Theor Appl Genet (1995) 90: 925–932

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Quantitative trait locus analysis of a recombinant inbred line population derived from a *Lycopersicon esculentum* × *Lycopersicon cheesmanii* cross

Received: 11 April 1994 / Accepted: 22 September 1994

Abstract Quantitative trait loci influencing fruit traits were identified by restriction fragment length polymorphism (RFLP) analysis in a population of recombinant inbred lines (RIL) derived from a cross of the cultivated tomato, *Lycopersicon esculentum* with a related wild species *Lycopersicon cheesmanii*. One hundred thirty-two polymorphic RFLP loci spaced throughout the tomato genome were scored for 97 F_8 RIL families. Fruit weight and soluble solids were measured in replicated trials during 1991 and 1992. Seed weight was measured in 1992. Significant ($P<0.01$ level) quantitative trait locus (QTL) associations of marker loci were identified for each trait. A total of 73 significant marker locus-trait associations were detected for the three traits measured. Fifty-three of these associations were for fruit weight and soluble solids, many of which involved marker loci signficantly associated with both traits. QTL with large effects on all three traits were detected on chromosome 6. Greater homozygosity at many loci in the RIL population as compared to F_2 populations and greater genomic coverage resulted in increased precision in the estimation of QTL effects, and large proportions of the total phenotypic variance were explained by marker class variation at significant marker loci for many traits. The RIL population was effective in detecting and discriminating among QTL for these traits previously identified in other investigations despite skewed segregation ratios at many marker loci. Large additive effects were measured at significant marker loci. Lower fruit weight, higher soluble solids, and lower seed weight were generally associated with RFLP alleles from the *L. cheesmanii* parent.

Key words Recombinant inbred line · Quantitative trait locus · Restriction fragment length polymorphism · Tomato

Communicated by M. Koornneef

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Introduction

Efforts to localize and characterize associations between segregating molecular marker loci and quantitative traits have expanded in recent years. Linkage between DNA markers and quantitative trait loci (QTL) controlling important agronomic traits has been reported (Beavis et al. 1991; Edwards et al. 1987; Lander and Botstein 1989; Paterson et al. 1988; Edwards et al. 1992). Much of the published QTL information in crop plants has been obtained from experiments conducted in early segregating generations, such as F_2 or F_3. Generally, mean phenotypic estimates have been regressed on genotypic marker classes at molecular marker loci in order to estimate QTL effects. Given the difficulty of obtaining replicated phenotypic data from individual F_2 plants in obligate sexually-propagated species, genetically advanced progeny (e.g., beyond the F_2 generation) should be better suited for QTL analysis. Populations advanced beyond the F_3 have only recently been utilized in QTL mapping efforts (Mansur et al. 1993; Eshed and Zamir 1994) Recombinant inbred lines (RIL), which are produced by inbreeding the progeny of an F_2 plant derived from two inbred lines, offer certain specific advantages in QTL analysis. Since each RIL family representing a segregate from the original F_2 population is in essence an inbred line, multi-environment trials can be conducted to obtain increased precision of genetic variance estimates for a particular trait (Burr et al. 1988). In addition, RIL constitute a permanent mapping population in which near-homozygosity is often obtained (Burr et al. 1988); thus multiple workers can contribute to genetic mapping and subsequent QTL analysis efforts.

A major objective in tomato breeding programs throughout the world is to improve the soluble solids (SS) content in fruits of high-yielding varieties. The amount of processed product which can be obtained from processing tomatoes is directly related to the SS content, and in fresh market tomatoes high SS is associated with superior taste. The cultivated tomato, *Lycopersicon esculentum* is relatively low in SS (approximately 5%). A source for increased SS content (approximately 15% SS) has been identified in two related wild species: *L. chmielewskii* and *L. cheesmanii*, both of which also possess much smaller fruit than *L. esculentum* (Rick 1974; Osborn et al. 1987, Tanksley and Hewitt 1988). Despite the economic importance of SS in tomatoes and the availability of donor germ plasm with high solids levels, efforts to improve this trait have generally been unsuccessful because of a negative correlation between yield and SS content. A number of recent investigations have identified QTL for SS in crosses of *Lycopersicon* species (Paterson et al. 1988, 1990, 1991; Tanksley and Hewitt 1988; Osborn et al. 1987), however these studies have been carried out on F_2 and F_3 populations, which render the estimation of quantitative effects more difficult than for inbred lines.

Due to its abundance of well-characterized molecular marker loci (Tanksley et al. 1993) the tomato has played an important role in the development of QTL analysis strategies (Paterson et al. 1988, 1990; Tanksley and Hewitt 1988). These contributions have also provided a wealth of information on QTL positions in tomato (DeVicente and Tanksley 1993; Osborn et al. 1987, Tanksley and Hewitt 1988, Paterson et al. 1988, 1991). Paterson et al. (1988) identified QTL for mass per fruit, soluble solids, and pH in F_2 and BC_1 populations derived from *L. esculentum* and *L. chmielewskii*. Collectively these QTL accounted for 44–58% of the total phenotypic variation for these traits. Subsequent fine-mapping of these QTL (Paterson et al. 1990) has revealed close marker-QTL associations. Recent work by Paterson et al. (1991) detailed the identification of 29 putative QTL for soluble solids, mass per fruit, and pH in a *L. esculentum* × *L. cheesmanii* cross. *Lycopersicon cheesmanii* is a wild red-fruited species related to *L. escuelntum* and native to the Galapagos Islands. Many of these QTL mapped to similar chromosomal locations as those identified in crosses with *L. chmielewskii*, suggesting an overall positional consistency for QTL in *Lycopersicon* species. Since phenotypic estimates were based upon F_2 and F_3 family data, experimental error associated with these measurements would be expected to be larger than for replicated progenies. More precise estimates of quantitative traits should be available with the use of RIL. The objective of this investigation was to utilize a RIL population in examining associations between polymophic molecular marker loci and quantitative traits in tomato.

Materials and methods

RIL families were developed from a cross of the inbred cultivar 'UC204C' with the *L. cheesmanii* accession LA483 (Paterson et al. 1991). Three hundred and fifty individual F_2 plants derived from this cross were grown in a completely randomized design in Davis, California, in 1987. Single-seed descent was practiced for six generations on all plants descended from the original F_2 population however, due to lethality and inbreeding depression, 97 F_8 RIL families remained following selfing. These RIL families formed the segregating population used in QTL analyses. Quantitative trait measurements were assessed with each RIL family represented by six replications of single plants. Measurements were based on mean values for all mature fruit harvested from each family. Plots containing families exhibiting the determinate and indeterminate growth habit were 0.5 m^2 and 1 m^2, respectively. The experiment was planted in a randomized complete block design and grown in 1991 and 1992 at the Acre Experiment Station in Acre, Israel. Fruit weight in grams per fruit (FW) and soluble solids (SS, °Brix) were determined as described by Tanksley and Hewitt (1988). RIL families were visually scored for fruit color (yellow/orange/red) and growth habit (determinate/indeterminate). These morphological traits correspond to the *B* and *SP* loci, respectively. Seed weight (SDWT) was measured on seed from the F_8 generation as the mass per 100 seeds.

DNA isolation, restriction digestion, Southern blotting, and hybridization were performed as described in Paterson et al. (1991). DNA was extracted from a bulk of 30 F_8 individuals from each RIL. Marker-restriction enzyme combinations were chosen for their ability to identify restriction fragment length polymorphism (RFLP) between *L. esculentum* and *L. cheesmanii*. Nine restriction enzymes were used for digesting total genomic DNA: *Bst*I, *Dra*I, *Eco*RI, *Eco*RV, *Hae*III, *Hin*dIII, *Msp*I, *Sca*I, *and Xba*I. A linkage map consisting of 132 RFLP markers was constructed in the population of RIL (see companion paper, Paran et al. 1995). General similarity and colinearity between this genetic map and published linkage maps derived from interspecific crosses (Tanksley et al. 1992) was observed. The probes used were a subset of those described in Tanksley et al. (1992) selected for thorough coverage of the tomato genome and polymorphism between the *L. esculentum* and *L. cheesmanii* species. Forty-five of the 73 markers used to construct the genetic map described in Paterson et al. (1991) were also included in this investigation. A single isozyme marker, *Adh1*, was scored in the RIL population.

Means and standard errors were determined for each trait for the RIL population (Table 1). Skewness and kurtosis of the phenotypic distribution for each of these traits was tested, and normality was improved by $\log_{10}$ transformation of all three traits (Fig. 1). Phenotypic correlations were calculated for all traits. One-way analysis of variance (ANOVA) was performed on all loci for each trait separately (Edwards et al. 1987) using an *F*-test (SAS Institute 1988). The heterozygous marker class was included in the ANOVA. Associations of marker loci with QTL linkage were considered to be significant when the *F*-test exceeded a value necessary for a probability value less than 0.01. The explained variance (R^2) value was calculated for each significant marker locus. The additive effects (a) were obtained for each locus by substracting one homozygous marker class from the other homozygous marker class and dividing by 2.

Results

Phenotypic evaluation of RIL families

Significant differences among RIL families were detected for each trait measured. No significant family × year interaction was measured for FW and SS; thus these traits were combined over years for analyses. SDWT was measured only once on F_8 seed; thus no environmental component existed for this trait.

The mean FW in the RIL population was 8.03 g (Table 1), which is close to values reported for F_2 and F_3 generations from which this RIL population was derived (Pa-

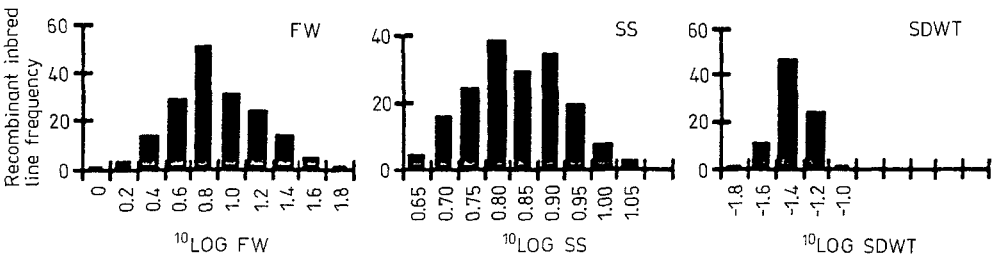


Fig. 1 Distribution of phenotypes for each trait in the RIL population

Table 1 Means, ranges, and standard errors for quantitative traits studied in the RIL population

Trait	Mean	Range	SD
FW (g fruit^{-1})	8.03	0.5–55.3	6.97
SS (Brix)	6.68	4.1–11.3	1.40
SDWT (g 100 seeds^{-1})	0.036	0.014–0.067	0.01

Table 2 Phenotypic correlations[a] among quantitative traits measured in the RIL population

	FW	SS
SS	–0.59**	
SDWT	0.62**	–0.37**

** Denotes significance at the $P<0.01$ level
[a] Correlations measured using Pearson correlation coefficients on mean FW, SS, and SDWT from 1991 and 1992

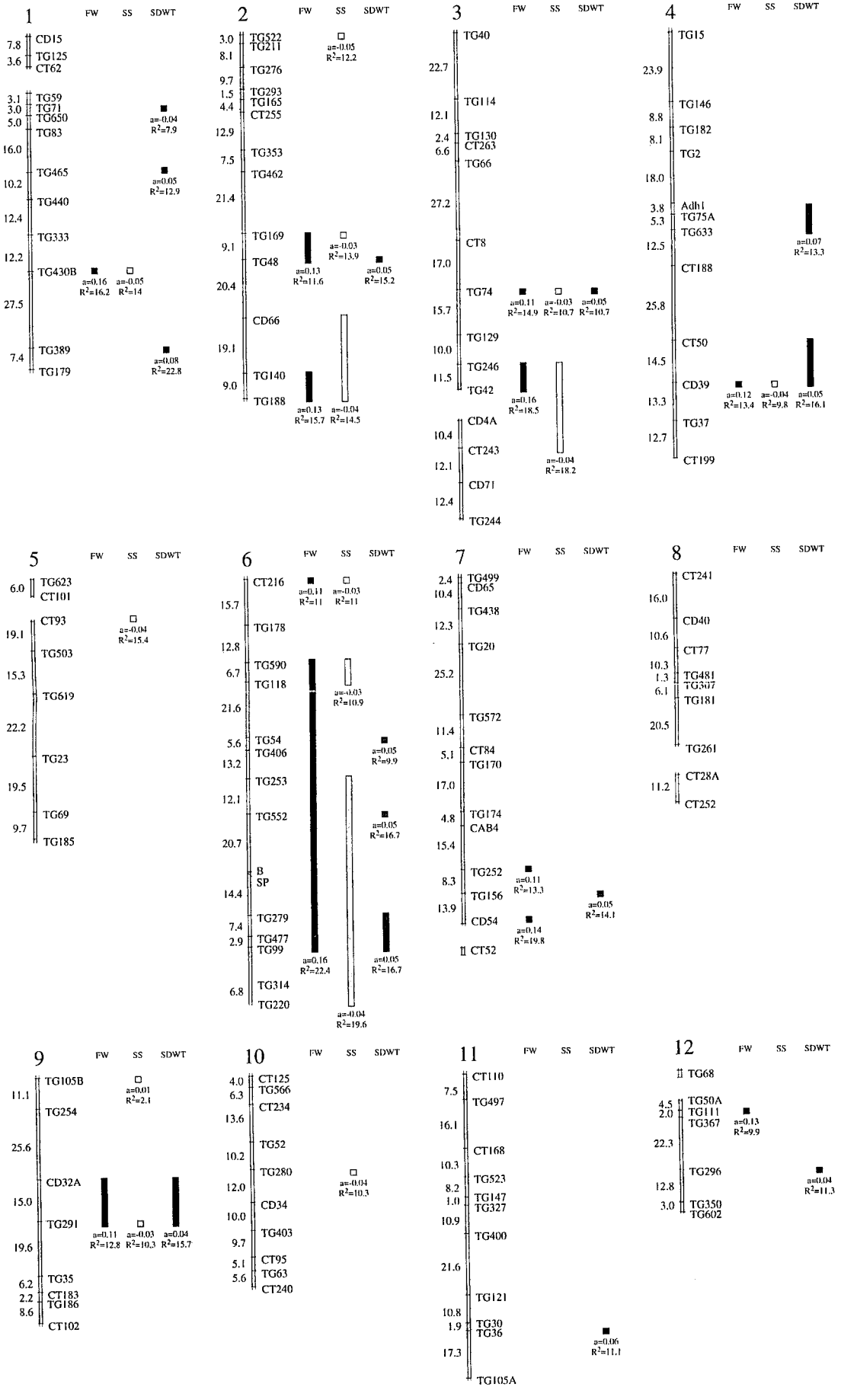
terson et al. 1991). FW values in the RIL ranged from 0.5 g to 55 g (Fig. 1). These workers reported that the *L. esculentum* accession (UC204B) exhibited a FW of approximately 82 g in contrast to the *L. cheesmanii* accession (LA483), which had a FW of less than 3 g.Thus, the average RIL more closely resembles the previously reported generations and the *L. cheesmanii* accession than the cultivated *L. esculentum*, however, variation approaching the parental accessions was observed. SS values in the RIL population averaged 6.7 Brix and ranged from 4.1 to 11.3. The mean SS value for the RIL population is consistent with F_3 data reported by Paterson et al. (1991). Strong negative correlation was observed between FW and SS (–0.59**, Table 2). A negative relationship between these two traits in tomato has been well-documented (Ibarbia and Lambeth 1969, Paterson et al. 1988, 1991). SDWT exhibited a significant negative correlation with SS and a significant positive correlation with FW in the RIL.

QTL associations in RIL families

Significant associations with FW were detected for 25 marker loci on 8 different chromosomes, based on a genetic linkage map created in this population (Paran et al. 1995; Fig. 2). At every significant marker locus, the RFLP allele from the *cheesmanii* parent was associated with lower FW. Eleven of these significant marker loci were located on chromosome 6. Twenty-eight significant marker loci were detected for SS on 8 different chromosomes. In each case, RFLP alleles donated by the *cheesmanii* parent were associated with high SS. Twelve of these marker loci were located on chromosome 6. Off the significant loci for these two traits, 43% were therefore found on chromosome 6. Six out of the 8 chromosomes exhibited significant marker loci for FW and SS, and 19 loci were significant for both traits. The *B* and *SP* loci on chromosome 6 were highly significantly associated with FW and SS in this investigation. The *SP* locus influences FW and SS in a range of genetic backgrounds (Emery and Munger 1970, Paterson et al. 1988). Indeterminate RIL families, characterized by the dominant *SP* allele, exhibited greater FW and SS than determinate RIL families (homozygous for the recessive *sp*) in this investigation. Twenty significant marker loci were detected for SDWT on 9 different chromosomes. One-fourth of these loci were located on chromosome 6. For nearly all 20 marker loci, RFLP alleles donated by the *cheesmanii* parent were associated with low SDWT.

Chromosomal regions exhibiting significant associations for 2 or more linked marker loci for FW were detected on chromosomes 2, 3, 6, 7, and 9. Clusters of two or more linked marker loci significantly associated with SS were detected on chromosomes 2, 3, 6, and 9. Clusters of 2 or more significant marker loci on chromosomes 2, 3, 6, and 9 were significant for both FW and SS. Clusters of 2 or more significant marker loci for SDWT were observed on chromosomes 1, 4, and 6; the latter 2 of which were also associated with FW and SS. The finding of several marker loci showing significant associations with FW, SS, and SDWT is in agreement with both the reported significant correlations among these traits (Paterson et al. 1991) and correlations measured in this investigation (Table 2).

Many of the reported significant marker-trait associations for FW and SS tended to exhibit large R^2 values (Fig. 2). Significant marker loci for FW on chromosome 6 exhibited R^2 values from 11.0% (CT216) to 32.9% (TG253). A large proportion of the total phenotypic variation for FW was explained by variation at the *B* locus (32.2%), also located on chromosome 6. Due to colinearity of markers on the same chromosome, it is quite likely these loci are explaining similar phenotypic variation. A number of marker loci which were significant for multiple traits, such as TG430 (chr. 1) and TG169 (chr. 2) for both FW and SS, explained similar amounts of variation. For example, variation at TG430 explained 16.2% of the total phenotypic


1
FW SS SDWT
7.8 CD15
3.6 TG125
CT62
3.1 TG59
3.0 TG71
5.0 TG650
TG83
16.0
TG465
10.2
TG440
12.4
TG333
12.2
TG430B
27.5
7.4 TG389
TG179
a=-0.04 R²=7.9
a=0.05 R²=12.9
a=0.16 R²=16.2
a=-0.05 R²=14
a=0.08 R²=22.8
2
FW SS SDWT
3.0 TG522
8.1 TG211
TG276
9.7
1.5 TG293
4.4 TG165
CT255
12.9
TG353
7.5
TG462
21.4
9.1 TG169
TG48
20.4
CD66
19.1
9.0 TG140
TG188
a=-0.05 R²=12.2
a=-0.03 R²=13.9
a=0.05 R²=15.2
a=0.13 R²=11.6
a=0.13 R²=15.7
a=-0.04 R²=14.5
3
FW SS SDWT
22.7 TG40
TG114
12.1
2.4 TG130
6.6 CT263
TG66
27.2
CT8
17.0
TG74
15.7
10.0 TG129
11.5 TG246
TG42
10.4 CD4A
CT243
12.1
CD71
12.4
TG244
a=0.11 R²=14.9
a=-0.03 R²=10.7
a=0.05 R²=10.7
a=0.16 R²=18.5
a=-0.04 R²=18.2
4
FW SS SDWT
23.9 TG15
TG146
8.8
TG182
8.1
TG2
18.0
3.8 Adh1
5.3 TG75A
TG633
12.5
CT188
25.8
CT50
14.5
CD39
13.3
TG37
12.7
CT199
a=0.07 R²=13.3
a=0.12 R²=13.4
a=-0.04 R²=9.8
a=0.05 R²=16.1
5
FW SS SDWT
6.0 TG623
CT101
19.1 CT93
TG503
15.3
TG619
22.2
TG23
19.5
9.7 TG69
TG185
a=-0.04 R²=15.4
6
FW SS SDWT
15.7 CT216
TG178
12.8
6.7 TG590
TG118
21.6
5.6 TG54
13.2 TG406
TG253
12.1
TG552
20.7
B
SP
14.4
7.4 TG279
2.9 TG477
TG99
6.8 TG314
TG220
a=0.11 R²=11
a=-0.03 R²=11
a=-0.03 R²=10.9
a=0.05 R²=9.9
a=0.05 R²=16.7
a=0.16 R²=22.4
a=0.05 R²=16.7
a=-0.04 R²=19.6
7
FW SS SDWT
2.4 TG499
10.4 CD65
TG438
12.3
TG20
25.2
TG572
11.4
5.1 CT84
TG170
17.0
4.8 TG174
CAB4
15.4
8.3 TG252
13.9 TG156
CD54
CT52
a=0.11 R²=13.3
a=0.14 R²=19.8
a=0.05 R²=14.1
8
FW SS SDWT
CT241
16.0
CD40
10.6
CT77
10.3
1.3 TG481
TG307
6.1
TG181
20.5
TG261
11.2 CT28A
CT252
9
FW SS SDWT
11.1 TG105B
TG254
25.6
CD32A
15.0
TG291
19.6
6.2 TG35
2.2 CT183
8.6 TG186
CT102
a=0.01 R²=2.1
a=0.11 R²=12.8
a=-0.03 R²=10.3
a=0.04 R²=15.7
10
FW SS SDWT
4.0 CT125
6.3 TG566
CT234
13.6
TG52
10.2
12.0 TG280
CD34
10.0
TG403
9.7
5.1 CT95
5.6 TG63
CT240
a=-0.04 R²=10.3
11
FW SS SDWT
CT110
7.5
TG497
16.1
CT168
10.3
8.2 TG523
1.0 TG147
TG327
10.9
TG400
21.6
TG121
10.8
1.9 TG30
TG36
17.3
TG105A
a=0.06 R²=11.1
12
FW SS SDWT
TG68
4.5 TG50A
2.0 TG111
TG367
22.3
TG296
12.8
3.0 TG350
TG602
a=0.13 R²=9.9
a=0.04 R²=11.3

variation for FW and 14% for SS. TG169 explained 12.4% of the total phenotypic variation for FW and 13.9% for SS.

RFLP segregation at QTL

Seventy-three percent of the RFLP loci deviated significantly from the expected 1:1 segregation expected between the two homozygous classes (Paran et al. 1995). For 98% of the deviant loci, *L. esculentum* alleles were present in greater frequency than *L. cheesmanii* alleles. This finding is in contrast to results reported by de Vincente and Tanksley (1993) and Zamir and Tadmor (1986) with respect to skewed segregation ratios in other interspecific crosses. Those workers reported that the majority of loci segregating in an *L. esculentum*×*L. pennellii* cross were skewed towards the *L. pennellii* allele; thus demonstrating skewness toward the wild species parent. The RIL population was also investigated in the F_2 and F_3 generations (Paterson et al. 1991) and found to possess some loci that deviated towards the *L. esculentum* parent. In most cases, these deviations were preserved in the RIL population (Paran et al. 1995). Unintentional selection for cultivated phenotype during the inbreeding process may have skewed segregation ratios toward the *L. esculentum* parent. This skewing did not affect the detection of significant QTL at marker loci previously shown to contain QTL in the F_2 and F_3 (Paterson et al. 1991).

Despite the relatively high level of heterozygosity present in the RIL population (15%), significantly greater FW and SS was not associated with the heterozygous marker class. All significant marker loci for FW and all but 2 significant marker loci for SS were characterized by intermediate performance of the heterozygous marker class. In the two cases where this was not true for SS, heterozygous marker class means were nearly identical to that of the homozygous *L. chessmanii* marker class. The number of observations in the heterozygous marker class were fewer than in the homozygous *L. cheesmanii* marker class for most loci; thus means comparisons with this marker class would generally be unbalanced. In general, marker classes at QTL for FW and SS were skewed more toward *L. esculentum* homozygotes as than to *L. cheesmanii* homozygotes, with an average of nearly 30% more *L. esculentum* homozygotes than *L. cheesmanii* homozygotes.

Gene action controlling QTL expression

Significant additive gene action was detected at all significant marker loci for FW and SS. In every case, a positive additive effect was associated with *L. esculentum* alleles, while the reverse was true of *L. cheesmanii* alleles (Fig. 2). Positive additive effects reflected a higher mean value of the *L. esculentum* homozygote. Additive effects were positive for FW and negative for SS, pointing out that RFLP alleles associated with high FW were also associated with the *L. esculentum* parent, while RFLP alleles associated with high SS were also associated with the *L. cheesmanii* parent. Both the presence of additive gene action and the sign of the effects are consistent with results reported by Paterson et al. (1991) using the F_2 and F_3 populations from which these RIL were derived.

Fig. 2 Figure 2. Distribution of significant ($P<0.01$) marker-QTL associations for FW, SS, and SDWT across the 12 tomato chromosomes. Map positions are based on Paran et al. (1995). *Bars to the right* of each chromosome indicate the presence of significant QTL for FW, SS, and SDWT, respectively ($P<0.01$). The magnitude of R^2 and values for a are given *under* each bar

Discussion

One hundred and thirty-two RFLP markers were screened on the RIL population in this investigation. Paterson et al. (1991) screened 73 RFLP markers in the F_2 and F_3 generations from which the RIL population was generated. The number of significant marker locus-QTL associations for FW and SS in this study was greater than that reported for these traits by Paterson et al. (1991). Although more significant associations were detected in this investigation, nearly twice as many markers were screened. Forty-five common marker loci were screened in the two investigations. Significant associations at 5 of the 6 same chromosomes found to be significant for FW (1, 2, 3, 6, 7, 11), and all of the same chromosomes for SS (2, 3, 6), in Paterson et al. (1991) were detected in this investigation; however, some marker locations varied. QTL for FW were found in similar chromosome positions in both studies on chromosomes 2, 3, 6, and 7. For example, several marker loci (such as TG42) in the region from TG74 to CD71 located on chromosome 3 were found to be significantly associated with FW in both investigations. Chromosome 6, which contains many significant marker loci for both FW and SS, exhibited consistent associations between this investigation and the Paterson et al. (1991) study for TG118 and TG253. TG54, located on chromosome 6, was significant for FW in both investigations. Although all marker loci were not common to both investigations, significant regions for FW were consistently observed in four primary regions: the short arms of chromosomes 2, 3, and 7, and in multiple regions on chromosome 6. A similar pattern was detected for SS, where marker loci on chromosomes 2, 3, and 6 were found to be significantly associated with SS in both investigations. CD66 on chromosome 2, TG74 and TG42 on chromosome 3, and TG118, TG253, *SP*, and TG314 on chromosome 6 were associated with SS in both investigations. Additional QTL were detected on chromosomes 1, 4, 5, 9, and 10 for SS in this investigation, suggesting the possibility that greater precision for QTL estimation in the RIL population may have resulted in the identification of more significant marker loci. In general, these additional QTL were not of a large magnitude (e.g., TG280 for SS on chromosome 10 and CD39 for FW and SS on chromosome 4). Many of these QTL, with the exception of chromosome 9, occurred in marker-linked regions eval-

uated by Paterson et al. (1991). However, genome coverage was significantly smaller in that investigation (73 loci) compared to the present study (132 loci), suggesting that Patterson et al. may not have detected QTL with small effects in the F_2 and F_3 generations. The QTL for FW and SS on chromosome 9 identified in this investigation were also of a relatively minor magnitude, but might have failed to have been detected by Paterson et al. due to their use of only 2 RFLP markers on this chromosome. The difference in number of QTL detected between the two studies may also reflect the potential for error associated with phenotypic data from individual F_2 or F_3 plants. Replicated evaluations over years, which are made feasible by the RIL population, may enable the detection of more QTL with smaller phenotypic differences between parents due to decreases in error variance (Soller and Brody 1976). Paterson et al (1990) and Shrimpton and Robertson (1988) have demonstrated that the detection of QTL with small effects becomes increasingly easier as QTL effects are fixed in a population. Fixation of QTL effects is a feature of the RIL population that may facilitate identification of minor QTL.

Genes controlling SDWT have not been determined in previous QTL mapping efforts. Given the large differences in SDWT between the parents used to develop the RIL, this population is ideally suited to the identification of QTL for this trait. QTL for SDWT often appeared in close proximity to QTL for FW and SS. Given the strong correlations between SDWT and both FW and SS it is not surprising that similar QTL positions were identified. The largest single QTL for SDWT was detected on chromosome 1 (TG389, R^2=22.8), while both chromosomes 4 and 6 contained 5 colinear QTL for SDWT each. Closely linked QTL for SDWT on chromosome 4 (*adh1*, TG75, TG633) and a single QTL on chromosome 11 (TG36) occurred in regions without QTL for FW and SS, suggesting the possibility of genes controlling only SDWT in this region.

The locations of QTL in this investigation are consistent with those reported by Paterson et al. (1988) in their analysis of a population derived from a cross of *L. esculentum* × *L. chmieliewskii*, again suggesting positional consistency of QTL in *Lycopersicon* species. Tanksley and Hewitt (1988) and Osborn et al. (1987) identified chromosomal regions associated with SS in a cross of *L. esculentum* × *L. chmielewskii*. Tanskley and Hewitt (1988) reported that these associated regions reside on chromosomes 7 and 10. No significant marker loci for SS were identified on chromosome 7 in this investigation; however significant associations between marker loci and FW were detected on the distal portion of the short arm of this chromosome, which was also identified as carrying an introgressed *L. chmielewskii* segment. Introgressed segments from *L. chmielewskii* which were responsible for changes in SS content also affected FW, suggesting the possibility that QTL for FW may reside in this location in *Lycopersicon* species.

Compared to other QTL mapping efforts, relatively large R^2 values were observed for FW and SS in this investigation. For example, QTL on the short arm of chromosome 6 were identified by a number of marker loci, including the morphological marker *B*. While variation at this locus explained approximately 7% of the total phenotypic variation in the F_2 studied by Paterson et al. (1991), variation at this locus explained 32.3% of the total phenotypic variation in our investigation. The relatively high proportion of phenotypic variance explained may simply be due to the inclusion of only the most significant marker loci in the QTL model. On the other hand, the increase in R^2 values may reflect the precision gained in quantitative trait estimation using RIL. Estimates of the percentage of total phenotypic variance explained would not include nonadditive genetic effects in an RIL population as compared to an F_2, thus potentially decreasing the gap between total phenotypic variance and the percentage of this variance that may be explained by variation at marker loci. Given their relatively high level of homozygosity, these RIL may function like inbred lines and allow for more accurate estimation of phenotypic data. Our results demonstrate larger amounts of phenotypic variance explained (based upon R^2 values) for FW and SS than in previous investigations (Paterson et al. 1991). This confirms one of the predicted advantages for RIL populations in QTL analysis and suggests that more accurate estimation of the total phenotypic variance may be estimable using RIL population.

The most significant QTL effects for FW and SS in this investigation were found on chromosome 6. This finding is in agreement with results reported by a number of investigators (Paterson et al. 1988, 1991) and suggests that QTL for these traits may reside in similar chromosomal locations in different tomato crosses. Paterson et al. (1988) detected QTL for FW and SS on the short arm of chromosome 6 in a backcross population derived from a cross of *L. esculentum* × *L. cheesmanii*. These QTL were also detected by Paterson et al (1991) using *L. cheesmanii* and in this investigation. Tanksley and Hewitt (1988) detected QTL for SS on chromosomes 7 and 10 using a set of *L. chmielewskii* introgression lines. Although QTL for SS were not detected in this investigation, Paterson et al. (1988, 1991) found QTL for SS in two different tomato crosses. Both the *B* and *SP* loci were significantly associated with FW and SS in this investigation. These loci are located in close proximity on the short arm of chromosome 6. The *SP* locus has been shown to influence FW and SS in other genetic backgrounds (Emery and Munger 1970) and an interspecific cross (Paterson et al. 1988), further demonstrating the importance of this region to these quantitative traits. RIL carrying the *sp* allele (determinate) had lower FW and SS than those RIL carrying the *SP* allele, a pattern which was first noted by Emery and Munger (1970). The importance of the *SP* locus to FW and SS content in tomato suggests that additional investigation of the physiological genetics of this response is warranted for further manipulation of these traits.

Fruit weight and SS appear as correlated traits in numerous investigations where processing tomato yield and its components are measured. A majority of the markers significantly associated with FW were also significantly associated with SS in this investigation. The genetic control of FW and SS has not yet been shown to be distinct,

thus leaving open the possibilities of either linkage or pleotropy as the cause of their correlation. Separation of QTL effects for FW and SS may be accomplished through the development of fine mapping approaches (Paterson et al. 1990) or QTL analysis in populations segregating for only one of these traits. At present there is little information regarding QTL analysis of correlated traits. Goldman et al. (1993) identified significant associations between RFLP alleles and QTL controlling protein and starch concentration in the maize kernel. Many of these QTL likely influenced both traits due to the inverse physiological relationship between protein and starch synthesis in maize. Nienhuis and Helentjaris (1990, 1989) proposed the use of a selection index as an aid to the development of high SS tomato germ plasm. This index was based on the standardized effects of specific RFLP loci found to be associated with SS and FW in a segregating population derived from a cross of the cultivar 'UC82' with a *L. chmielewskii* accession, LA1028. By standardizing the SS and FW values for each line at specific QTL, these workers proposed that manipulation of these traits in a breeding program could be managed successfully.

In conclusion, results from this investigation demonstrate the effectiveness of using RIL populations in QTL analysis. The RIL population was effective in the identification of large QTL in tomato, many of which are supported by findings from other investigations (Paterson et al. 1988, 1991). Thus, there is evidence for the idea that some QTL controlling these traits may reside in similar chromosomal locations in different genetic backgrounds. Additional QTL were identified for FW and SS, two traits which have been extensively studied in tomato. These QTL were primarily of small magnitude and likely detectable in the RIL due to additional marker saturation of the genome and greater precision in estimation resulting from inbreeding and controlling error in field trials. A number of genomic regions controlling these traits were identified by clusters of linked RFLP markers, suggesting the introgression of QTL alleles for desirable traits such as high SS may be possible with marker-assisted selection. Because most QTL identified showing favorable effects for SS also had unfavorable effects for FW, care will need to be taken when using marker-assisted or conventional selection for SS to assure maintenance of FW. Results from this investigation demonstrate that the RIL population should become a useful tool for the dissection of QTL and contribute to our understanding of quantitative genetics in tomato.

Acknowledgements The authors wish to thank E. Harel, T. Pleban, M. Emanuel, and A. Natur for technical assistance, B. S. Yandell, G. Coors for assistance with statistical analyses, and Y. Eshed for helpful discussions. This work was supported in part by grant FU-0164 from the Binational Agricultural Research and Development Fund, the Ministry of Science and Technology of Israel, and the Commission of the European Communities.

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