eggplant. Institute National de la Researche Agronomique, Avignon, France, pp 227–230

Ku HM, Doganlar S, Chen KY, Tanksley SD (1999) The genetic basis of pear-shaped tomato fruit. Theor Appl Genet 99:844–850

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln, SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lee M (1996) Comparative genetic and QTL mapping in sorghum and maize. Symp Soc Exp Biol 50:31–38

Lefebvre V Palloix A (1996) Both epistatic and additive effects of QTL are involved in polygenic-induced resistance to disease: a case study, the interaction pepper-*phytophthora capsici* Leon. Theor Appl Genet 94:503–511

Lefebvre V, Palloix A, Caranta C, Pochard E (1995) Construction of an intra-specific integrated linkage map of pepper using molecular markers and doubled-haploid progenies. Genome 38:112–121

Legg PD, Lippert LF (1966) Estimates of genetic and environmental variability in a cross between two strains of pepper (*Capsicum annuum* L.). Proc Am Soc Hortic Sci 89:443–448

Lin YR, Schertz KF, Paterson AH (1995) Comparative analysis of QTL affecting plant height and maturity across the Poaceae, in reference to an interspecific Sorghum population. Genetics 141:391–411

Livingstone KD, Lackney VK, Blauth J, van Wijk R, Jahn MK (1999) Genome mapping in Capsicum and the evolution of genome structure in the Solanaceae. Genetics 152:1183–1202

McArdle RN, Bouwkamp JC (1983) Inheritance of several fruit characters in *Capsicum annuum* L. J Hered 74:125–127

Murphy JF, Blauth JR, Livingstone KD, Lackney VK, Jahn MK (1998) Genetic mapping of the *pvr1* locus in *Capsicum* spp. and evidence that distinct Potyvirus resistance loci control responses that differ at the whole plant and cellular levels. Mol Plant Microbe Interact 11:943–951

Nelson CJ (1997) QGENE software for marker-based genomic analysis and breeding. Mol Breed 3:229–235

Paran I, Aftergoot E, Shifriss C (1998) Variation in *Capsicum annuum* revealed by RAPD and AFLP markers. Euphytica 99:167–173

Peterson PA (1959) Linkage of fruit shape and color genes in *Capsicum*. Genetics 44:407–419

Prince JP, Pochard E, Tanksley SD (1993) Construction of molecular linkage map of pepper and a comparison of synteny with tomato. Genome 36:404–417

Prince JP, Zhang Y, Radwanski ER, Kyle MM (1997) A high-yielding and versatile DNA extraction protocol for *Capsicum*. HortScience 32:937–939

SAS Institute (1989) SAS/STAT version 6. SAS Institute, Cary, N. C.

Tanksley SD McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277: 1063–1066

Tanksley SD, Bernatzky R, Lapitan NL, Prince JP (1988) Conservation of gene repertoire but not gene order in pepper and tomato. Proc Natl Acad Sci USA 85:6419–6423

Tanksley SD, Ganal MW, Prince JP, deVicente MC, Bonierbale MW, Broun P, Fulton TM, Giovanonni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Pineda O, Roder MS, Wing RA, Wu W, Young ND (1992) High-density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160

Thakur PC, Gill HS, Bhagchandani PM (1980) Diallel analysis of some quantitative traits in sweet pepper. Indian J Agric Sci 50:811–817

Van Deynze AE, Nelson JC, Yglesias ES, Harrington SE, Braga DP, McCouch SR, Sorrells MR (1995) Comparative mapping in the grasses: wheat relationships. Mol Gen Genet 248:744–754

Vos P, Hogers R, Bleeker M, Reijans M, van de Lee T, Hornes M, Frijters A, Pot J, Peleman J, Kuiper M, Zabeau M (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res 23:4407–4414

Xiong LZ, Liu KD, Dai XK, Xu CG, Zhang Q (1999) Identification of genetic factors controlling domestication-related traits of rice using an F_2 population of a cross between *Oryza sativa* and *O. rufipogon*. Theor Appl Genet 98:243-251

Yu SB, Li JX, Xu CG, Tan YF, Gao YJ, Li XH, Zhang Q, Saghai Maroof MA (1997) Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. Proc Natl Acad Sci USA 94:9226–9231