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Dynamic QTL analysis for fruit lycopene content and total soluble solid content in a *Solanum lycopersicum* x *S. pimpinellifolium* cross

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ABSTRACT. Fruit lycopene content and total soluble solid content are important factors determining fruit quality of tomatoes; however, the dynamic quantitative trait loci (QTL) controlling lycopene and soluble solid content have not been well studied. We mapped the chromosomal regions controlling these traits in different periods in $F_{2:3}$ families derived from a cross between the domestic and wild tomato species *Solanum lycopersicum* and *S. pimpinellifolium*. Fifteen QTLs for lycopene and soluble solid content and other related traits analyzed at three different fruit ripening stages were detected with a composite interval mapping method. These QTLs explained 7-33% of the individual phenotypic variation. QTLs detected in the color-changing period were different from those detected in the other two periods. On chromosome 1, the soluble solid content QTL was located in the same region during the color-changing and full-ripe periods. On chromosome 4, the same QTL for lycopene content was found during the color-changing and full-ripe periods. The QTL for lycopene content on chromosome 4 co-located with the QTL for soluble solid content during the full-ripe period. Co-location of lycopene content QTL

and soluble solid content QTLs may be due to pleiotropic effects of a single gene or a cluster of genes via physiological relationships among traits. On chromosome 9, the same two QTLs for lycopene content at two different fruit ripening periods may reflect genes controlling lycopene content that are always expressed in tomato fruit development.

Key words: Lycopene content; *Solanum lycopersicum* tomato; Total soluble solid content; QTL mapping

INTRODUCTION

Tomato (*Solanum lycopersicum*) is widely consumed, and its health benefits are well known. Antioxidants in tomato fruits have been a public health focus for many years. The lycopene content (LYC) in tomato fruit is an important source of lipid-soluble antioxidants in the human diet and can prevent the initiation or propagation of oxidizing chain reactions (Rousseaux et al., 2005; Wu and Kubota, 2008; Riadh et al., 2011). Total soluble solid content (SSC) is one of the main components of tomato flavor (Kader, 1986), and it is the property in tomato most likely to match the consumer perception of internal quality (Arazuri et al., 2007). LYC and SSC are the main quality traits of tomato fruit. However, a range of genetic and environmental factors that result in quantitative variation across varieties governs tomato fruit quality, and the inheritance is complex. Therefore, overcoming the genetic linkage between fruit quality traits presents a challenge for conventional breeding methods. The use of quantitative trait locus (QTL) mapping to find major genes and functional markers and improve the ability to control quantitative traits is an effective way to solve these problems.

Conventional breeding methods provide little information on the chromosomal regions controlling these complex quality traits or the simultaneous effects of each chromosomal region on other traits such as epistasis, pleiotropy, and linkage (Semel et al., 2006; Kuan-Hung et al., 2010). If based only on phenotype analysis, selection by conventional breeding methods is extremely difficult when genotype-environment interactions are substantial. No reliable field screening technique exists that can be used year after year and generation after generation.

One approach to facilitate the selection and breeding of complex quality traits is to identify genetic markers linked to the traits of interest. DNA markers have facilitated QTL mapping studies in segregated population and shown that certain genomic regions derived from wild germplasm have the potential to improve related traits (Gur and Zamir, 2004). Molecular maps are more useful for identifying and exploiting variations within these genetic resources through marker analysis (Kuan-Hung et al., 2010). Tomato is one of the first plant species in which researchers have began to map QTL traits of agronomic importance using molecular markers (Cagas et al., 2008). During the past decades, QTL studies conducted for tomato have revealed more than 50 traits, and most are fruit-related traits (Eshed and Zamir, 1996; Grandillo and Tanksley, 1996; Tanksley et al., 1996; Bernacchi et al., 1998; Chen et al., 1999; Grandillo et al., 1999; Fulton et al., 1997, 2000; Ku et al., 2000; Causse et al., 2002; Doganlar et al., 2002; Lecomte et al., 2004; Rousseaux et al., 2005; Chaib et al., 2006; Foolad, 2007; Kuan-Hung et al., 2010). Current studies on the

traits of LYC or SSC have suggested the existence of 17 QTLs for LYC in all of the tomato chromosomes except 9 (Thorup et al., 2000; Saliba-Colombani et al., 2001; Heather et al., 2004; Foolad, 2007; Shirasawa et al., 2010), and 109 QTLs for SSC in all chromosomes (Saliba-Colombani et al., 2001; Heather et al., 2004; Foolad, 2007; Causse et al., 2007; Gur et al., 2011). With the exception of 2 QTLs for LYC, none of these QTLs has been used for marker-assisted selection (MAS) in breeding, this suggests that constructing a static model of genetic roles at only one development point is inadequate, and more effort should be directed toward examining the stability and effectiveness of the target trait QTLs with the view of using a dynamic model in the genetic variation.

Tomato LYC and SSC change during the course of fruit development and maturation. In this study, the phenotype in a time-varying function model of the LYC and SSC dynamic traits was analyzed using simple sequence repeat (SSR) molecular markers to detect the major genes that impact changes in dynamic processes. Fifteen QTLs controlling LYC, SSC, and other fruit-related traits during specific periods of tomato fruit development were detected, and the stability and effectiveness of the dynamic QTLs were analyzed. This information will be useful for developing a strategy for gene functional markers that can be used in MAS, and will also enable the implementation of fine mapping and map-based cloning in the future.

MATERIAL AND METHODS

Mapping population

Two hundred and fourteen $F_{2:3}$ families developed from a cross between an inbred line S0805 (*S. lycopersicum*) and S0801 (*Solanum pimpinellifolium*) were cultivated at the research greenhouse of the Northwest A & F University, China. The LYC and SSC genetic backgrounds of S0805 and S0801 are quite different, and all of the samples were from the World Vegetable Center (Tainan, Taiwan). In August 2009, the F_1 generation was obtained by crossing S0801 (male) with S0805 (female), and in January 2010, the F_2 population was created from the F_1 single seed descent. In February 2010, 214 F_2 plants were planted, yielding 214 $F_{2:3}$ family seeds in July 2010. The $F_{2:3}$ families were planted, and the related traits were measured between August and December, 2010.

Phenotypic evaluation

LYC, SSC, and other fruit-related traits were measured at 3-fruit development stages: the color-changing period (CP: fruit coloring area is 10-20%), half-ripe period (HP: fruit coloring area is 60-80%) and full-ripe period (FP: all fruit is colored and non-softening). During the growing season, 5 fruits were harvest randomly from each plant during these three ripening periods, and the following traits were measured with 3 repetitions; fruit weight (FW) was measured using an electronic balance, in grams to the one-thousandth gram.

Five fruits per period were used to measure LYC (in milligrams per 100 grams of fruit); determination of LYC was based on the method of Lavecchia and Zuorro (2008). For each tomato fruit, chromaticity values were measured at 4 positions in the equatorial regions of the fruit, and the average value was used to estimate LYC.

SSC mixed fresh juice (homogenized in a blender) of fruits from each period studied

was used to measure SSC in Brix using PAL-1 refractometer.

Fruit ascorbic acid (AsA) was determined from the mixed fresh juice of fruits from each period studied using the method of Ma and Cheng (2003).

The fruit juice sample used to measure SSC was also used to measure fruit pH (FpH) with a pH meter.

Statistical analysis

Means, standard deviations, Pearson's correlation coefficients, and frequency distributions were calculated for each trait for the parents and 214 $F_{2:3}$ families using SPSS 19.0 and Microsoft Office Excel 2003. Tests for significant differences in means for each trait among the parents and the $F_{2:3}$ families were carried out using the univariate analysis of variance model.

DNA extraction and SSR reaction

The DNA of the 214 F_2 plants and 2 parents were extracted from fresh leaf tissue following the method of Fulton et al. (1995). A total of 300 SSR markers were obtained from the SOL Genomics Network (http://sgn.cornell.edu/ [accessed January 23, 2012]) and the VegMarks database (http://vegmarks.nivot.affrc.go.jp/ [accessed January 23, 2012]), and 45 SSR markers were selected to construct a linkage map. Polymerase chain reaction (PCR) consisted of 2.0 µL 10X PCR buffer, 2.0 µL 2.0 mM $MgCl_2$, 2.0 µL 0.2 mM deoxyribonucleotide triphosphate mixture, 4.0 µL 0.05 U/µL Taq DNA polymerase, 0.5 µL 100 µM forward and reverse primers, 4.0 µL 50 ng/µL template DNA, and 5.0 µL double-distilled water; the total volume was 20.0 µL. PCR was performed in an Eppendorf Mastercyler using the following thermal program: initial denaturation at 94°C for 3 min, followed by 40 cycles of 94°C for 1 min, 42-55°C (depending on the primer) for 1 min, and 72°C for 2 min, and a final extension at 72°C for 10 min. The products were separated on 6% vertical polyacrylamide gels at 75 W constant power for 90-120 min until xylene cyanol settled toward the bottom of the gel. After electrophoresis, the gel was stained with silver nitrate solution.

Linkage map construction and QTL analysis

Composite interval mapping was used to detect the QTLs for LYC, SSC and other fruit-related traits using the following linear model:

$$y_i = b_0 + b^* x_j^* + \sum b_k x_{jk} + \varepsilon_i,$$

where b_0 is the mean of $K \neq i, j + 1$, the population b^* is the effect of the potential QTL, x_j^* is a variate and its value is 1 or 0, b_k is the partial regression coefficient of y phenotype on the k^{th} marker, x_{jk} is the genotype of the k^{th} marker on the individual j and its value is 1 or 0, and ε_i is post-fit residuals. All polymorphic SSR molecular markers were tested with chi-square goodness-of-fit analysis to determine whether the detected stable molecular markers were in accordance with Mendelian segregation. The JoinMap 4.0 software was used to construct a genetic map, and QTL analysis was conducted using MapQTL 6.0.

RESULTS

Trait variation

Phenotypic values were obtained for LYC, SSC, and other related traits of the $F_{2:3}$ family and its parents at 3 developmental periods (Table 1). Within each period, all of these traits followed a continuous distribution pattern typical of quantitative traits. Each physiological index increasing clearly showed the dynamic changes of all physiological indexes within the 3 progressive periods (Figure 1). In the normal distribution test of LYC and SSC within each period, the LYC coefficients of skewness were 0.887 (CP), 0.915 (HP), and 0.424 (FP); the SSC were 0.351 (CP), 0.073 (HP), and 0.002 (FP); the AsA coefficients were 0.889 (CP), 0.618 (HP), and 0.122 (FP); the FpH coefficients were 0.194 (CP), 0.189 (HP), and 0.192 (FP), and the FW coefficients were 0.108 (CP), 0.413 (HP), and 0.227 (FP), which were in accordance with normal distribution (Figures 2-6).

Table 1. Phenotypic values of each trait for $F_{2:3}$ families and its parents at three periods.

Traits	Periods	Parents		$F_{2:3}$ families	
		S0805	S0801	Mean	Range
LYC	CP	0.36 ± 0.00	1.73 ± 0.00	1.18 ± 0.00	0.34-2.94
	HP	3.51 ± 0.01	6.27 ± 0.10	2.03 ± 0.01	0.42-6.27
	FP	4.23 ± 0.05	11.66 ± 0.33	5.89 ± 0.94	3.05-11.77
SSC	CP	2.70 ± 0.14	5.73 ± 0.32	4.53 ± 0.54	2.86-6.48
	HP	3.12 ± 0.11	6.24 ± 0.41	5.67 ± 0.38	3.04-7.54
	FP	3.53 ± 0.18	8.97 ± 0.68	6.81 ± 0.46	3.67-9.76
AsA	CP	8.67 ± 1.00	12.84 ± 1.08	9.60 ± 1.70	8.01-12.54
	HP	11.27 ± 1.05	16.69 ± 1.76	12.48 ± 1.12	10.41-15.73
	FP	13.77 ± 1.14	20.38 ± 1.94	15.24 ± 1.82	12.72-20.41
FpH	CP	3.15 ± 0.18	3.57 ± 0.20	3.26 ± 0.18	2.62-3.73
	HP	3.93 ± 0.22	4.46 ± 0.24	4.07 ± 0.22	3.28-4.66
	FP	4.15 ± 0.25	4.71 ± 0.36	4.29 ± 0.24	3.46-4.92
FW	CP	126.28 ± 6.1	2.30 ± 0.01	5.93 ± 0.10	2.16-11.44
	HP	138.11 ± 8.2	2.51 ± 0.01	6.94 ± 0.15	2.36-12.51
	FP	173.63 ± 9.4	3.16 ± 0.01	8.15 ± 0.20	2.97-15.73

LYC = lycopene content; SSC = soluble solid content; AsA = ascorbic acid; FpH = fruit pH; FW = fruit weight; CP = color-changing period; HP = half-ripe period; FP = full-ripe period

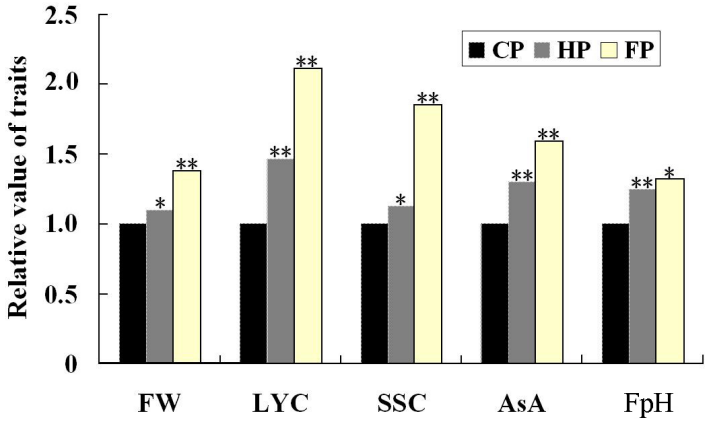

Figure 1. Difference of each trait among the three periods. **P < 0.01,*P < 0.05 (*t*-test). For abbreviations, see legend to Table 1.

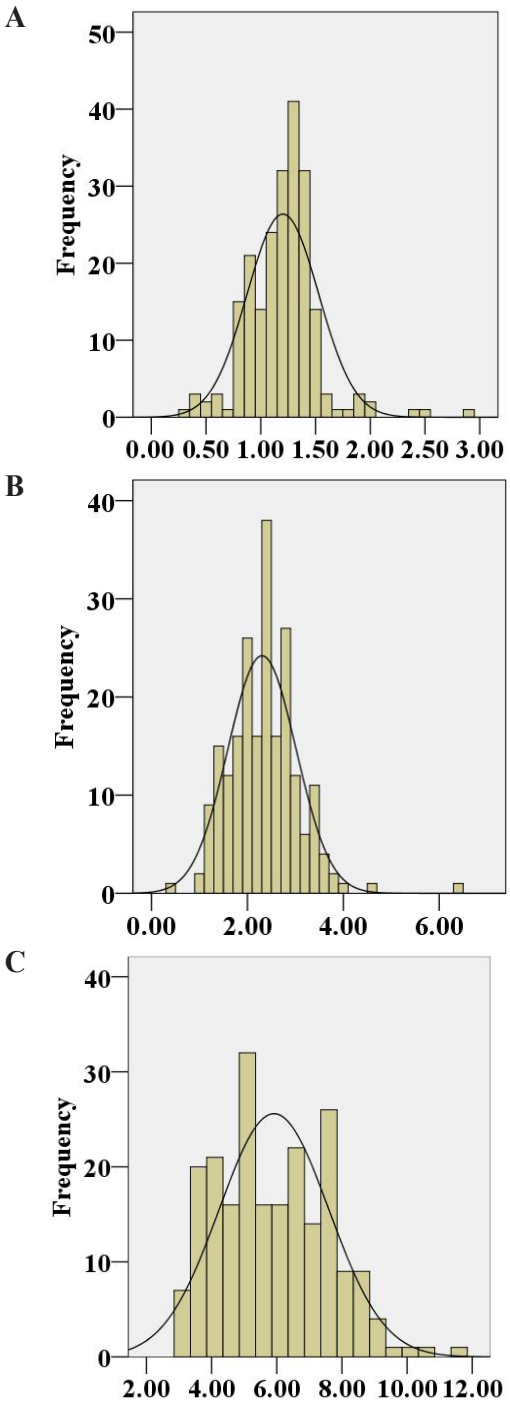

Figure 2. Frequency distribution of lycopene content at the three periods [color changing period (**A**), half-ripe period (**B**) and full-ripe period (**C**)] in the $F_{2:3}$ families.

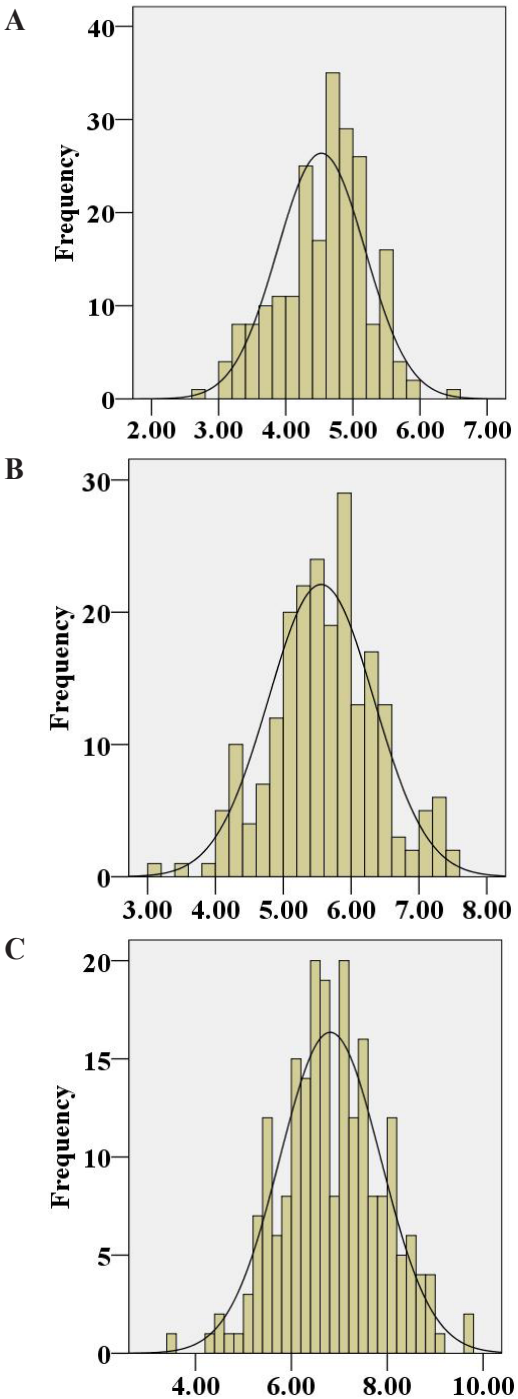

Figure 3. Frequency distribution of soluble solid content at the three periods [color changing period (**A**), half-ripe period (**B**) and full-ripe period (**C**)] in the $F_{2:3}$ families.

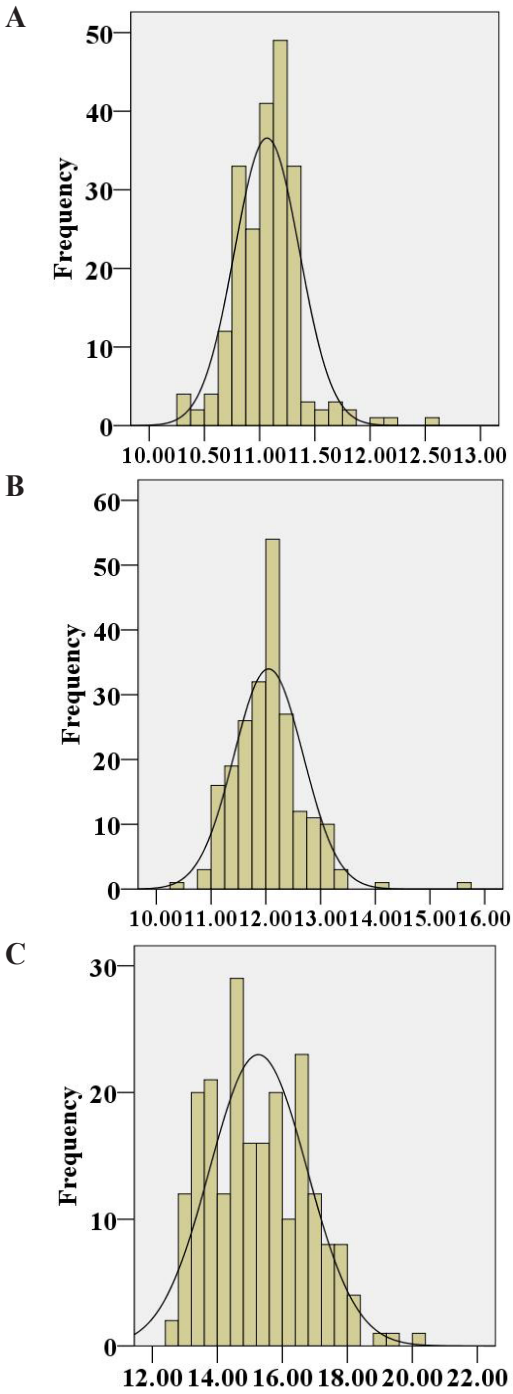

Figure 4. Frequency distribution of ascorbic acid at the three periods [color changing period (**A**), half-ripe period (**B**) and full-ripe period (**C**)] in the $F_{2:3}$ families.

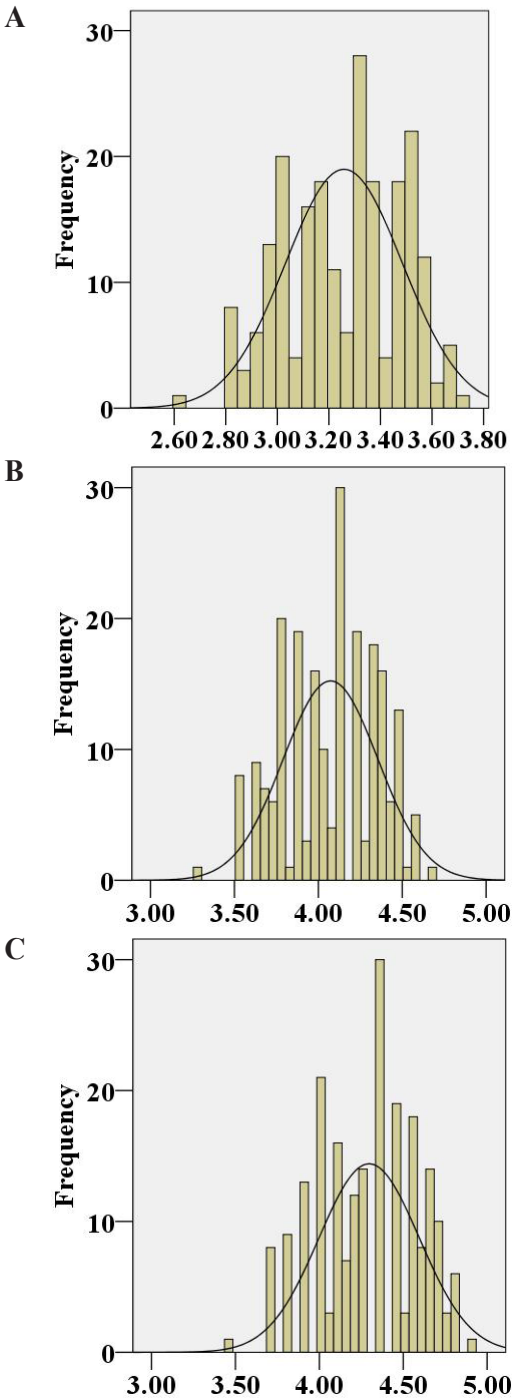

Figure 5. Frequency distribution of fruit pH at the three periods [color changing period (**A**), half-ripe period (**B**) and full-ripe period (**C**)] in the $F_{2:3}$ families.

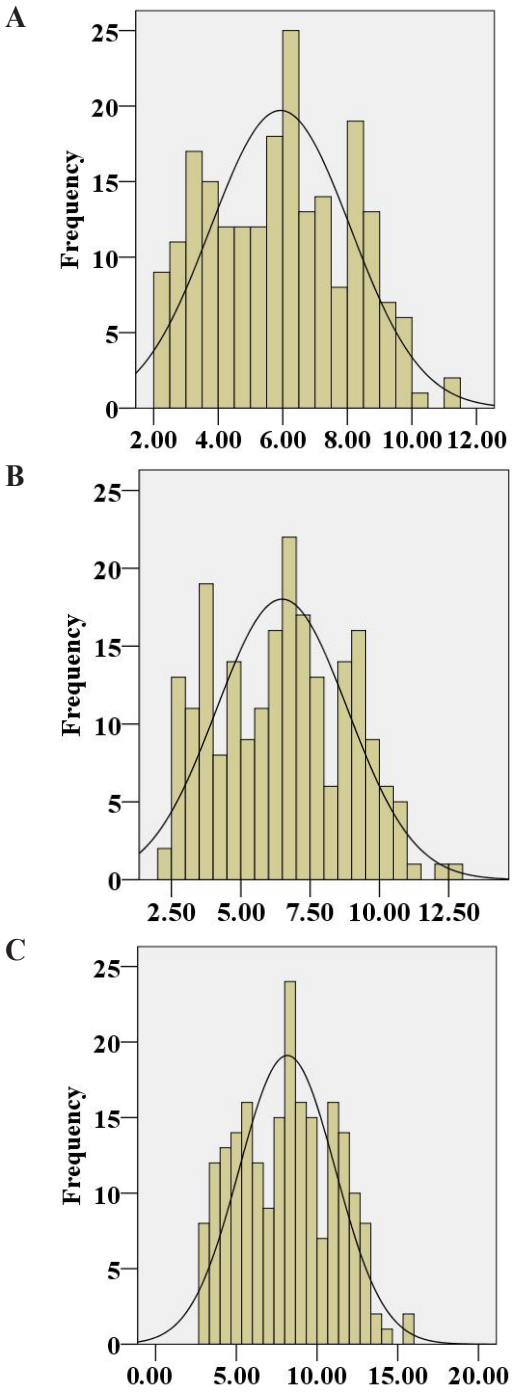

Figure 6. Frequency distribution of fruit weight at three periods (color changing period (**A**), half-ripe period (**B**) and full-ripe period (**C**), respectively) in the $F_{2:3}$ families.

Correlations among traits

Family mean correlation coefficients for traits measured during the 3 periods are presented in Tables 2-4.

The strongest negative correlations were observed between LYC and FW in the 3 periods. LYC was positively correlated with AsA in the HP and FP. A negative correlation was observed between SSC and FW in the CP and strongest negative correlations were observed in other periods. SSC was highly positive correlated with FpH in the HP, and positively correlated in the FP. Otherwise, the strongest negative correlations were observed between FW and AsA in the HP, and the strongest positive correlations were observed between AsA and FpH in the CP and HP. LYC was positively correlated with SSC in the HP and highly positively correlated in the FP.

Table 2. Correlations among traits in the color-changing period.

	FW	LYC	SSC	AsA
LYC	-0.402**			
SSC	-0.189*	0.146		
AsA	-0.151	0.131	0.093	
FpH	0.114	-0.142	0.087	0.179**

*P < 0.05; **P < 0.01. For abbreviations, see legend to Table 1.

Table 3. Correlations among traits in the half-ripe period.

	FW	LYC	SSC	AsA
LYC	-0.317**			
SSC	-0.249**	0.181*		
AsA	-0.257**	0.175*	0.149	
FpH	0.105	-0.149	0.251**	0.234**

*P < 0.05; **P < 0.01. For abbreviations, see legend to Table 1.

Table 4. Correlations among traits in the full-ripe period.

	FW	LYC	SSC	AsA
LYC	-0.420**			
SSC	-0.430**	0.276**		
AsA	-0.123	0.211*	0.050	
FpH	0.091	-0.147	0.222*	-0.109

*P < 0.05; **P < 0.01. For abbreviations, see legend to Table 1.

Genetic map and QTL analysis

The linkage map totaled 218 cM of the tomato genome with an average genetic distance between markers of 4.84 cM. The lowest genetic distance was 0.047 cM. Fifteen QTLs were detected for LYC and SSC evaluated in the 3 periods evaluated (Table 5 and Figure 7), which explained 7-33% of the individual phenotypic variation. All of the detected QTLs were co-located in a single locus on chromosomes 1, 4, and 9. The QTLs identified for LYC and SSC are summarized in Table 5.

Two QTLs for LYC in the CP were detected on chromosomes 4 and 9. Molecular marker SSR146 (chromosomes 4) accounted for 15% of the phenotypic variation, and SSR110 (chromosomes 9) accounted for 31% of the phenotypic variation. In contrast, only one LYC

QTL in the HP was detected on chromosomes 9 by SSR237, and it explained as much as 16% of the phenotypic variation. Three QTLs were detected in the FP for LYC by SSR146 (chromosomes 4), SSR111 (chromosomes 4) and SSR237 (chromosomes 9), the phenotypic variations were 20, 16, and 17%, respectively.

Table 5. Quantitative trait loci, their position, additive effects, and percentage of phenotypic variation explained (R^2) for LYC and SSC in the $F_{2:3}$ population developed from *Solanum lycopersicum* x *S. pimpinellifolium*.

Traits	Period	QTL molecular marker	Chromosome	QTL position (cM)	LOD score	Additive effect	R^2
LYC	CP	SSR146	4	22.164	3.33	2.1224	0.15
		SSR110	9	18.691	4.43	-1.1597	0.31
	HP	SSR237	9	22.108	2.78	2.1752	0.16
	FP	SSR146	4	22.164	5.84	1.5446	0.20
		SSR111	4	30.094	2.99	1.1434	0.16
		SSR237	9	22.108	4.53	1.7675	0.17
SSC	CP	SSR67	1	55.811	2.68	-0.8373	0.12
	FP	SSR67	1	55.811	3.07	-0.7898	0.33
		SSR111	4	30.094	2.66	2.3282	0.23
FW	HP	SSR300	4	52.411	3.05	-2.1264	0.24
	FP	SSR45	7	5.864	2.94	-1.1649	0.19
AsA	FP	SSR111	1	10.005	2.73	0.9781	0.07
FpH	CP	LEaat004	1	42.814	3.32	-0.1732	0.11
	HP	SSR304	7	15.722	4.25	1.3427	0.21
	FP	SSR85	10	13.126	2.84	-1.7934	0.13

QTL = quantitative trait locus; LOD = logarithm of the odds. For abbreviations, see legend to Table 1.

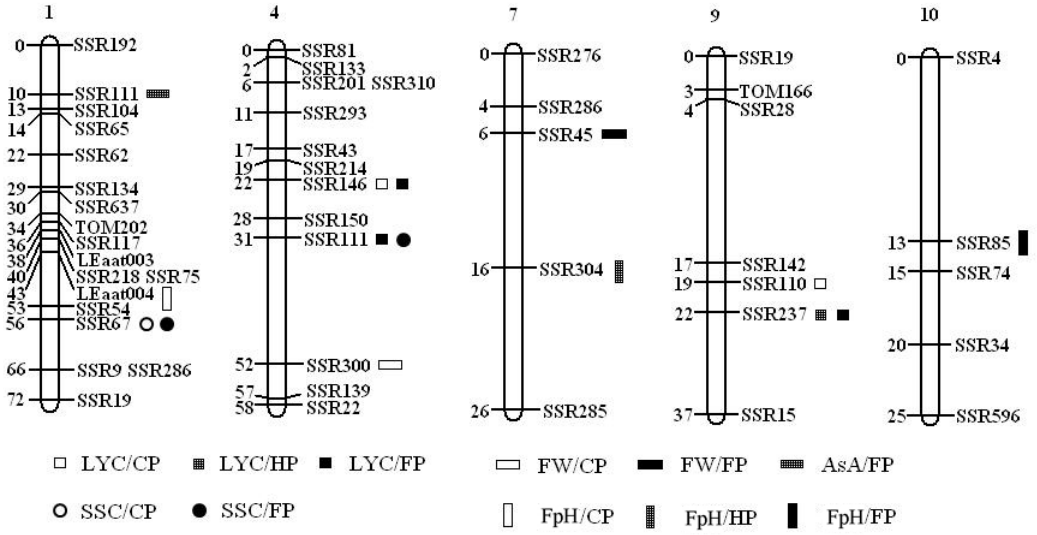

Figure 7. Mapping quantitative trait loci for lycopene content and soluble solid content in tomato. SSR = simple sequence repeat. For abbreviations, see legend to Table 1.

One QTL for SSC was detected in the CP and 2 QTLs for SSC were detected in the FP. The SSC QTL in the CP was co-located with the SSC QTL in the FP on chromosome 1 by SSR67, accounting for 12% of the phenotypic variation in the CP and 33% of the phenotypic variation in the FP. Another SSC QTL in the FP was detected on chromosome 4 by SSR111 and accounted for 23% of the phenotypic variation.

Two QTLs for FW in the HP and FP were detected on chromosomes 4 (SSR300) and 7 (SSR45). The molecular marker SSR300 accounted for 24% of the phenotypic variation, whereas SSR45 accounted for 19% of the phenotypic variation. Only one QTL was detected on chromosome 1 (SSR111) and accounted for 7% of the phenotypic variation. One QTL for FpH was detected in each period on chromosomes 1 (LEaat004), 7 (SSR304), and 10 (SSR85), and the phenotypic variations were 11, 21, and 13%, respectively.

DISCUSSION

S. pimpinellifolium has repeatedly served as a source of many important traits for horticulture improvement, making it an important genetic resource and a conservation priority (Cagas et al., 2008). *S. pimpinellifolium* harbors numerous desirable horticultural and agronomic characteristics, such as good fruit quality. The LYC and SSC of *S. pimpinellifolium* are higher than those of the cultivated tomato, and high LYC and SSC gene introgression to cultivated tomatoes would be beneficial for the implementation of tomato fruit qualities.

As indicated earlier, several major genes with significant contribution to high LYC and SSC contents were previously identified and mapped onto the classical linkage map of tomato (Foolad, 2007). In this study, the dynamic QTLs for LYC and SSC were first developed using a crossed population from *S. lycopersicum* and *S. pimpinellifolium*. The molecular markers SSR146 in the CP and FP, and SSR237 in the HP and FP for LYC were identified, which may reflect that some genes for controlling LYC are always expressed in tomato fruit development. The molecular marker SSR110 for LYC was identified in the CP, but not in the HP or FP. The molecular marker SSR146 for LYC was not identified in the HP, and the molecular marker SSR237 for LYC was not identified in the CP, which may reveal that some genes for controlling the LYC are ever changing in tomato fruit development, and the expression of these genes would be limited by time. We also identified the SSC molecular marker SSR67 in the CP and FP, and identified SSC molecular marker SSR111 in the FP, but we did not identify any SSC molecular markers in the HP. The genetic molecular markers may cover only a few genomes, and the SSC molecular markers could exist in other chromosomes.

LYC and SSC were the target traits for several QTL mapping studies in tomato using interspecific crosses between a cultivated tomato and a related wild species. Several reports (Chen et al., 1999; Yong-Sheng et al., 2003; Foolad, 2007; Sonah et al., 2011) have concluded that QTLs for LYC are present in all tomato chromosomes except chromosome 9, but we identified LYC QTL on chromosome 9 in the CP (SSR110), HP and FP (SSR237) that accounted for 16-17% of the phenotypic variation. This discovery may be useful for tomato breeders using MAS.

The LYC QTL on chromosome 4 in the FP was co-located with the SSC QTL. Cagas et al. (2008) have reported that QTLs for tomato FW and days to flowering were co-located. Kuan-Hung et al. (2010) have reported a co-location of FW and Brix QTLs. In most case, traits that were co-localized showed significant correlations with each other (Doganlar et al., 2002). Thus, the co-localization of QTLs and correlations between LYC and SSC may be due to pleiotropic effects of a single gene or a cluster of genes via physiological relationships among traits because they were found to be highly significantly correlated. However, separating linkage and pleiotropy is nearly impossible, unless QTLs have been cloned. Several novel QTLs for LYC and SSC were identified in this study, which aimed to assess the implication of dynamic changes during the course of fruit development and maturation. Our study could

contribute in helping to breeding programmes as tomato breeders are more likely to seek improvements to LYC and SSC.

We detected one QTL in each period for FpH, and detected 2 QTLs for FW in the HP and FP. Molecular mapping studies have revealed that the genetic control of FW and FpH are extraordinarily complex (Chen et al., 1999; Causse et al., 2004; Frary et al., 2004; Foolad, 2007; Cagas et al., 2008; Sonah et al., 2011). Several QTLs were co-located with the FW and FpH QTLs, but our study revealed few QTLs co-located with those for FW and FpH. Only one QTL for AsA was found in the FP, and few studies have investigated the AsA of tomato. Confirmation of these QTLs is currently in progress in our laboratory.

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