Theor Appl Genet (2003) 106:1457–1466
DOI 10.1007/s00122-003-1204-5

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Mapping of yield-related QTLs in pepper in an interspecific cross of *Capsicum annuum* and *C. frutescens*

Received: 8 May 2002 / Accepted: 15 October 2002 / Published online: 14 February 2003

Abstract An advanced backcross QTL study was performed in pepper using a cross between the cultivated species *Capsicum annuum* cv. Maor and the wild *C. frutescens* BG 2816 accession. A genetic map from this cross was constructed, based on 248 BC_2 plants and 92 restriction fragment length polymorphism (RFLP) markers distributed throughout the genome. Ten yield-related traits were analyzed in the BC_2 and BC_2S_1 generations, and a total of 58 quantitative trait loci (QTLs) were detected; the number of QTLs per trait ranged from two to ten. Most of the QTLs were found in 11 clusters, in which similar QTL positions were identified for multiple traits. Unlike the high percentage of favorable QTL alleles discovered in wild species of tomato and rice, only a few such QTL alleles were detected in BG 2816. For six QTLs (10%), alleles with effects opposite to those expected from the phenotype were detected in the wild species. The use of common RFLP markers in the pepper and tomato maps enabled possible orthologous QTLs in the two species to be determined. The degree of putative QTL orthology for the two main fruit morphology traits – weight and shape – varied considerably. While all eight QTLs identified for fruit weight in this study could be orthologous to tomato fruit weight QTLs, only one out of six fruit shape QTLs found in this study could be orthologous to tomato fruit shape QTLs.

Keywords *Capsicum* · Yield · Advanced backcross QTL analysis · Molecular markers · Comparative mapping

Communicated by J. Dvorak

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Introduction

Pepper (*Capsicum* spp.) is a New World crop with enormous genetic and phenotypic diversity (Bosland and Votava 2000). Most of the exotic genetic resources available in the genus have not yet been effectively exploited. Although there are five known domesticated species of *Capsicum*, the breeding of large-fruited sweet cultivars has been based entirely on a fraction of the variation in one species, *C. annuum*. The utilization of unadapted germplasm for improvement of such cultivars has been restricted to the introgression of disease resistance genes (Palloix 1992).

Yield in pepper is a complex trait, affected by factors such as the number of fruits, and their weight, dimensions and maturity. Previous studies have strongly indicated that selection for fruit number, fruit weight and early flowering can substantially enhance yields in various horticultural types of pepper (Gill et al. 1977; Gopalakrishnan et al. 1985; Gupta and Yadav 1984; Legg and Lippert 1966; Ramana Rao et al. 1974). However, selection for yield components should not compromise other fruit traits such as shape or quality. Most of the traits mentioned above are quantitatively inherited, and it is imperative to discover the quantitative trait loci (QTLs) that govern these traits in various backgrounds and to transfer them to elite varieties in order to develop viable commercial varieties.

Recent advances in marker technologies have made it possible to discover several agronomically important QTLs in exotic germplasm and to introgress them into major crop species (Paran 2003; Zamir 2001). It has also been possible to extend these developments to other related crop species on the basis of synteny of genomes in related species. Advanced backcross (AB) QTL analysis has been proposed as an efficient new molecular breeding method that can integrate QTL discovery and variety development while exploiting the full potential of the genetic variation available in unadapted germplasm for the improvement of quantitative traits (Tanksley and Nelson 1996). By means of this approach, specific regions

of the genome, derived from wild sources of germplasm, can be tagged with molecular markers and can be tested for association with traits that segregate in the offspring of the cross between the cultivated and the exotic parents.

In tomato, the genetic system most closely comparable with pepper, use of the advanced backcross strategy (Bernacchi et al. 1998; Fulton et al. 1997, 2000; Tanksley et al. 1996) and of introgression lines of wild species (Eshed and Zamir 1995) has led to much progress in recent years with respect to the discovery and exploitation of many beneficial alleles at QTLs originated from exotic germplasm. Similar studies have also identified beneficial QTL alleles for yield-related traits in rice (Moncada et al. 2001; Xiao et al. 1998). These studies demonstrated that high percentages of trait-enhancing QTLs for diverse traits can be discovered in the wild species related to crop plants.

The objectives of the study reported here were: (1) to use the AB-QTL mapping strategy to test the potential utilization of a wild pepper (*C. frutescens*) accession as a source of valuable QTL alleles that control yield-related traits; (2) to assess the degree of QTL conservation within *Capsicum* by comparing the present data with previously identified QTLs for similar traits in an intra-specific cross of *C. annuum*; (3) to determine whether there is any evidence for orthology between QTLs in pepper and in tomato that control the same morphological traits.

Materials and methods

Plant material

An interspecific BC_2 population was constructed by crossing the bell-type *C. annuum* cv. Maor with the small oval-fruited *C. frutescens* wild accession BG 2816, with Maor as the recurrent parent. Seeds of Maor were obtained from Dr. C. Shifriss, of the Volcani Institute, Israel, and those of BG 2816 from Prof. Molly Jahn, Cornell University, USA. Approximately 350 BC_2 plants were grown in a net house in Qiryat Gat, Israel during 1999, and 248 normal fertile plants from among them were used for phenotyping, harvesting leaves for DNA extraction and seed collection. All 248 BC_2 plants were selfed to generate BC_2S_1 families in which further phenotypic evaluations were carried out.

Trait evaluation

The parents, F_1, and 248 BC_2S_1 families were grown in an open field at Qiryat Gat, Israel during the summers of 2000 and 2001. Spacing between the plants was maintained at 30 cm within the rows and 100 cm between rows. Each year 20 individual plants from each family were used for scoring the phenotypes, which were arranged in two replicates of ten plants in a non-random block design. The seeds were germinated in the nursery, and the population was transplanted during April in each year. All traits were measured in both seasons unless mentioned otherwise.

The following traits were evaluated for each plant (three fruits per plant) in the BC_2 generation in 1999 and in the BC_2S_1 generation in 2001 and 2002 (for the latter generation, individual plant measurements were used to calculate the mean of each family): (1) fruit weight (in grams); (2) fruit length (in millimeters); (3) fruit diameter (in millimeters); (4) fruit shape (ratio of fruit length to fruit diameter); (5) pericarp width (in millimeters). The following traits were measured only in the BC_2S_1 generation: (6) number of fruits – total number of fruits found on plants at the time of harvest (2001 only); (7) yield – total weight of fruits from individual plants of each family (in kilograms); (8) flowering – scores of one to five were given based on the developmental stage of the flower/fruit at the third node on day 88; the scores represented: 1 = flower bud/flower, 2 = small fruits, 3 = small to medium size fruits, 4 = medium size fruits and 5 = mature fruits; (9) maturity – the developmental stage of the flower/fruit at the third node 1 week before harvest was scored as for the flowering scores, and a family value of 1–5 was given based on the overall maturity status of the family: 1 = only green fruits; 2 = more than 50% green fruits and the rest at the breaker stage; 3 = 50% green and 50% breaker; 4 = a few green and the majority in breaker; 5 = at least 50% breaker and the rest red. Lastly, the seed weight (in milligrams) was determined by weighing 30 BC_2S_1 seeds collected from the BC_2 plants. A more detailed description of the measurements of the fruit-related traits is provided by Ben Chaim et al. (2001). Heritability was calculated according to Ben Chaim and Paran (2000) by determining the components of variance between (σ^2b) and within (σ^2w) families by applying one-way analysis of variance (ANOVA) and adjusting the estimates for BC_2S_1 generation $h^2 = 1.1667\ \sigma^2b/(\sigma^2w + \sigma^2b)$. Pearson correlation coefficients ($P < 0.05$) were calculated for each trait/experiment combination by applying the QGENE software package (Nelson 1997) to the BC_2 and BC_2S_1 data.

Marker analysis and map construction

Total genomic DNA from young leaves of the parents and their offspring were prepared according to Prince et al. (1997). Restriction digestion was applied to 20 μg of total genomic DNA that had been separated in 1% agarose gels and blotted onto Hybond N+ membranes. A total of seven restriction enzymes (*Bcl*I, *Bst*NI, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII and *Xba*I) were used to survey the polymorphism between the parents. Tomato restriction fragment length polymorphism (RFLP) markers described in Tanksley et al. (1992) were used as probes in the survey (parents) and in the population filters. Pepper (PG) clones were obtained from Prof. Molly Jahn, Cornell University. Additional clones and their GenBank accession numbers were: MYB (AJ277944), Q2 (AF404416), Q7 (AF404421), fw2.2 (AF261774), COMT (AF081214) and CrtR-1 (Y14809). Clones 6.16-2 and TG420-P are pepper markers produced in our laboratory. Labeling and hybridization conditions were as described by Ben Chaim et al. (2001). Mapping was performed with the MAPMARKER v. 2.0 program (Lander et al. 1987). Markers were grouped at high LODs of 15–25 and a maximum recombination fraction of 30 cM. The order within each linkage group was determined at LOD 3.0. Map distances were calculated by means of the Kosambi mapping function.

QTL analysis

All QTL analyses were performed with the QGENE software (Nelson 1997). The significance threshold (LOD $\geq$ 3.4) for detecting QTLs by interval mapping was established by doing 1,000 permutations at $P < 0.01$. Estimates of percentage phenotypic variations accounted for by individual QTLs (R^2) were obtained for the single markers with the highest LOD value within a given QTL interval. The percentage phenotypic change (A%) of each significant QTL, associated with the BG 2816 allele at a given marker locus was estimated as 100 × (AF-AA)/AA, where AF is the phenotypic mean of the heterozygous individuals at a given marker locus and AA is the phenotypic mean for individuals homozygous for the *C. annuum* allele at the same locus. The +/– sign of % A of each QTL indicates an increasing or reducing effect of the BG2816 allele on the trait, respectively.

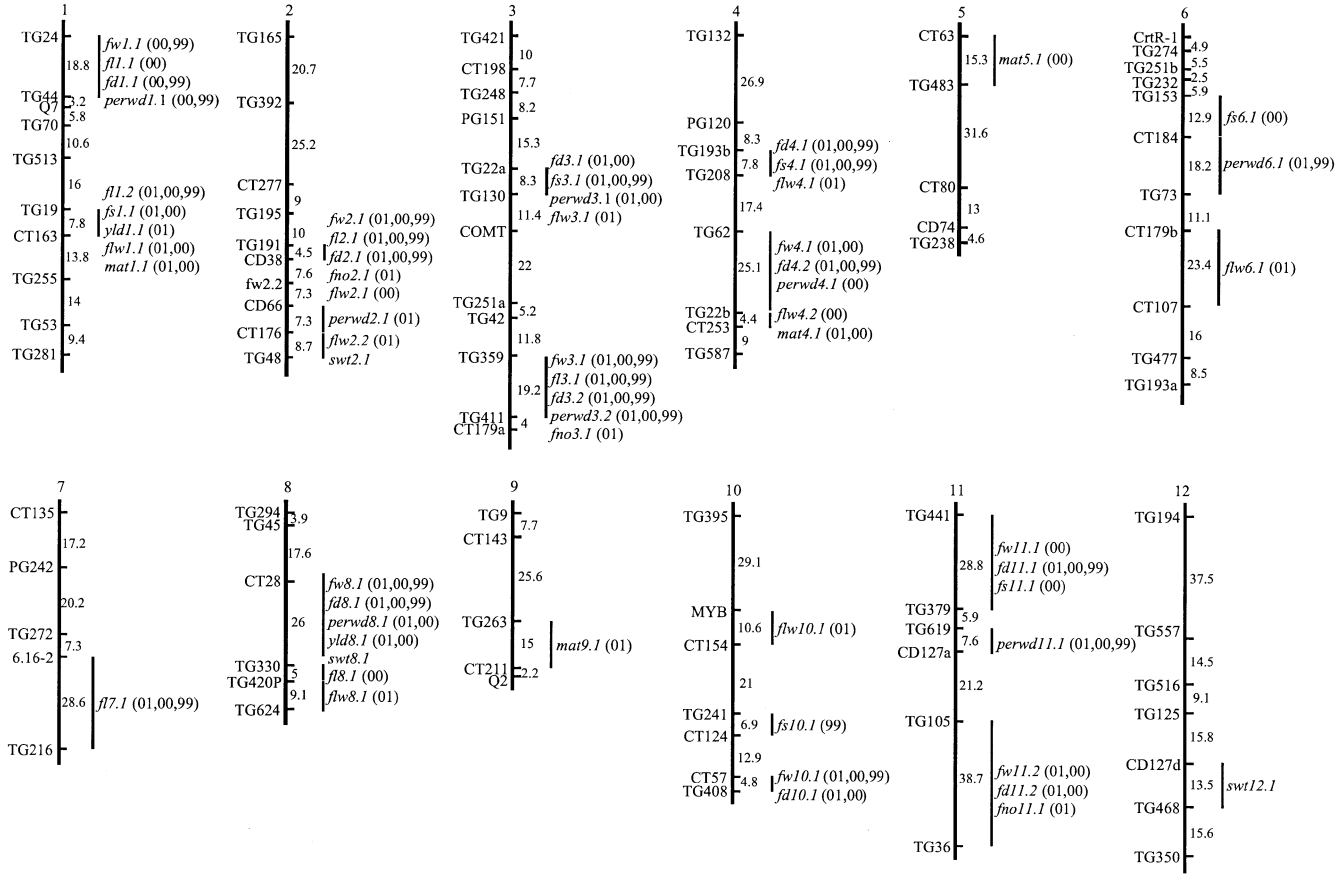

Fig. 1 Positions of QTLs in the BC_2 map from the cross of *Capsicum annuum* × *C. frutescens*. Linkage groups are *numbered* according to the chromosome number given by Livingstone et al. (1999). RFLP markers are to the *left* of each linkage group. QTL intervals are presented as *bars* to the *right* of the linkage groups, and the QTL symbols are to the *right* of the *bars*. *fw* Fruit weight, *fd* fruit diameter, *fl* fruit length, *fs* fruit shape, *perwd* pericarp width, *yld* yield, *fno* fruit number, *flw* flowering, *mat* maturity, *swt* seed weight. The years in which the QTLs were detected are *abbreviated* in *parentheses*

Results

Map construction

The linkage map created from the cross of Maor × BG 2816 is the first to be reported from the cross of *C. annuum* × *C. frutescens*. The F_1 was completely fertile and revealed no indication of translocations that differentiate the two genomes as had been observed in the *C. annuum* × *C. chinense* cross (Livingstone et al. 1999). Ninety-two RFLP markers were used to construct the linkage map (Fig. 1). The average heterozygosity percentage per locus in the BC_2 was 22%, very close to the 25% to be expected in this generation. These markers were distributed across the 12 pepper chromosomes with a total length of 1,100 cM (compared with 1,246 cM) in the map of Livingstone et al. (1999). Except for the most distal markers in some of the linkage groups and for chromosome 7, a major portion of which [70 cM, according to the map of Livingstone et al. (1999)] was not included because of a lack of polymorphism, all chromosomes were represented in the map. The overall linkage assignment and the order of the markers were similar to those in the map of Livingstone et al. (1999). A few differences were: CD74 was mapped to the bottom of chromosome 5, similarly to the findings of Ben Chaim et al. (2001), instead of to chromosome 7 as reported by Livingstone et al. (1999); TG153 that had been assigned to chromosome 5 by Livingstone et al. (1999) was mapped to the top of chromosome 6 in the present study, in a similar location to that in the tomato map of Tanksley et al. (1992); the order of TG9 and CT143 at the top of chromosome 9 was inverted compared with the order of Livingstone et al. (1999), but was the same as that of Tanksley et al. (1992).

Traits variation and correlations

Maor is a common large-fruited blocky cultivar, while BG 2816 is a wild accession with a small, more elongated, oval fruit. Accordingly, the fruit of Maor was heavier and larger than that of BG2816, and it ripened earlier than that of BG 2816 (Table 1). Fruit number and yield were calculated only for Maor because both BG 2816 and the F_1 carried very many (hundreds) small

Table 1 Means, standard errors (SE) and heritabilities of quantitative traits in the parents, BC_2 (1999) and BC_2S_1 (2000 and 2001) generations

Trait	Year	Maor		BG 2816		F_1		BC_2S_1		Heritability
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Fruit weight (g)	2001	159.6	5.30	0.2	0.02	11.55	3.42	70.11	0.48	0.49
	2000	107.6	7.05	0.4	0.00	14.66	0.91	61.68	0.48	0.43
	1999	131.3	8.10	0.3	0.01	12.63	0.04	59.81	0.65	–
Fruit length (mm)	2001	95.4	1.37	11.2	0.12	26.04	1.57	77.74	0.28	0.54
	2000	76.2	1.21	12.5	0.07	32.22	0.27	72.73	0.25	0.56
	1999	73.6	2.10	11.6	0.17	24.48	0.64	68.94	0.36	–
Fruit diameter (mm)	2001	76.8	0.89	7.14	0.11	13.40	0.74	54.52	0.16	0.53
	2000	74.2	1.18	8.28	0.65	17.36	0.12	56.89	0.17	0.51
	1999	72.3	1.28	7.01	0.19	13.93	0.39	49.13	0.22	–
Fruit shape	2001	1.2	0.02	1.57	0.02	1.92	0.05	1.46	0.01	0.59
	2000	1.0	0.01	1.63	0.02	1.86	0.01	1.31	0.01	0.60
	1999	1.0	0.03	1.66	0.05	1.76	0.05	1.43	0.01	–
Pericarp width (mm)	2001	5.3	0.10	0.58	0.02	1.83	0.08	4.28	0.01	0.43
	2000	5.0	0.11	0.62	0.03	2.21	0.02	4.37	0.01	0.26
	1999	4.7	0.11	0.63	0.04	1.80	0.06	4.59	0.02	–
Fruit number	2001	7.9	0.38	–	–	–	–	23.76	0.24	0.33
Yield (kg)	2001	1.0	0.04	–	–	–	–	1.05	0.01	0.16
	2000	0.9	0.34	–	–	–	–	0.67	0.01	–
Flowering	2001	3.8	0.14	1.32	0.25	4.83	0.17	2.79	0.04	0.09
	2000	3.7	0.68	1.94	0.23	–	–	2.80	0.03	0.20
Maturity	2001	5.0	0.00	1.00	0.00	3.00	0.00	3.32	0.08	0.24
	2000	4.5	0.00	1.00	0.00	–	–	3.39	0.09	–
Seed weight (mg)	1999	178.4	2.64	91.0	1.91	145.0	3.21	205.73	1.37	–

fruits. The F_1 exhibited characteristics intermediate between those of the two parents for all traits. Similarly, the means of BC_2/BC_2S_1 did not indicate the occurrence of transgressive variation in this population. The heritability estimates were moderate for the fruit weight and dimensions and were low for yield and for the two earliness parameters.

High correlation coefficients between years were observed for most traits (Table 2); the lowest between-years correlation was for yield (r = 0.36). In 2000, the highest correlation between traits was that between fruit weight and diameter, with r = 0.89, compared with r = 0.66 for the correlation between weight and length, indicating that the contribution of the width to fruit weight was stronger than that of the length. There was a strong negative correlation between fruit number and fruit dimensions, as expected. Yield was positively correlated with fruit dimensions and negatively correlated with fruit number. Seed weight was positively correlated with fruit weight.

QTL identification

Fruit weight

In 2000, eight QTLs were detected for fruit weight, of which five and six were also detected in 1999 and 2001, respectively (Fig. 1, Table 3). For all the QTLs detected in 2000 but not in 1999 (*fw4.1*, *fw11.1* and *fw11.2*) or in 2001 (*fw1.1* and *fw11.1*), an effect slightly below the threshold was detected (LOD > 3). At all QTLs, Maor (the large-fruited parent) alleles were associated with increased fruit weight. The QTL with the largest effect on fruit weight in each year was *fw2.1* at which the wild allele decreased weight by 27–37%.

Fruit length

In 2000, six QTLs for fruit length were detected, of which four were also detected in 1999 and 2001. *fl1.1* and *fl8.2*, which were not detected in 1999 and in 2001, had effects slightly below the threshold (LOD > 3). For all QTLs, Maor alleles were associated with increased fruit length. Similarly to *fw2.1*, the QTL with the largest effect on fruit length was *fl2.1*, located at CD38y the wild allele in 1999 and 2001. For all fruit length QTLs except *fl1.2* and *fl7.1*, identical positions were found for fruit weight QTLs.

Fruit diameter

In 2000, ten QTLs for fruit diameter were detected; the same QTLs except for *fd1.1* were detected in 2001, and seven out of the ten QTLs were detected in 1999. Of the remaining QTL, only *fd3.1* in 1999 had an LOD value above 3. As with fruit weight and length, Maor alleles at all QTLs were associated with increased fruit diameter. Two QTLs – *fd2.1* and *fd3.1* – had the greatest effects on

Table 2 Pearson correlation coefficients ($P < 0.05$) between traits and between years for the same trait measured in the BC_2 and BC_2S_1 progeny (*ns* not significant)

Trait	fw (01)	fw (00)	fw (99)	fl (01)	fl (00)	fl (99)	fd (01)	fd (00)	fd (99)	fs (01)	fs (00)	fs (99)	pw (01)	pw (00)	pw (99)	fno (01)	yld (01)	yld (00)	flw (01)	flw (00)	mat (01)	mat (00)
Fruit weight (fw) 2000	0.86																					
Fruit weight 1999	0.81	0.83																				
Fruit length (fl) 2001	0.60	0.58	0.57																			
Fruit length 2000	0.53	0.66	0.55	0.89																		
Fruit length 1999	0.46	0.53	0.66	0.76	0.75																	
Fruit diameter (fd) 2001	0.88	0.76	0.74	0.31	0.26	0.26																
Fruit diameter 2000	0.81	0.89	0.77	0.31	0.36	0.33	0.87															
Fruit diameter 1999	0.73	0.72	0.84	0.35	0.34	0.45	0.75	0.77														
Fruit shape (fs) 2001	ns	ns	ns	0.71	0.64	0.53	–0.42	–0.32	–0.20													
Fruit shape 2000	ns	ns	ns	0.62	0.68	0.46	–0.40	–0.41	–0.25	0.89												
Fruit shape 1999	–0.21	ns	ns	0.44	0.44	0.59	–0.44	–0.36	–0.42	0.75	0.71											
Pericarp width (pw) 2001	0.74	0.55	0.54	0.24	0.16	0.19	0.75	0.61	0.53	–0.31	–0.31	–0.30										
Pericarp width 2000	0.69	0.77	0.63	0.31	0.37	0.32	0.65	0.77	0.58	–0.18	–0.23	–0.20	0.71									
Pericarp width 1999	0.51	0.52	0.56	0.20	0.19	0.28	0.51	0.55	0.57	–0.17	–0.23	–0.23	0.48	0.52								
Fruit number (fno) 2001	–0.81	–0.75	–0.67	–0.54	–0.50	–0.41	–0.76	–0.72	–0.65	ns	ns	0.19	–0.61	–0.65	–0.45							
Yield (yld) 2001	0.54	0.48	0.49	0.48	0.44	0.42	0.46	0.39	0.38	ns	ns	ns	0.41	0.37	0.27	–0.20						
Yield 2000	0.38	0.34	0.28	0.37	0.33	0.18	0.28	0.22	0.18	0.13	0.16	ns	0.25	0.26	0.14	–0.29	0.35					
Flowering (flw) 2001	0.27	0.31	0.27	0.53	0.51	0.32	ns	ns	0.13	0.41	0.42	0.20	ns	Ns	ns	–0.20	0.34	0.29				
Flowering 2000	0.29	0.34	0.23	0.40	0.43	0.21	0.16	0.16	0.14	0.25	0.30	ns	ns	0.20	ns	–0.25	0.16	0.25	0.45			
Maturity (mat) 2001	0.23	0.28	0.23	0.43	0.44	0.24	ns	ns	0.15	0.32	0.36	ns	ns	Ns	ns	–0.25	ns	0.21	0.68	0.53		
Maturity 2000	0.21	0.29	0.24	0.35	0.42	0.23	ns	ns	0.15	0.24	0.32	ns	ns	0.16	ns	–0.22	ns	0.20	0.49	0.59	0.68	
Seed weight	0.41	0.39	0.41	0.27	0.23	0.30	0.38	0.40	0.37	ns	ns	ns	0.31	0.36	0.23	–0.33	0.20	ns	0.16	0.20	0.24	0.16

fruit diameter: for each, the wild allele decreased the diameter by approximately 10%. Out of the ten QTLs, all except *fd3.1* and *fd4.1* were found in similar positions for fruit weight.

Fruit shape

A total of six QTLs for fruit shape were detected in the three experiments, two of which – *fs3.1* and *fs4.1* – were detected in all the experiments. Except for *fs1.1*, which was detected in 2 out of the 3 years, the other three QTLs were found in only 1 year. However, for *fs11.1* in 2000, a sub-threshold LOD (LOD = 3.3) was detected in 2001. For all QTLs except *fs1.1*, the wild alleles were associated with an increased fruit shape index. The QTL with the largest effect ($14 < \%A < 22$) on fruit shape in the 3 years was *fs3.1*. The same position (TG130) that was significant for *fs3.1* was also significant for fruit diameter (*fd3.1*) but not for fruit length, indicating that fruit shape at this locus in this cross was determined primarily by the width of the fruit.

Pericarp width

Seven QTLs for pericarp width were detected, of which only *perwd3.2* and *perwd11.1* appeared in all 3 years. Two additional QTLs – *perwd3.1* and *perwd8.1* – that were significant in 2000 and 2001 had sub-threshold peaks (LOD>3) in 1999. For all the QTLs, Maor alleles were associated with increased pericarp width. The same markers that were associated with pericarp width QTLs (except for *perwd6.1*) were also found as QTLs for fruit diameter. For *perwd11.1*, multiple peaks above the threshold level appeared along chromosome 11, which may indicate the existence of more than one QTL for this trait in this chromosome.

Fruit number

Three QTLs for fruit number were identified. For all of these QTLs, the same markers were also identified as QTLs for fruit weight and diameter, and the wild alleles were associated with increased fruit number, reflecting the high negative correlation between these traits. As with fruit weight, for which the QTL with the largest effect was *fw2.1, fno2.1* had the largest effect on fruit number, and the wild allele increased fruit number by 45% at this locus.

Yield

Two QTLs for yield were detected, of which *yld8.1* appeared in both years for which yield was measured, and *yld1.1* was detected only in 2001. For both QTLs, Maor alleles were associated with increased yield. The region

Table 3 List of QTLs detected in the BC_2 (1999) and BC_2S_1 (2000 and 2001) experiments

QTL	Year	Marker interval[a]	Direction	Variation	LOD	%A
Fruit weight						
fw1.1	1999	TG24-**TG44**	Maor	0.07	5.02	–31.91
	2000	TG24-**TG44**	Maor	0.12	7.32	–31.11
fw2.1	1999	**CD38**-TG191	Maor	0.16	9.75	–37.17
	2000	**CD38**-TG191	Maor	0.14	8.64	–27.63
	2001	**CD38**-TG191	Maor	0.19	11.35	–29.51
fw3.1	1999	**TG359**-TG411	Maor	0.13	7.84	–33.17
	2000	**TG359**-TG411	Maor	0.11	6.59	–23.88
	2001	**TG359**-TG411	Maor	0.10	5.98	–21.29
fw4.1	2000	**TG22b**-TG62	Maor	0.05	5.74	–18.00
	2001	**TG22b**-TG62	Maor	0.05	4.71	–14.97
fw8.1	1999	**CT28**-TG330	Maor	0.08	5.57	–24.78
	2000	**CT28**-TG330	Maor	0.06	4.68	–17.30
	2001	**CT28**-TG330	Maor	0.08	5.56	–17.84
fw10.1	1999	**CT57**-TG408	Maor	0.11	5.83	–27.92
	2000	**CT57**-TG408	Maor	0.06	3.60	–16.86
	2001	**CT57**-TG408	Maor	0.08	4.95	–18.11
fw11.1	2000	**TG441**-TG379	Maor	0.04	3.80	–14.84
fw11.2	2000	**TG105**-TG36	Maor	0.03	4.75	–11.39
	2001	TG105-**TG36**	Maor	0.04	4.60	–10.68
Fruit length						
fl1.1	2000	TG24-**TG44**	Maor	0.07	4.90	–13.78
fl1.2	1999	**TG19**-CT163	Maor	0.07	3.42	–13.18
	2000	**TG19**-CT163	Maor	0.11	5.67	–14.48
	2001	**TG19**-CT163	Maor	0.08	3.56	–12.34
fl2.1	1999	**CD38**-TG191	Maor	0.18	10.86	–19.37
	2000	**CD38**-TG191	Maor	0.22	11.92	–17.29
	2001	**CD38**-TG191	Maor	0.25	15.27	–18.40
fl3.1	1999	**TG359**-TG411	Maor	0.15	9.26	–17.36
	2000	**TG359**-TG411	Maor	0.09	6.00	–12.20
	2001	**TG359**-TG411	Maor	0.10	6.67	–12.27
fl7.1	1999	6.16-2-**TG216**	Maor	0.03	3.72	–8.50
	2000	6.16-2-**TG216**	Maor	0.08	4.47	–11.88
	2001	6.16-2-**TG216**	Maor	0.08	3.44	–10.97
fl8.1	2000	TG330-**TG420P**	Maor	0.08	4.50	–11.46
Fruit diameter						
fd1.1	1999	TG24-**TG44**	Maor	0.07	5.48	–14.48
	2000	TG24-**TG44**	Maor	0.08	5.62	–11.94
fd2.1	1999	CD38-**TG191**	Maor	0.13	6.55	–15.04
	2000	**CD38**-TG191	Maor	0.10	6.06	–10.50
	2001	**CD38**-TG191	Maor	0.10	7.61	–10.23
fd3.1	2000	TG22a-**TG130**	Maor	0.12	6.85	–11.66
	2001	TG22a-**TG130**	Maor	0.10	5.33	–10.39
fd3.2	1999	**TG359**-TG411	Maor	0.07	4.28	–11.28
	2000	**TG359**-TG411	Maor	0.08	4.80	–9.47
	2001	**TG359**-TG411	Maor	0.06	3.60	–7.73
fd4.1	1999	TG193b-**TG208**	Maor	0.06	4.09	–11.47
	2000	TG193b-**TG208**	Maor	0.06	5.80	–9.15
	2001	TG193b-**TG208**	Maor	0.07	5.62	–9.37
fd4.2	1999	**TG22b**-TG62	Maor	0.05	3.40	–10.04
	2000	TG22b-**TG62**	Maor	0.08	6.14	–9.71
	2001	TG22b-**TG62**	Maor	0.06	4.60	–8.33
fd8.1	1999	**CT28**-TG330	Maor	0.08	5.13	–11.76
	2000	**CT28**-TG330	Maor	0.06	3.78	–7.76
	2001	**CT28**-TG330	Maor	0.07	4.96	–7.72
fd10.1	2000	**CT-57**-TG408	Maor	0.04	3.48	–6.56
	2001	**CT-57**-TG408	Maor	0.06	3.73	–6.83
fd11.1	1999	**TG441**-TG379	Maor	0.08	5.71	–11.43
	2000	**TG441**-TG379	Maor	0.08	6.33	–8.76
	2001	**TG441**-TG379	Maor	0.06	4.7	–7.19
fd11.2	2000	TG105-**TG36**	Maor	0.04	4.30	–5.63
	2001	TG105-**TG36**	Maor	0.05	5.19	–5.86
Fruit shape						
fs1.1	2000	**TG19**-CT163	Maor	0.09	4.25	–13.64
	2001	**TG19**-CT163	Maor	0.07	3.45	–13.42
fs3.1	1999	TG22a-**TG130**	BG 2816	0.09	4.73	14.71
	2000	TG22a-**TG130**	BG 2816	0.24	14.63	22.76
	2001	TG22a-**TG130**	BG 2816	0.17	9.54	20.00

Table 3 (continued)

QTL	Year	Marker interval[a]	Direction	Variation	LOD	%A
fs4.1	1999	TG193b-**TG208**	BG 2816	0.07	4.41	10.95
	2000	TG193b-**TG208**	BG 2816	0.05	3.91	10.24
	2001	TG193b-**TG208**	BG 2816	0.09	4.98	13.99
fs10.1	1999	TG241-**CT124**	BG 2816	0.02	4.54	6.94
fs11.1	2000	TG441-**TG379**	BG 2816	0.05	3.67	8.80
Pericarp width						
perwd1.1	1999	TG24-**TG44**	Maor	0.05	3.61	–13.57
	2000	TG24-**TG44**	Maor	0.08	5.45	–8.60
perwd2.1	2001	CD66-**CT176**	Maor	0.06	3.81	–6.22
perwd3.1	2000	TG22a-**TG130**	Maor	0.04	4.60	–4.76
	2001	TG22a-**TG130**	Maor	0.09	5.32	–6.88
perwd3.2	1999	**TG359**-TG411	Maor	0.06	4.78	–12.19
	2000	**TG359**-TG411	Maor	0.10	7.10	–7.66
	2001	**TG359**-TG411	Maor	0.06	5.41	–5.96
perwd4.1	2000	TG22b-**TG62**	Maor	0.05	5.41	–6.12
perwd6.1	1999	**CT184**-TG73	Maor	0.06	3.81	–11.39
	2001	**CT184**-TG73	Maor	0.05	3.85	–5.29
perwd8.1	2000	**CT28**-TG330	Maor	0.09	6.44	–6.76
	2001	**CT28**-TG330	Maor	0.08	5.79	–6.18
perwd11.1	1999	**TG619**-CD127a	Maor	0.06	5.30	–11.27
	2000	**TG619**-CD127a	Maor	0.08	5.26	–6.07
	2001	**TG619**-CD127a	Maor	0.07	4.39	–5.49
Fruit number						
fno2.1	2001	**CD38**-TG191	BG 2816	0.23	14.44	45.62
fno3.1	2001	**TG359**-TG411	BG 2816	0.12	8.71	31.36
fno11.1	2001	TG105-**TG36**	BG 2816	0.02	3.88	13.12
Yield						
yld1.1	2001	**TG19**-CT163	Maor	0.08	5.03	–10.38
yld8.1	2000	CT28-**TG330**	Maor	0.06	4.59	–24.66
	2001	CT28-**TG330**	Maor	0.09	4.26	–9.43
Flowering						
flw1.1	2000	TG19-**CT163**	Maor	0.08	4.88	–15.92
	2001	**TG19**-CT163	Maor	0.14	7.34	–16.67
flw2.1	2000	**TG191**-CD38	Maor	0.09	4.56	–15.46
flw2.2	2001	CT176-**TG48**	Maor	0.08	4.55	–11.15
flw3.1	2001	TG22a-**TG130**	BG 2816	0.06	3.68	10.58
flw4.1	2001	TG193b-**TG208**	BG 2816	0.01	3.75	3.90
flw4.2	2000	**TG22b**-CT253	Maor	0.11	6.37	–18.34
flw6.1	2001	**CT179b**-CT107	BG 2816	0.01	3.88	3.94
flw8.1	2001	**TG420P**-TG624	Maor	0.06	3.95	–10.14
flw10.1	2001	MYB-**CT154**	BG 2816	0.01	5.89	4.26
Maturity						
mat1.1	2000	**TG19**-CT163	Maor	0.11	5.73	–31.92
	2001	**TG19**-CT163	Maor	0.14	6.78	–38.29
mat4.1	2000	**TG22b**-CT253	Maor	0.07	4.15	–25.36
	2001	TG22b-**CT253**	Maor	0.13	6.79	–28.93
mat5.1	2000	CT63-**TG483**	Maor	0.09	4.71	–28.90
mat9.1	2001	**TG263**-CT211	Maor	0.07	3.84	–27.22
Seed weight						
swt2.1		CT176-**TG48**	Maor	0.095	5.90	–7.34
swt8.1		**CT28**-TG330	Maor	0.072	4.10	–6.31
swt12.1		**CD127d**-TG468	BG 2816	0.010	3.72	2.63

[a]Estimates of variation explained LOD and %A were calculated for the marker in bold that had the highest LOD within the QTL interval

that contains *yld8.1* also contains a QTL for fruit weight; therefore, the yield reduction caused by the wild allele at this locus was associated with the production of smaller fruits. The region of *yld1.1* was found as a QTL for flowering and maturity (see below), indicating that the yield reduction caused by the wild allele at this locus is a pleiotropic effect of late flowering and fruit setting.

Flowering

Nine QTLs for flowering were detected, of which only *flw1.1* was found in both 2000 and 2001. Four additional QTLs were detected in only 1 year (*flw4.1, flw4.2, flw6.1* and *flw10.1*), with sub-threshold LOD values (LOD > 3) observed in the other year. The wild alleles in the QTLs

had mixed effects on flowering; i.e., those in five QTLs caused late flowering, whereas those in the others caused early flowering.

Maturity

Four QTLs for fruit maturity were detected, of which two (*mat1.1* and *mat4.1*), were found in both years and had the greatest effect on flowering and maturity. At all QTLs, Maor alleles contributed to early maturity.

Seed weight

Three QTLs were detected that affected seed weight. For *swt2.1* and *swt8.1*, Maor alleles were associated with increased seed weight and QTLs in the same positions were found to affect fruit weight, whereas for *swt12.1*, the wild allele was associated with increased seed weight.

Discussion

Yield of pepper is a complex trait that derives from the cumulative action of genes that control several different traits, including fruit size, weight, number and earliness. Hitherto, studies on yield-related traits in pepper were mostly focused on evaluating heterosis in diallelic intraspecific crosses of *C. annuum* [reviewed by Poulos (1994)]. None of these studies used wild germplasm or interspecific crosses. Moreover, molecular markers were not employed in any of the studies to identify the individual loci that affected yield-related traits. In the present study, we analyzed the major yield components that affect the production of blocky-type pepper cultivars and used an advanced backcross QTL detection design to identify QTLs that control these traits. Previous studies of tomato and rice, involving advanced backcross QTL analysis in crosses with wild species, revealed a high percentage of favorable alleles affecting yield-related traits that had originated from the wild parents (Bernacchi et al. 1998; Fulton et al. 1997, 2000; Moncada et al. 2001; Tanksley et al. 1996; Xiao et al. 1998). We were, therefore, interested to assess the potential of advanced backcross QTL analysis in pepper and to determine the possibility that favorable QTL alleles could be found in and introgressed from a wild *C. frutescens* accession.

A total of 58 QTLs were discovered for ten different traits spanning over 26 intervals of the pepper genome in three experiments conducted over 3 years. The vast majority of the QTLs were located in 11 clusters in chromosomes 1, 2, 3, 4, 8, 10 and 11 and resulted from linkage or pleiotropy. Fruit weight was primarily correlated with fruit diameter and, to a lesser extent, with fruit length. Accordingly, all of the QTLs associated with fruit weight were also found to be associated with fruit diameter, except for two additional QTLs (*fd3.1* and *fd4.1*) that were associated only with fruit diameter. In contrast, only half of the QTLs for fruit length had positions in common with QTLs for fruit weight. Pericarp width was also highly correlated with fruit weight and with fruit diameter, and six out of the seven identified QTLs for pericarp width shared positions with QTLs for the other two traits. Fruit weight was highly negatively correlated with fruit number, and the three QTLs identified for fruit number were also found to be significant for fruit weight and diameter.

Out of ten traits evaluated, five were repeated in all three experiments, three in two experiments and two in only one experiment. Out of the 37 QTLs detected for the five traits measured in the three experiments, 18 (48%) were identified in all 3 years and 31 (83%) were detected in at least two experiments, indicating a low environment-by-QTL interaction. Overall, the two BC_2S_1 experiments identified higher percentages of QTLs common to the 2 years (70%) than the BC_2 and either of the two BC_2S_1 generations (59%). This difference probably resulted from the smaller variation in the BC_2S_1 generation than among the data obtained from single plants in the BC_2 generation because of the use of family means in the former case. The level of QTL consistency across the years was generally related to the heritability of the traits; for example, flowering, which exhibited very low heritability (0.1), had only one QTL common to both years, whereas fruit diameter, which exhibited high heritability (0.5), had seven out of ten QTLs in common to all three experiments.

Unlike the high percentage of transgressive and favorable QTL alleles that had previously been found to originate from the wild donors in tomato and rice, only a few such QTL alleles were detected in the present study. For all of the major fruit traits (weight, diameter, length, pericarp width and yield), only Maor alleles were associated with an increased phenotype. The wild alleles were associated, as expected, with increased fruit number, elongated fruit shape, and late flowering and fruit setting. For three out of the ten traits measured (fruit shape, flowering and seed weight), QTL alleles with mixed origins were detected. Only six QTLs (10%) had alleles opposite to those expected according to the parental phenotype. Because this study presents the first QTL analysis in pepper that involved a wild parent relatively closely related to *C. annuum*, additional crosses with more widely diverged *Capsicum* species will be required for a more complete exploration of the potential of marker utilization of exotic germplasm in pepper improvement.

The major QTL affecting fruit weight in this study was *fw2.1*. Although the peak LOD at *fw2.1* was at CD38, almost the entire chromosome 2 (TG48-CT277 interval) had LOD values higher than the threshold, indicating the likely occurrence in this chromosome of several linked QTLs for fruit weight. The corresponding region in tomato was previously found to contain three linked QTLs with similar effects on fruit weight (Eshed and Zamir 1996; Grandillo et al. 1999). Since CD38 had been mapped to chromosomes 5 and 10 in tomato (Tanksley et al. 1992), we could not determine which of the tomato

QTLs corresponded to pepper *fw2.1*. However, *fw2.2*, which was recently cloned in tomato (Frary et al. 2000), was shown to reside outside the peak region of the pepper QTL (Fig. 1). We are currently constructing near-isogenic lines that contain overlapping segments of pepper chromosome 2 in order to do fine mapping of fruit weight QTLs in this chromosome. The major QTL that affected fruit number in the present study was *fno2.1*, which was in the same position as the major fruit weight QTL *fw2.1*; this indicates a pleiotropic effect of this gene on fruit weight and fruit number. Similar results were recently obtained in tomato for the adjacent *fw2.2* gene, for which the reduction in fruit weight caused by the wild *fw2.2* allele was compensated by an increased number of fruits, with no change in total yield (Nesbitt and Tanksley 2001).

Fruit size, fruit number and maturity have been considered to be the major components of yield in pepper. In the present study, only two QTLs for yield were detected: one (*yld8.1*) was also associated with fruit weight and the other (*yld1.1*) with flowering and fruit setting. Therefore, most of the QTLs affecting fruit weight, fruit number and flowering/maturity did not have an effect on total yield. Our inability to detect a larger number of yield QTLs may have been because the inheritance of yield is more complex than that of the various components, i.e. that it involves the interaction of genes that control yield and yield components, as has been found for yield QTLs in barley (Kandemir et al. 2000; Zhu et al. 1999) and rice (Li et al. 1997), or it might have been because of QTLs with small effects, below the detection threshold of the present study.

The major QTL affecting fruit shape in the present study was *fs3.1*. The same QTL was previously found to be the major one affecting fruit shape in *C. annuum*, in which it accounted for more than 60% of the phenotypic variation for this trait (Ben Chaim et al. 2001). However, the effect of the oval-fruited BG 2816 allele at *fs3.1* on fruit elongation, in the present study, was less than that found by Ben Chaim et al. (2001), who crossed Maor with the elongated-fruited parent, Perennial.

The present paper is our second report on fruit-related QTLs in pepper. In the first study (Ben Chaim et al. 2001), the same blocky-fruited parent, Maor, was used in an F_2 cross with the Indian *C. annuum* accession Perennial to map QTLs for 14 traits. A total of 76 QTLs were identified for the seven traits analyzed in both studies. Although at least one possible orthologous QTL (QTLs were considered to be orthologous if both were mapped within the same 15-cM region) was found for each trait in both studies, only ten (13%) QTLs were found to be possibly orthologous. These included *fw2.1, fw3.1* and *fw4.1* for fruit weight, *fl2.1* for fruit length, *fd2.1* and *fd3.1* for fruit diameter, *fs3.1* for fruit shape, *perwd3.1* and *perwd4.1* for pericarp width, *flw2.1* and *flw3.1* for flowering and *swt2.1* for seed weight. This level of QTL orthology was similar to the percentages of QTLs in common between advanced backcross populations of tomato; those ranged from 11 to 19% (Fulton et al. 2000).

The use of tomato RFLP markers for mapping the pepper and tomato genomes enabled us to detect possible orthology of QTLs for similar traits in these two solanaceous species. Out of the eight fruit weight QTLs identified in the present study, five (*fw1.1, fw2.1, fw3.1, fw4.1* and *fw11.2*) may be orthologous to tomato fruit weight QTLs that were identified in at least two previous studies (Grandillo et al. 1999). The other three fruit weight QTLs found in the present study (*fw8.1, fw10.1* and *fw11.1*) may be orthologous to tomato QTLs found in only one previous study (Grandillo et al. 1999). In contrast to the high putative conservation of fruit weight QTLs in the two species, only one (*fs3.1*) out of the six fruit shape QTLs identified in the present study could correspond to a tomato fruit shape QTL (Grandillo et al. 1999). Out of the six fruit length and ten fruit diameter QTLs detected in the present study, two (*fl2.1* and *fl3.1*) and four (*fd1.1, fd2.1, fd4.1* and *fd11.2*) might correspond to tomato fruit length and fruit diameter QTLs, respectively (Lippman and Tanksley 2001). Out of the seven pericarp width QTLs detected in the present study, one (*perwd1.1*) could correspond to a tomato pericarp thickness QTL (Fulton et al. 2000). The two yield QTLs identified in the present study could correspond to tomato yield QTLs (*ydt1.2* and *ydt8.1*) identified by Bernacchi et al. (1998). All the three seed weight QTLs observed in the present study were possibly orthologous to tomato seed weight QTLs identified by Doganlar et al. (2000), while two of them (*swt2.1* and *swt12.1*) were found in corresponding positions by Goldman et al. (1995). Because hundreds of QTLs have been identified in numerous studies in tomato, it is possible that some of the putative pepper/tomato orthologous QTLs were found because of type-I errors. Therefore, improved mapping resolution and use of a common set of markers will be required to increase the confidence of declaring QTL orthology in these two species.

Acknowledgements This research was supported by The Israel Science Foundation (Grant no. 643/00) and by Hazera Genetics.

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