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Quantitative trait loci analysis of the time of floral initiation in tomato

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ABSTRACT

The potential of a single-truss tomato production system is dependent on earliness, but few genetic studies have investigated QTLs for earliness component traits in tomatoes. Thus, QTL analyses were performed using a backcross inbred line (BIL) population after dissecting days to the ripening of the first fruit into two stages, i.e., days from sowing to anthesis and days from anthesis to first fruit ripening, in one experiment. In other experiments, the days to flowering (DTF) were further dissected into several stages, i.e., days from sowing to germination or cotyledon expansion and days from cotyledon expansion to floral initiation. A BIL family comprising 111 lines of the BC_1F_8 generation was derived from a cross between *Solanum lycopersicum* and *Solanum pimpinellifolium*. Two DTF, three FMP (fruit maturation period), two LN (number of leaves preceding inflorescence) and four DFI (days to floral initiation) QTLs with additive effects were identified in the present study. One pair of DTF QTLs exhibited epistatic effects. Additive QTLs for DTF, LN and DFI were co-located on chromosome 7, whereas LN and DFI QTLs were co-located on chromosome 3. An additive QTL for DFI located on chromosome 3 was co-located with an epistatic QTL for DTF. In the regions on chromosome 4 where an additive QTL for DFI was located, a DTF QTL was not detected, but additive QTLs for germination-related traits, such as the mean germination time (MGT), time to 90% of the final germination percentage (GT_{90}) and hypocotyl length (HYL), were clustered. In conclusion, it is likely that DFI QTLs are one of the important components of DTF QTLs, but other QTLs controlling early seedling development, such as the MGT and days to cotyledon expansion (COT), may also become important components of DTF QTLs. Furthermore, DFI QTLs could be classified into two types: the first type of QTLs hasten the developmental stage up to floral initiation, whereas those classified as belonging to the second type shorten the plastochron without any effect on the developmental stage.

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1. Introduction

The annual yield of greenhouse tomatoes in Japan has remained approximately 30 kg m^{-2} for more than 30 years, whereas the annual tomato yield in the Netherlands has doubled from 30 to 60 kg m^{-2} during this period. This low yield of tomatoes in Japan could be ascribed to differences in climate conditions and cultivars; summer temperatures reach extreme high levels in Japan, and Japanese cultivars have been bred mainly for quality and not for yield (Higashide and Heuvelink, 2009; Higashide et al., 2012). To attain an annual tomato yield of 50 kg m^{-2}, Dutch cultivation systems have been adopted and high-yielding cultivars are being bred in Japan. However, it is not easy to attain an annual yield greater than 40 kg m^{-2} in Japan without integrated environmental control because the plant vigor decreases in summer (Yasuba et al., 2011). In the 1960's, Cooper developed a single-truss tomato production system (Morgan, 2003) in which tomato plants are planted at high density but only the fruits of the first truss are harvested (Hisatomi and Fujimoto, 1978). It has been proven that the annual yield of single-truss tomatoes is comparable to that of multi-truss tomatoes, possibly because the negative long-term effect of non-optimal weather conditions could be averted in the single-truss tomato production system (Hisatomi and Fujimoto, 1978). Thus, some Japanese researchers proposed the use of single-truss tomato cultivation methods to achieve high yield. Kobayashi (1997, 1999) estimated that this method achieved an annual yield of 36 kg m^{-2} through the sequential cultivation of the Momotaro and House Momotaro cultivars and an annual yield greater than 50 kg m^{-2} by the cultivation of the Multi First cultivar. Using this cultivation method, the annual production is dependent on the number of tomato crops per year; thus, earliness should be one of the important characteristics of cultivars. The genetic and environmental factors that regulate earliness in tomatoes have been studied by many researchers (Peirce and Currence, 1959; Banerjee and Kalloo, 1989). Earliness in tomatoes has usually been evaluated as the number of days from sowing or transplanting to the ripening

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of the first fruit in the first cluster. Powers and Lyon (1941) divided days to the ripening of the first fruit into three stages, i.e., days from sowing to anthesis, days from anthesis to fruit set, and days from first fruit set to first fruit ripening, and concluded that days from sowing to anthesis had a greater impact on earliness compared with days from anthesis to fruit set.

Because the flowering time is quantitative, similarly to many other agronomic traits, quantitative trait locus (QTL) analyses have been performed by many researchers. Jiménez-Gómez et al. (2007) reported that nine QTLs for days to flowering (DTF) have been identified on chromosomes 1, 2, 3, 5, 10, 11 and 12 (De Vicente and Tanksley, 1993), chromosomes 1 and 2 (Grandillo and Tanksley, 1996), chromosomes 3 and 4 (Doganlar et al., 2002) and chromosome 11 (Lindhout et al., 1994) in previous studies using interspecific crosses of tomato. Of these DTF QTLs, *dtf2* detected by De Vicente and Tanksley (1993) is considered to correspond to *dtf2* detected by Grandillo and Tanksley (1996), and *dtf3* detected by De Vicente and Tanksley (1993) is considered to correspond to *dtf3* detected by Doganlar et al. (2002). After the report published by Jiménez-Gómez et al. (2007), Cagas et al. (2008) identified three DTF QTLs on chromosomes 1, 3 and 7, whereas Sumugat et al. (2010) and Sumugat and Sugiyama (2010) identified two DTF QTLs on chromosomes 1 and 6 and three DTF QTLs on chromosomes 1, 4 and 7, respectively.

In rice, 15 QTLs for heading date (Hd QTLs) were identified in the early 2000s through a cross between *japonica* cultivar Nipponbare and *indica* cultivar Kasalath (Monna et al., 2002). Of these QTLs, six Hd QTLs (*Hd1*, *Hd6*, *Hd3a*, *Ehd1*, *RFT1* and *Ghd7*) were cloned by map-based cloning before 2008 (Xue et al., 2008). In addition to these six Hd QTLs, six flowering-time QTLs (*DTH8*, *DTH3*, *Hd17*, *DTH 2*, *Hd16* and *OsPRR37*) have been cloned in rice to date (Matsubara et al., 2014). Some Hd QTLs, such as *Hd1* and *Hd3a*, were identified as floral initiation genes homologous to *CONSTANS* (*CO*) and *FLOWERING LOCUS T* (*FT*) in *Arabidopsis*, respectively. Kojima et al. (2002) found that *Hd3a* functioned downstream of *Hd1*, similarly to *FT* and *CO* in *Arabidopsis*, suggesting the presence of a similar flowering pathway in *Arabidopsis* (long-day plant) and rice (short-day plant), i.e., *GI*/*OsGI*−*CO*/*Hd1*−*FT*/*Hd3a*, even though rice has a unique *Ghd7*−*Ehd1*−*Hd3a*/*RFT1* flowering pathway.

In contrast, several late-flowering mutants, including *single flower truss* (*sft*), *falsiflora* (*fa*), *uniflora* (*uf*), *blind* (*bl*) and jointless (*j*), have been reported in tomato (Dielen et al., 1998; Lozano et al., 2009). *SELF-PRUNING* (*SP*) and *SFT* are tomato orthologs of *Arabidopsis TFL1* (Pnueli et al., 1998) and *FT* (Lifschitz et al., 2006), respectively, and *FA* is a tomato ortholog of *Arabidopsis LEAFY* (Molinero-Rosales et al., 2004). Molinero-Rosales et al. (2004) reported that the *sft* and *fa* double-mutant showed an additive effect in delaying flowering time and that the *sft* phenotype is epistatic to that of *sp*. These researchers assumed that *SFT* and *FA* participate independently in switching the phase change, whereas *SFT* may act upstream of *SP* in the same floral induction pathway. Périlleux et al. (2014) recently proposed that floral initiation in the primary shoot of tomato is controlled by *FA* in the shoot apical meristem and systemic *SFT* signals independently and that *FA* acts downstream of *TERMINATING FLOWER* (*TMF*) and upstream of *ANANTHA* (*AN*).

Regarding QTLs for floral initiation and flowering time, Jiménez-Gómez et al. (2007) reported that the *PHYE*, *FA*, *FLOWERING LOCUS C* (*FLC*)*-like*, *CRY1*, *PHYB2*, *SP* and *JOINTLESS* (*J*) genes are co-located with DTF and/or LN (number of leaves preceding the first inflorescence) QTLs on chromosomes 2, 3, 3, 4, 5, 6 and 11, respectively. The co-localization of genes regulating floral initiation and DTF QTLs suggests a key role of genes regulating floral initiation in the determination of days to flowering. However, flowering genes corresponding to DTF QTLs have not been clarified in tomato. It is possible that some DTF QTLs are independent of floral initiation because flowering time is a complex trait, i.e., the flowering time depends on not only floral initiation but also floral development. Sumugat and Sugiyama (2010) detected DTF QTLs on chromosomes 1 and 6, and both of these were found to be co-located with QTLs for DMB (days to macroscopic flower bud appearance) and FDD (flower development duration, DTF-DMB). These researchers hypothesized that the genetic factors controlling several flowering time processes occur as a functional gene clusters that synergistically drives the flowering time or as a gene with pleiotropic effects on different flowering processes. In studies of QTLs for flowering time, however, DTF has generally not been dissected into different stages, i.e., time to cotyledon expansion, time from cotyledon expansion to floral initiation, and time from floral initiation to anthesis. Therefore, it is not clear whether a DTF QTL plays a role in floral initiation or roles in developmental processes other than floral initiation. The aims of the present study were to detect QTLs involved in floral initiation and the early stage of development and to confirm whether these QTLs are co-located with DTF QTLs. Furthermore, the co-localization of DTF QTLs with FMP QTLs was examined to determine whether DTF QTLs play an important role in determining earliness.

2. Materials and methods

2.1. Mapping population

A backcross inbred line (BIL) population of 111 lines was used in the present study. One hundred and eleven BC_1F_7 lines were derived from an initial cross between the commercial cultivar *Solanum lycopersicum* 'M570018' and its early flowering wild-type relative, *Solanum pimpinellifolium* (PI124039), and a backcross of the F_1 to the M570018 cultivar. The resultant BC_1F_1 population was advanced using the single-seed descent (SSD) method to obtain the BC_1F_7 population, which was used for genotyping (Supplementary Fig. 1). The subsequent BC_1F_8 population was used for phenotypic evaluation.

Supplementry material related to this article found, in the online version, at http://dx.doi.org/10.1016/j.scienta.2016.02.009.

2.2. Growth condition

2.2.1. Flowering time and fruit maturation period

Seeds from the 111 BC_1F_8 families, together with seeds from their parents, were sown into 0.2-L pots (7.5 cm in diameter) containing growth medium mixed with equal amounts of Nippi-Engei-Baido-1gou (Nihon Hiryo, Tokyo, Japan) and Supermix A (Sakata, Yokohama, Japan) under greenhouse conditions on April 11, 2012 (spring experiment) and on September 13, 2012 (autumn experiment). Supplementary Table 1 shows the properties of these commercial growth media. The seedlings were transplanted to 4-L pots (18 cm in diameter) containing the same commercial compost on May 3, 2012, and October 3, 2012 (23 and 20 days after sowing, respectively). In the spring and autumn experiments, the plants were trained to a single stem and pinched above the second and third leaf after the third and second inflorescences, respectively. The plant density was 5.7 plants m^{-2} in both experiments. The plants were fertilized with 300 mL pot^{-1} 1000-fold diluted liquid fertilizer Hyponex (6-10-5; Hyponex Japan, Osaka) every other day starting eight weeks after sowing. The experimental design was a randomized complete block with five replications. The days to flowering (DTF) were counted as the number of days from sowing to anthesis of the first flower of the first inflorescence, and fruit maturation period (FMP) was recorded as the days from anthesis to the breaker stage of the first fruit at the first inflorescence (Kemble and Gardner, 1992). The numbers of leaves preceding the

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