J. ISSAAS Vol. 16, No. 2:1-9 (2010)

QUANTITATIVE TRAIT LOCI CONTROLLING FLOWERING PROPERTIES IN TOMATO

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(Received: September 4, 2009; Accepted: August 25, 2010)

ABSTRACT

To understand better the factors influencing the days to anthesis and the number of flowers in tomato inflorescences, quantitative trait loci (QTLs) for these traits were studied in winter and summer using a BC_1F_6 population derived from *Solanum lycopersicum* and *S. pimpinellifolium*. Plants from 110 accessions were grown in 4 L pots, trained as single stems, and pinched above the third leaf after the second inflorescence. The number of flowers on the first (NFI_1) and second inflorescences (NFI_2), the number of days from sowing to anthesis of the first inflorescence (DTF) and between the antheses of the first and second inflorescences (DTF_1F_2), and the number of leaves before the first inflorescence (LN_{01}) and between the first and second inflorescences (LN_{12}) were counted. Nine additive QTLs were detected, three of which (LN_{01}, LN_{12}, and DTF_1F_2) exhibited additive × environment interaction. Two additive LN_{12} QTLs showed epistatic effects. Epistatic effects were also identified for three QTLs pairs for DTF_1F_2, LN_{01}, and inflorescence branching (DBI), all of which had no additive effects. These results suggest that the number of leaves preceding the first inflorescence (LN) and the period between the flowering of the first and second inflorescences (DTF_1F_2) are subject to environmental modification and that QTL × environment and epistatic effects should be considered when pyramiding QTLs to breed early flowering tomatoes.

Key words: breeding, epistasis, flowering time, inflorescence, QTL × environment interaction

INTRODUCTION

Recently in Japan, some farmers maximize their yield by harvesting tomato fruits only from the first inflorescence or from the first to the third inflorescences and transplanting seedlings at high densities in plastic houses several times a year (Watanabe, 2006). This high-density short-term cultivation method (the HDSC method) offers several advantages: healthy and vigorous seedlings with flower buds can be cultivated even in summer, during which tomato plants grown in plastic houses for long periods lose their vigor; and the short cultivation period helps to reduce the damage caused by pests and diseases. Thus, the HDSC method may be an effective way of cultivating tomato plants in humid tropical countries, such as those in Southeast Asia, where tomato plants are prone to high-temperature stress and pest damage.

In tomato plants, the shoot apical meristem of the primary shoot usually produces 7–11 leaves and then transforms into the first inflorescence. Vegetative growth is succeeded by the axillary bud (sympodial meristem) in the axil of the last-initiated leaf (Heuvelink, 2005). The number of leaves preceding the first inflorescence (LN_{01}) in tomato seedlings usually increases in summer in response to high temperatures (Oda *et al*., 2005). Therefore, tomato seedlings raised in summer flower later than those raised in other seasons, leading to a reduction in early yields. To overcome this problem, Oda *et al*. (2005) proposed that tomato seedlings should be raised in plug trays in the highlands and then transported to the lowlands in summer.

Because the tomato stem exhibits a sympodial growth habit, the sympodial shoot terminates at the second inflorescence after developing approximately three leaves. However, the number of leaves formed between the first and second inflorescences (LN_{12}) occasionally diverges from three, with an increase in LN_{12} at a small LN_{01} (Klapwijk and Wubben, 1984). Calvert (1964) reported that the initiation of the second inflorescence is delayed in the Ailsa Craig cultivar when the initiation of the first inflorescence is accelerated by low temperatures, resulting in an increase in LN_{12}. With the HDSC method, a small LN_{12} is necessary to achieve a high early yield because high LN_{12} may prolong the period between the flowering of the first and second inflorescences (DTF_1F_2). However, little is known about the effects of genotype and the genotype × environment interaction on LN_{12} and DTF_1F_2. Furthermore, the number of flowers per inflorescence (NFI) should be high to produce a high yield with the HDSC method. Wittwer and Teubner (1957) reported that low temperatures increased NFI, whereas Fukushima and Masui (1962) found that low night temperatures during the first two weeks after cotyledon expansion did not affect NFI of the first inflorescence. Lohar and Peat (1998) compared the effects of night temperature on NFI among heat-sensitive and heat-tolerant cultivars, and concluded that genotype × environmenl interactions affect NFI.

Several studies have been conducted at the QTL level on the flowering times of the tomato. QTLs for days to flowering (DTF) have been detected on chromosomes 1–5, 7, and 10–12 in interspecific crosses involving *Solanum lycopersicum* and wild species, such as *S. pennellii*, *S. pimpinellifolium*, *S. chmielewskii*, and the hybrid IVT-KT_1 (Cagas *et al*., 2008; de Vicente and Tanksley, 1993; Doganlar *et al*., 2002; Grandillo and Tanksley, 1996; Jimenez-Gomez *et al*., 2007; Lindhout *et al*., 1994). Jimenez-Gomez *et al*. (2007) and Cagas *et al.* (2008) demonstrated the colocalization of DTF and LN QTLs. Cagas *et al*. (2008) also investigated the effects of season on DTF and LN in a BC_1F_4 population derived from a cultivated tomato and *S. pimpinellifolium*, and found that DTF QTLs colocalized with QTLs for other traits, such as leaf length, number of lateral shoots, plant height, and fresh weight.

Grandillo and Tanksley (1996) detected three NFI QTLs on chromosomes 3, 6, and 9 using an interspecific F_2 cross between *S. lycopersicum* and *S. pimpinellifolium*. In contrast, van der Knaap and Tanksley (2003) identified a total of nine NFI QTLs on chromosomes 1–5, 7, and 9 in a similar population. To the best of our knowledge, QTLs for the period between the flowering of the first and second inflorescences (DTF_1F_2) and LN_{12} have not yet been studied. In this study, we examined DTF, DTF_1F_2, LN_{01}, LN_{12}, NFI, and inflorescence branching (DBI) in different seasons to identify these traits at the QTL level.

MATERIALS AND METHODS

Plant Material and Growth Conditions

The BC_1-derived recombinant inbred lines used in this study have been described previously by Cagas *et al*. (2008). In brief, 110 BC_1F_6 lines were derived from an initial cross between the commercial cultivar *S. lycopersicum* 'M570018' and its close wild relative *S. pimpinellifolium* (PI124039), and the backcross of the F_1 generation to 'M570018'. The resultant BC_1F_1 population was advanced by the single-seed method to produce the BC_1F_5 population, which was used for genotyping. The subsequent BC_1F_6 generation was used for phenotypic evaluation.

Phenotypic Evaluation of Flowering Properties

Seeds from 110 and 108 BC_1F_6 families, together with those of their parents, were sown into 10.5 cm pots filled with commercial compost (Soilmix, Sakata Seed Co., Yokohama, Japan) under greenhouse conditions on December 29, 2007 (winter experiment) and on May 8, 2008 (summer experiment). The seedlings were transplanted to 4 L pots (18 cm in diameter) containing the same

commercial compost on February 17, 2007, and June 12, 2008 (50 days and 35 days after sowing, respectively). In both experiments, the plants were trained to one stem and pinched above the third leaf after the second inflorescence.

The experimental design was a randomized complete block, consisting of five replications. Days to flowering (DTF) were counted as the number of days from sowing to first anthesis, whereas DTF_1F_2 was the number of days between the first anthesis in the first inflorescence and the first anthesis in the second inflorescence. The number of leaves preceding the first inflorescence (LN_{01}) and the number of leaves between the first and second inflorescences (LN_{12}) were counted at the end of the experiments. The numbers of flowers in the first (NFI_1) and second (NFI_2) inflorescences were monitored at each inflorescence. The branching of the inflorescence was evaluated in both the first (DBI_1) and second (DBI_2) inflorescences, with a score of 1 given for a simple cyme inflorescence and of 2 for a double-branched cyme inflorescence.

Marker Analysis

The overall genotyping protocol was as described by Cagas *et al*. (2008). In brief, DNA from the 110 BC_1F_5 lines and parent lines was extracted from 0.1 g of leaf material using the Nucleon PhytoPure plant DNA extraction kit (Amersham Biosciences, Buckinghamshire, UK), following the manufacturer's protocol. The PCR consisted of 200 ng of template DNA, 2 μM forward and reverse primers, 0.2 mM dNTP mixture, 1.8 mM $MgCl_2$, 1 μL of 10× NH_4 buffer, and 0.25 units of Bio*Taq* DNA Polymerase (Bioline, London, UK) in a 10 μL total reaction solution. The PCR consisted of one cycle of 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 50–55 °C for 45 s, and 72 °C for 45 s, and one last cycle of 72 °C for 5 min for final extension.

Ninety-three polymorphic markers (46 SSR, 13 COSII, 33 CAPS, and two SNP) were used to construct a linkage map. Polymorphic COSII and CAPS markers were identified by digestion with 14 restriction enzymes, *Afa*I, *Alu*I, *Bam*HI, *Bgl*II, *Dra*I, *Dpn*II, *Eco*RI, *Eco*RV, *Hinc*II, *Hin*dIII, *Hinf*I, and *Kpn*I, at 37 °C for 12 h. The amplified products were separated on a 13% acrylamide/bisacrylamide running gel (18 × 6 cm) with a 5% acrylamide/bisacrylamide stacking gel in a NB-5010 Nihon Eido (Tokyo, Japan) electrophoresis apparatus for 3 h at 120 V. The gels were stained with SYBR Green I (Lonza, Rockland, Maine, USA) and visualized under UV.

QTL Mapping

QTL analysis was performed with the QTLNetwork 2.0 software (http://ibi.zju.edi.cn/software/qtlnetwork) based on a linkage map calculated using MAPMAKER/EXP ver. 3.0b (Lander *et al.*, 1987). QTLNetwork uses a mixed-model-based composite-interval mapping technique capable of estimating additive, epistatic, and QTL × environment interaction effects. The walking speed and test window size were set as 1 cM and 10 cM, respectively. A filtration window size of 10 cM was used to distinguish whether two adjacent test statistic peaks were derived from two QTLs. One thousand permutation tests were performed on each trait in the combined data from the two seasons to calculate the critical F value at $P < 0.05$. Accessions between experiments not used were treated as missing data.

Statistical Analysis

Single-factor analysis of variance (ANOVA), Least Significant Difference (LSD), and Pearson correlation coefficient analysis were performed using SPSS for Windows (release 11.01).

RESULTS

Trait Variation

All the traits analyzed followed continuous normal distributions typical of quantitative traits, except for DBI_1 and DBI_2, in which the distributions were left skewed (data not shown). *S. pimpinellifolium* (PI124039) flowered earlier than *S. lycopersicum* 'M570018' (Table 1). DTF was generally shorter in summer, with the BC_1F_6 family and its parents flowering 10 days earlier than when grown in winter. DTF_1F_2 was 4–5 days shorter in summer than in winter for the BC_1F_6 family and its parents, and shorter in *S. pimpinellifolium* than in *S. lycopersicum*.

LN_{01} was almost the same for both parents, regardless of the growing season. The genotype × environment interaction on LN_{12} was statistically significant. Compared with winter LN_{12}, *S. lycopersicum* had an average of 0.6 more leaves in summer, whereas *S. pimpinellifolium* had an average of 1.1 fewer leaves in summer. The number of flowers in the first inflorescence (NFI_1) was much smaller in *S. lycopersicum* than in *S. pimpinellifolium* in both seasons. The genotype × environment interaction in NFI_1 was significant, with a larger difference between parents in summer. Conversely, no environmental effect or genotype × environment interaction was evident in NFI_2. The occurrence of double-branched cymes (greater DBI value) was higher in winter than in summer in the BC_1F_6 families and its parents for the first inflorescence, but no differences were observed for the second inflorescence.

Correlations among Traits

DTF negatively correlated with DTF_1F_2 in both seasons (Table 2). LN_{01} and LN_{12} negatively and positively correlated with DTF_1F_2, respectively, in winter but positively correlated with DTF in summer. NFI_1 and NFI_2 were highly correlated with each other in both seasons. NFI_2 negatively correlated with DTF in both seasons but with DTF_1F_2 only in winter. The occurrence of double-branched cymes in the first inflorescence (DBI_1) positively correlated with NFI_1, whereas DBI_2 positively correlated with NFI_2 in both seasons. DBI_1 positively correlated with DBI_2.

Table 2. Correlation coefficients among eight flowering traits in the BC_1F_6 families in winter, 2007 (above diagonal), and in summer, 2008 (below diagonal).

Trait	DTF	DTF_1F_2	LN_{01}	LN_{12}	NFI_1	NFI_2	DBI_1	DBI_2
DTF		–0.20*	0.12	0.06	–0.09	–0.20*	–0.19*	–0.30**
DTF_1F_2	–0.56**		–0.30*	0.37**	–0.10	–0.22*	0.12	–0.04
LN_{01}	0.61**	–0.14		0.09	–0.18	–0.09	–0.16	0.17
LN_{12}	0.43**	0.04	0.37**		0.03	0.12	–0.03	0.01
NFI_1	–0.09	–0.03	0.08	–0.14		0.56**	0.63**	0.18
NFI_2	–0.23*	–0.07	–0.17	–0.23**	0.60**		0.18	0.36**
DBI_1	–0.07	–0.01	–0.01	–0.23*	0.26**	0.17		0.19*
DBI_2	–0.18	0.12	–0.04	–0.12	0.16	0.34**	0.36**	

* significant at $P < 0.05$, ** significant at $P < 0.01$.

Table 1. Descriptive statistics of phenotypic values for flowering traits of the parents and BC_1F_6 families.

Trait	P_1		P_2		BC_1F_6		Contrast				
	Winter	**Summer**	**Winter**	**Summer**	**Winter**	**Summer**	**P_1/P_2**	**P_1/BC_1F_6**	**P_2/BC_1F_6**	**E**	**G × E**
DTF	66.0±0.7	56.2±2.6	66.0±0.7	56.2±2.6	66.0±0.7	56.2±2.6	*	*	*	*	N.S.
DTF_1F_2	12.6±0.9	8.5±1.6	8.3±1.7	3.4±3.8	11.9±2.2	6.9±2.5	*	N.S.	*	N.S.	N.S.
LN_{01}	8.6±0.5	8.3±0.7	6.8±0.5	8.0±0.7	8.4±0.9	8.6±1.4	N.S.	N.S.	*	N.S.	N.S.
LN_{12}	2.8±0.4	3.4±0.8	4.0±0.8	2.9±0.4	3.3±0.5	3.5±0.7	N.S.	N.S.	*	N.S.	*
NFI_1	6.4±1.5	5.1±0.7	16.3±0.5	18.1±4.7	8.1±2.4	6.5±2.2	*	*	*	N.S.	*
NFI_2	6.2±0.4	5.5±1.1	2.3.5±7.1	19.8±7.3	7.6±2.0	8.1±3.0	*	*	*	N.S.	N.S.
DBI_1	1.2±0.4	1.0±0.0	1.3±0.5	1.0±0.2	1.1±0.2	1.0±0.1	N.S.	N.S.	N.S.	*	N.S.
DBI_2	1.0±0.0	1.0±0.0	1.0±0.0	1.0±0.0	1.1±0.1	1.1±0.1	N.S.	*	*	N.S.	N.S.

P1, *Solanum lycopersicum*; P2, *Solanum pimpinellifolium*; E, environmental effects; G × E, genotype × environment interaction;
*, significant at $P < 0.05$; N.S., not significant at $P < 0.05$.

QTL Analysis

Nine main QTLs with additive effects were detected by QTL mapping using QTLNetwork software (Table 3). These nine QTLs were mapped to chromosomes 1, 3, 4, and 12. Three QTLs (*ln_{01}-3*, *ln_{12}-1.1*, and *dtf_1f_2-12*) exhibited significant QTL × environment interaction effects, in which the presence of *S. lycopersicum* alleles increased LN_{01} by 0.2216 leaves in winter, and increased LN_{12} and DTF_1F_2 by 0.1039 leaves and 0.6505 days, respectively, in summer. No QTL × environment interactions were detected for DTF, NFI_1, or NFI_2. Two QTLs for DTF were identified in the intervals between markers C2_At5g49480 and SSR105 on chromosome 1 (*dtf-1*), and between markers SSR306 and LEOH37 on chromosome 4 (*dtf-4*). These QTLs explained 6.64% and 3.55% of the phenotypic variation, respectively. *S. lycopersicum* alleles at *dtf-1* and *dtf-4* on chromosomes 1 and 4, respectively, increased DTF. A DTF_1F_2 QTL (*dtf_1f_2-12*) was detected in the interval between CLET8K4 and CT99 on chromosome 12. This QTL explained 2.08% of the phenotypic variation, and the presence of *S. lycopersicum* alleles increased DTF_1F_2. One LN_{01} QTL (*ln_{01}-3*) was detected in the interval between C2_At5g51110 and SSR111 on chromosome 3, and explained 16.31% of the phenotypic variation. At the same location on chromosome 3, Cagas *et al*. (2008) found LN_{01} QTLs using the earlier BC_1F_4 generation of this population. *S. pimpinellifolium* alleles at the *ln_{01}-3* QTL increased LN_{01} by 0.5636 leaves because of its additive effect. Two LN_{12} QTLs were detected in the intervals between C2_At5g49480 and SSR105 (*ln_{12}-1.1*) and between SSR308 and SSR117 (*ln_{12}-1.2*) on chromosome 1. These two QTLs explained 9.08% and 12.28% of the phenotypic variation, respectively. *S. lycopersicum* alleles at *ln_{12}-1.1* and *ln_{12}-1.2* increased and decreased LN_{12} by 0.3121 and 0.2393 leaves, respectively. One QTL for NFI_1 (*nfi_1-4*) was detected in the interval between Hero and LEOH361 on chromosome 4, whereas one QTL for NFI_2 (*nfi_2-4*) was detected in the interval between SSR603 and SSR306 on the same chromosome. *nfi_1-4* and *nfi_2-4* explained 15.18% and 7.89% of the phenotypic variation, respectively, and the presence of alleles from *S. pimpinellifolium* at these QTLs increased NFI. One QTL associated with inflorescence type, *dbi_1-4*, was detected in the same interval as *nfi_1-4* on chromosome 4. This QTL explained 4.83% of the phenotypic variation, and alleles from *S. pimpinellifolium* increased the occurrence of double-branched inflorescences.

Epistatic QTLs Controlling Flowering Properties

A total of four digenic epistatic interactions were identified for LN_{01}, LN_{12}, DTF_1F_2, and DBI_1 (Table 4). Variations explained by these epistatic interactions ranged from 2.89% for LN_{12} to 8.98% for LN_{01}, which are lower than those for the additive QTLs. The two main LN_{12} QTLs detected in this study (*ln_{12}-1.1* and *ln_{12}-1.2*) showed epistatic effects and explained 2.89% of the phenotypic variation. For DBI, an epistatic interaction was detected between QTLs *dbi_1-1.2* and *dbi_1-2*, and this pair also exhibited epistasis × environment interaction. The epistatic and epistasis × environment interaction effects of this QTL pair explained 4.83% and 5.78% of the phenotypic variation, respectively, indicating a high contribution of these effects. The epistatic or additive × additive effects were positive for LN_{01} and negative for LN_{12}, DTF_1F_2, and DBI_1.

DISCUSSION

Tomato plants usually develop 7–11 leaves before the formation of the first inflorescence (Heuvelink, 2005). The number of leaves preceding the first inflorescence (LN_{01}) is reportedly affected by the genotype and environmental factors, such as light and temperature (Heuvelink, 2005), but little is known about the number of leaves between the first and second inflorescences (LN_{12}). In this study, LN_{01} QTL *ln_{01}-3* and LN_{12} QTL *ln_{12}-1*, mapped to chromosomes 1 and 3, respectively, exhibited both additive and additive × environment interaction effects. Furthermore, one epistatic interaction each was observed for LN_{01} (*ln_{01}-2* and *ln_{01}-5*) and LN_{12} (*ln_{12}-1.1* and *ln_{12}-1.2*). To the best of our knowledge, this is the first report to identify QTL × environment interaction effects and epistatic effects for LN_{01} and LN_{12}. Additive, additive × environment interaction, and epistatic effects explained 16.31%, 3.47%, and

Table 3. Estimated additive and additive × environment interaction effects of QTLs for flowering properties of tomato in two different seasons (environments).

Trait	QTL	Interval	Position (cM)	a	h_a^2	ae_1	ae_2	h_{ae}^2
DTF	*dtf-1*	C2_At5g49480–SSR105	46.9	2.05	0.07			
	dtf-4	SSR306–LEOH37	36.8	1.25	0.04			
DTF_1F_2	*dtf_1f_2-12*	CLET8K4–CT99	86.8	0.69	0.02	–0.65	0.65	0.03
LN_{01}	*ln_{01}-3*	C2_At5g51110–SSR111	76.8	–0.56	0.16	0.22	–0.22	0.03
LN_{12}	*ln_{12}-1.1*	C2_At5g49480–SSR105	45.9	0.31	0.09	–0.11	0.10	0.02
	ln_{12}-1.2	SSR308–SSR117	93.7	–0.24	0.12			
NFI_1	*nfi_1-4*	Hero–LEOH361	2.0	–1.14	0.15			
NFI_2	*nfi_2-4*	SSR603–SSR306	25.7	–0.72	0.08			
DBI_1	*dbi_1-4*	Hero–LEOH361	0.0	–0.03	0.05			

Position (cM) denotes the genetic distance in centiMorgans on each chromosome. a, ae_1 and ae_2 denote additive effects and additive × environment interaction effects of QTLs in winter and summer, respectively. h_a^2 and h_{ae}^2 represent the contribution ratios of aa and aae.

Table 4. Estimated epistasis and epistasis ´ environment interaction effects of QTLs for flowering properties of tomato in two different seasons (environments).

Trait	QTL	Interval	Position (cM)	QTL	Interval	Position (cM)	aa	h_{aa}^2	aae_1	aae_2	h_{aae}^2
DTF_1F_2	*dtf_1f_2-6*	SSR47–SSR128	3.0	*dtf_1f_2-11*	SSR80–C2_At5g44880	11.6	–0.92	0.05			
LN_{01}	*ln_{01}-2*	SSR5–SSR32	107.8	*ln_{01}-5*	C2_At3g55360–SSR162	58.2	0.40	0.09			
LN_{12}	*ln_{12}-1.1*	C2_At5g49480–SSR105	45.9	*ln_{12}-1.2*	SSR308–SSR117	93.7	–0.14	0.03			
DBI_1	*dbi_1-1*	LEATPACAB–C2_At5g49480	17.4	*dbi_1-2*	ORFX2–T1566	220.6	–0.04	0.05	–0.03	0.03	0.06

8.98% of the total phenotypic variations in LN_{01}, respectively, whereas the corresponding values for LN_{12} were 21.36%, 2.03%, and 2.89%. This indicates that LN is subject to environmental modification.

It also shows that both the additive and epistatic effects are important genetic bases of LN_{01}, whereas the additive effect plays an important role in the genetic control of LN_{12}. Of the DTF_1F_2 QTLs, additive, additive × environment interaction, and epistatic effects explained 2.08%, 2.61%, and 5.40% of the total phenotypic variations in DTF_1F_2, respectively. This result suggests that epistatic effects play an important role in the genetic control of DTF_1F_2, although DTF_1F_2 is also subject to environmental modification. The negative epistatic effects suggest that two epistatic loci with homozygous alleles from the same parents reduced LN_{12}, DTF_1F_2 and DBI_1. Therefore, it is important that epistatic effects be taken into account when pyramiding the QTLs that control LN_{12} or DTF_1F_2 in breeding tomato plants with low LN_{12} and short DTF_1F_2.

One QTL each for NFI_1 and NFI_2 were identified at different locations on chromosome 4. *nfi$_1$-4* colocalized with *dbi$_1$-4*, reflecting the high correlation between the occurrence of double-branched inflorescences and high NFI_1. The colocalization of these two QTLs also suggests that the *nfi$_1$-4* locus is closely linked to *dbi$_1$-4* or that a single QTL exerts pleiotropic effects on the branching of the inflorescence and the number of flowers. Further studies involving the fine mapping of these colocalized QTLs may resolve whether the region contains two linked loci or a single locus with pleiotropic effects. In contrast, *nfi$_2$-4* is located close to *dtf-4*, suggesting that these two QTLs are closely linked. Because presence of *S. pimpinellifolium* alleles in this location increased NFI_2 and decreased DTF, introgression of this location should be important in breeding early-flowering tomato cultivars producing a large number of flowers.

Grandillo and Tanksley (1996) detected three NFI QTLs on chromosomes 3, 6, and 9 using an interspecific F_2 cross between *S. esculentum* and *S. pimpinellifolium* but did not detect any NFI QTLs on chromosome 4. In contrast, van der Knaap and Tanksley (2003) identified nine NFI QTLs on chromosomes 1–5, 7, and 9 using a similar population. Further study is required to ascertain whether *nfi$_1$-4* and *nfi$_2$-4* identified in this study correspond to the NFI QTL detected by van der Knaap and Tanksley (2003).

CONCLUSION

Of the nine additive QTLs detected in this study, three QTLs, i.e., LN_{01}, LN_{12}, and DTF_1F_2, exhibited additive × environment interaction. Additionally, two additive LN_{12} QTLs showed epistatic effects. Epistatic effects were also identified for three QTLs pairs for DTF_1F_2, LN_{01}, and inflorescence branching (DBI), all of which had no additive effects. These results suggest that the number of leaves preceding the first inflorescence (LN) and the period between the flowering of the first and second inflorescences (DTF_1F_2) are subject to environmental modification and epistatic interaction. Thus, QTL × environment and epistatic effects should be considered when pyramiding QTLs to breed early flowering tomatoes.

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