論文の内容の要旨

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QTL analysis of flowering time and related traits in an interspecies cross of tomato (*Solanum lycopersicum* ×*Solanum pimpinellifolium*)

(トマトの種間交雑系統群における開花時期とその関連特性のＱＴＬ解析)

In Japan, tomatoes are produced all year round to meet the high demand for fresh tomatoes. They are cultivated in cool or highland areas under rain shelter in summer and in plastic houses during the cooler seasons. However, growing tomatoes in the same plastic houses all year round is not easy because plants lose vigor due to very high temperatures in summer. Therefore, some farmers try to cultivate tomatoes within a shorter period but more frequently per year than usual. In this cultivation system, only fruits in the first truss are harvested and the low yield per plant is compensated by frequent cropping. Thus, early flowering is a pre-requisite for an increase in fruit production.

Although tomato is an autonomous plant, flower initiation is directly or indirectly influenced by light, temperature, carbon dioxide, nutrition, moisture and

growth regulators. However, no single environmental factor can be considered as critical for the regulation of flowering time in tomato. Furthermore, it is well-known that vigorous vegetative growth hinders reproductive development but the physiological and genetic background of this phenomenon is not clear. In this study, quantitative trait analysis (QTL) analysis was performed to explore the genetic control of flowering time as affected by growing season, temperature and mineral nutrition. QTLs controlling flowering time and related traits, such as number of leaves preceding the first inflorescence (LN), length of the largest leaf (LL), number of lateral shoots (LS), fresh weight (FRW), and plant height (PH), were characterized and mapped concurrently. Backross inbred lines developed from a cross between the commercial cultivar, *S. lycopersicum* and the wild species, *S. pimpinellifolium* were used as a mapping population. *S. pimpinellifolium* is the closest relative of the cultivated tomato and flowers earlier than the cultivated tomato.

1. QTLs controlling flowering time and related traits grown in spring and summer.

In January 2004, *S. pimpinellifolium* 'PI124039' (male) was crossed to *S. lycopersicum* cv. 'M570018' (female). The F_1 was backcrossed to 'M570018' in May 2004, the latter being used as a male parent. The resultant BC_1F_1 plants were advanced by the single seed descent method until BC_1F_3 were obtained in June 2005. A linkage map was constructed using the 114 BC_1F_3 families, and a phenotypic evaluation was done in spring and summer using the resultant BC_1F_4 families.

The two parents differed significantly in all traits examined, except for PH. On the other hand, the growing season affected all traits significantly, except for LL. DTF was generally hastened in summer, with the parents and progeny flowering 7-10 days earlier than those grown in spring. Moreover, DTF was found to be highly correlated with all traits, except LS in summer.

Composite interval mapping detected 16 QTLs for the six traits evaluated in

spring and summer, individually explaining 10%-42% of the phenotypic variation. In chromosome 1, a major DTF QTL was detected near marker C2_At5g49480, which accounted for about 40% of the phenotypic variation in spring with contributing alleles from *S. lycopersicum*. However, in summer this QTL was responsible for only 16% of the phenotypic variation, while the DTF QTL in chromosome 3 near marker C2_At5g51110 explained more of the variance for DTF (24%). The alleles derived from *S. pimpinellifolium* in chromosome 3 resulted in early flowering.

Most of the QTLs were co-located in a single locus in chromosomes 1 and 3, while the other QTLs were sparsely mapped in chromosomes 5, 7 and 10. The DTF QTLs in chromosome 1 were co-located with QTLs for LL, LS and FRW. This locus also corresponds to the same region to which a QTL was previously mapped for DTF, days to emergence and days to third leaf in a BC_1 population derived from a cross between *S. lycopersicum* and *S. pimpinellifolium*. The number of days to third leaf is considered to reflect the rate of leaf initiation. On the other hand, in chromosome 3, the DTF QTL was found to be co-located with QTLs for LN, FRW (summer) and PH. Co-localization of DTF and LN QTLs have been also observed in previous studies, indicating that the same gene/s may be controlling these traits. These results suggest that the DTF QTLs in chromosomes 1 and 3 probably control the rate of leaf initiation and the period from the vegetative to reproductive stage, respectively.

2. QTL analysis of traits related to flowering time under low and high temperature regimes

The growing season was found to affect the flowering time of tomato. Thus, the effect of temperature was investigated in this experiment. The BC_1F_3 plants were selfed by the single seed descent method and BC_1F_5 seeds were obtained in July 2006. A linkage map was constructed using 105 BC_1F_5 families. For phenotyping, tomato plants from the resultant BC_1F_6 families were subjected to low (23/18^{o}C) and high (30/25^{o}C) temperature regimes for 20 days from sowing. After the temperature treatment, all plants were transplanted to the glasshouse in June 2007.

Results showed that *S. esculentum* differed significantly from *S. pimpinellifolium* in all traits evaluated. DTF, LL, FRW and PH were not significantly different between temperatures, while LN significantly increased at high temperature. The LN QTL in chromosome 7 was detected only at low temperature. It reduced the number of leaves preceding the first inflorescence, suggesting that low temperatures hastened the phase change from vegetative to reproductive growth. It has been previously reported that high temperatures stimulate flower development and hasten anthesis in tomato. Therefore, it is possible that the temperature treatments affect the time to flower initiation but flower development proceeds rapidly under high temperature treatments after flower induction, thereby masking the effects of the treatments on flower initiation.

3. QTLs controlling flowering time and related traits in tomato grown under low and high nutrient levels

Besides temperature, flowering time of tomato is affected by other factors, including mineral nutrition. Previous studies have shown that nutrient deficiencies prolong the vegetative phase, thereby delaying flower initiation. In this experiment, therefore, the genetic basis of flowering in tomato under two different nutrient levels was investigated.

The traits evaluated showed genetic variability in the parental lines. The nutrient treatments significantly affected the vegetative growth and reproductive development of the BC_1F_6 families. Flowering was delayed by 8-10 days in all genotypes under low nutrient condition. LN was not affected by the nutrient level, but nutrient deficiency reduced LL by almost 50%.

The QTL analysis detected a total of 24 QTLs. Six DTF QTLs were identified, half of which were detected in both nutrient treatments, while the other half were detected only in high nutrient levels. The major DTF QTLs in chromosomes 2 (near marker SSR32) and 3 (near marker C2_At5g51110) exerted more in high nutrient level than in low nutrient level, leading to early flowering in plants grown under high nutrient conditions. Moreover, the DTF QTLs co-localized with QTLs for

other traits; with LL QTLs (low nutrient level) in chromosome 1, LN and PH QTLs in chromosome 2, LN (low nutrient level) and PH QTLs in chromosome 3 near marker SSR231, and with LN and PH QTLs in chromosome 3 near marker C2_At5g51110. The co-location of major QTLs for DTF and LN in chromosomes 2 and 3 in both nutrient levels further suggests that the same genes control these traits. On the other hand, 7 QTLs (1 LN, 3 LL, 1 LS, and 2 PH) were detected only in low nutrient level, whereas 6 QTLs (3 DTF, 1LL, 1FRW and 1 PH) were detected only in high nutrient level. No LL QTLs were common in both nutrient treatments, confirming previous reports that leaf elongation and shoot growth are highly responsive to differences in nitrogen levels.

In conclusion, a total of 8 DTF QTLs were detected in chromosomes 1, 2, 3, 7 and 12. Major DTF QTLs were detected in chromosomes 1, 2, and 3, while 6 DTF QTLs were found to be co-located with QTLs for other traits, indicating the presence of loci with pleiotropic effects on these traits. Most of the QTLs identified in this study were conferred by the *S. pimpinellifolium* alleles, indicating the great importance of this wild species in the genetic improvement of the cultivated tomato.