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RESEARCH ARTICLE

QTL Identification of Yield-Related Traits and their Association with Flowering and Maturity in Soybean

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Abstract

Two soybean recombinant inbred line populations, Jinpumkong 2 x SS2-2 (J x S) and Iksannamulkong x SS2-2 (I x S) showed population-specific quantitative trait loci (QTLs) for days to flowering (DF) and days to maturity (DM) and these were closely correlated within population. In the present study, we identified QTLs for six yield-related traits with simple sequence repeat markers, and biological correlations between flowering traits and yield-related traits. The yield-related traits included plant height (PH), node numbers of main stem (NNMS), pod numbers per plant (PNPP), seed numbers per pod (SNPP), 100-seed weight (SW), and seed yield per plant (SYPP). Eighteen QTLs for six yield-related traits were detected on nine chromosomes (Chrs), containing four QTLs for PH, two for NNMS, two for PNPP, three for SNPP, five for SW, and two for SYPP. Two highly significant QTLs for PH and NNMS were identified on Chr 6 (LG C2) in both populations where the major flowering gene, *E1*, and two DF and DM QTLs were located. One other PNPP QTL was also located on this region, explaining 12.9% of phenotypic variation. Other QTLs for yield-related traits showed population-specificity. Two significant SYPP QTLs potentially related with QTLs for SNPP and PNPP were found on the same loci of Chrs 8 (Satt390) and 10 (Sat_108). Also, highly significant positive phenotypic correlations ($P < 0.01$) were found between DF with PH, NNMS, PNPP, and SYPP in both populations, while flowering was negatively correlated with SNPP and SW in the J x S ($P < 0.05$) and I x S ($P < 0.01$) populations. Similar results were also shown between DM and yield-related traits, except for one SW. These QTLs identified may be useful for marker-assisted selection by soybean breeders.

Key words: days to flowering, days to maturity, quantitative trait loci, simple sequence repeat marker, soybean, yield-related trait

Introduction

Yield is the most important and complex trait and many morphological characteristics and physiological processes in soybean contribute to seed yield. Yield-related traits may also directly influence yield by affecting the yield-component traits (Chapman et al. 2003). Soybean seed yield is a functional product of the mean number of plants per unit area, pod numbers per plant (PNPP), seed numbers per pod (SNPP), and the average mass of the individual seed. Each of these components is sequentially fixed during specific phases of soybean development. Sharma and Juneja (1971) reported that seed yield in soybean was positively correlated with PNPP and days to flowering (DF). Ariyo (1995) also reported that days to maturity (DM) and numbers of flowers per plant were correlated with seed yield. Seed yield had a highly significant positive genetic correlation with total PNPP, 100-seed weight (SW), and DF (Arshad et al. 2006).

Recent developments with molecular markers could help plant breeding for artificial selection of agronomically interesting traits via marker-assisted selection (MAS) (Paterson and Tanksley 1991). Identification of stable quantitative trait loci (QTLs) among populations might have practical applications for plant breeders. Therefore, based on the soybean genetic linkage map and QTL mapping for major agronomical important traits,

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such as DF and DM, lodging, plant height (PH), nod numbers on main stem (NNMS), SW, PNPP, and seed yield, have been investigated in several studies (Chapman et al. 2003; Cober et al. 2010; Keim et al. 1990; Lee et al. 1996; Mansur et al. 1996; Panthee et al. 2007; Zhang et al. 2004). Most of the QTLs for these traits overlapped and were mapped on the same loci or gene clusters. Mansur et al. (1996) used recombinant inbred lines (RILs) to map QTLs for 15 agronomic traits and the majority of QTLs were located on the same chromosomal regions; especially DF and DM were tightly linked with PH, lodging, and seed yield QTLs. Between their traits, correlation coefficients were highly significant ranging from 0.58 to 0.84. All QTLs of DF, PH, lodging and NNMS were mapped on chromosome (Chr) 6 (Zhang et al. 2004). A PH QTL was located on Chr 19 which is associated with lodging and *Dt1* locus and was explained by 67.7% of total phenotypic variation for PH and 56.4% for lodging (Lee et al. 1996). QTLs for flower number and PNPP with related genes were located on Chrs 11 and 19 and these QTLs were governed by time-dependent gene expression (Zhang et al. 2010a). Patterson et al. (1977) reported that yield increases in late flowering induced by longer day length, which resulted in increased node numbers per plant in soybean.

QTL analysis of these agronomic important traits were also well characterized with rice, wheat, chickpea, and oil seed rape (*Brassica napus*) (Brondani et al. 2002; Chen et al. 2010; Cobos et al. 2007; Zhang et al. 2010b). By interval mapping analysis, it was revealed that QTLs for DF and seed yield on Chr 4 were related with at least nine traits. And, in rice, at least eight QTLs of the yield-related traits were present in the same genomic position on Chr 2 (Brondani et al. 2002). QTLs responsible for different traits were co-localized in three linkage groups (LGs). LG 7 had a QTL for oil content with a QTL for seed yield and a QTL for DF. On LG 13, a QTL for seed yield was co-localized with a QTL for DF. A QTL for oil content located on LG 2 was closely positioned with a QTL for DF in oilseed rape (Chen et al. 2010). A QTL associated with DF on LG 4 was closely linked with seed size and seed yield QTLs, which explained more than 10% of phenotypic variation in chickpea (Cobos et al. 2007).

The objectives of the present study were to identify QTLs for six yield-related traits including PH, NNMS, PNPP, SNPP, SW, and SYPP using two RIL populations of Jinpumkong 2 x SS2-2 (J x S) and Iksanamulkong x SS2-2 (I x S). These two populations eventually showed population-specificity of the identified QTLs, except for PH and NNMS traits. Association of yield-related traits was compared with flowering time and maturity based on the mapping positions of QTLs for each phenotypic trait.

Materials and Methods

Plant materials and evaluation of six yield-related traits

Two mapping populations derived from J x S and I x S were used to construct a genetic linkage map and QTL analysis for six yield-related traits. Their particular descriptions of parents and two RIL populations were explained by previous studies (Kim et al. 1997; Kim et al. 2005; Liu et al. 2010; Suh et al. 1997). Six yield-related traits, PH, NNPP, PNPP, SNPP, SW, and SYPP, were measured in the farm of Suwon 2008 (Table 1). DF and DM of RILs from two populations and their parents were also previously evaluated (Liu et al. 2010). A total of 30 seeds from each individual were planted in 1.5-m-wide plots. PH was measured from the soil surface to the top of the plant at maturity. NNMS indicated the number of nodes from cotyledonary node to the top of the plant. PNPP indicated the number of pods per plant. SNPP is the number of seeds per pod. SW is the mean value of 100 normal seed weight (g) of five plants for each line.

SSR marker analysis

Table 1. Statistical analysis for six yield traits of the parents and two RIL populations derived from the cross Jinpumkong 2 x SS2-2 and Iksannamulkong x SS2-2

Traits†	Parents			RIL populations			
				Jinpumkong 2 x SS2-2		Iksannamulkong x SS2-2	
	Jinpumkong 2	Iksannamulkong	SS2-2	Mean ± SD	2Range	Mean ± SD	Range
PH (cm)	80	75	43	58.9 ± 27.5	6.0 - 116.2	74.5 ± 23.7	26.0 - 114.0
NNMS	13	13	10	13.0 ± 4.7	3.0 - 23.0	14.9 ± 3.8	4.0 - 22.0
PNPP	89	98	61	98.9 ± 60.8	16.0 - 360.0	122.6 ± 52.1	28.0 - 290.0
SNPP	1.7	1.8	2.0	1.7 ± 0.4	0.2 - 2.9	1.7 ± 0.4	1.0 - 3.1
SW (g)	24.64	15.1	23.5	22.1 ± 4.7	11.7 - 31.1	19.2 ± 3.1	12.7 - 29.4
SYPP (g/plant)	0.3	27.2	24.7	35.9 ± 20.3	4.7 - 10.8	40.6 ±19.2	8.6 - 119.9

†PH: plant height, NNMS: Node numbers of main stem, PNPP: pod numbers per plant, SNPP: seed numbers per pod, SW: 100-seed weight, SYPP: seed yield per plant.

The DNA was extracted from leaves of the two sets of mapping parents and RILs according to the procedure of Shure et al. (1983). Simple sequence repeat (SSR) markers were selected from Soybase (http://www.soybase.com/resources/ssr.php) and were used to screen polymorphisms between parents of two mapping populations. The optimal polymerase chain reaction (PCR) system was performed in 5 µL reaction volume containing 10 ng of genomic DNA, 1x reaction buffer (w/$MgCl_2$), 160 M dNTP, 0.4 unit *Taq* DNA polymerase (Applied Biosystems, Foster City, CA, USA), and 0.5 µM of primer mixture. The PCR reaction was operated in a MJ Research PCT-25 TM Thermal Controller (MJ research, Watertown, MA, USA) at 94°C for 10 min, then 30 cycles at 94°C (25 s) / 46°C (25 s) / 68°C (25 s), and a final extension at 72°C for 10 min. Allelic differences of SSR markers were analyzed using GeneMapper version 3.7 (Applied Biosystems) to determine SSR genotypes of RILs and their parents.

Construction of genetic map and QTL mapping

MAPMAKER/EXP V3.0b (Lander et al. 1993) was used to establish two soybean genetic linkage maps with SSR markers. The parameters included the Kosambi mapping function, a logarithm of the odds (LOD) score of 3.0, and a maximum distance of 50 cM. Map distance (cM) and marker order were in agreement with the soybean linkage map (Choi et al. 2007). The PROC GLM procedure in the statistic analysis system (SAS) version 9.1 (SAS institute, 2002-2003) was used to determine the associations between SSR markers and QTLs for six yield-related traits. The significant level $P < 0.01$ was also used to identify loci affecting quantitative traits.

Results

Evaluation of yield-related traits

Phenotypic data of six yield-related traits among RILs and their parents showed significant differences (Table 1), providing a good genetic background for QTL analysis using both mapping populations. In the present study, all six yield-related traits involving PH, NNMS, PNPP, SNPP, SW, and SYPP showed transgressive segregation in both RIL populations of J x S and I x S. High correlations of SYPP were observed with PH, NNMS, and PNPP at $P < 0.01$ in both populations. In the I x S population, SYPP was correlated with SNPP and SW (0.24* and 0.31**, respectively), while there were no significant correlations in the J x S population (0.05 and 0.13, respectively) (data not shown). These results suggested the yield components used in this study could be effective factors for yield in general conditions.

Correlations between flowering and yield-related traits

Two RIL populations showed population-specific traits for DF and DM in previous research (Liu et al. 2010). In the present study, DF showed correlations with six yield-related traits and similar results were also shown between DM and these six traits, except between DM and SW in the I x S population (Table 2). Highly positive phenotypic correlations of DF and DM were observed with PH, NNMS, PNPP, and SYPP in both populations. In the J x S population, negative correlations were observed among DF with SNPP and SW, but no significant difference was found between DM and SW (Table 2). Among them, DF with NNMS and DM with NNMS displayed higher correlations in both populations, ranging from 0.74** to 0.85**, but between DF with SYPP correlations were lower, ranging from 0.23** to 0.35** in both populations. These results suggested that tall plants could ordinarily produce more numbers of nodes per plant, which could eventually lead to produce more numbers of pods per plant. However, DF and DM may exhibit higher direct and positive contributions towards seed yield.

QTL analysis of yield traits

Chromosomal regions with QTLs for DF and DM in two RIL populations were detected in the previous study, showing a high correlation within populations by linkage analysis for two traits (Liu et al. 2010). In the present study, QTLs for six yield-related traits by SF-ANOVA with P value and R^2 are summarized in Table 3. A total of 18 QTLs were associated with SSR markers from two populations and distributed on nine different chromosomes (Chrs 1, 2, 6, 8, 10, 14, 15, 19, and 20). Their phenotypic variations were explained by an individual QTL ranging from 7.8 to 23.3%. Four QTLs on three chromosomes (Chrs 6, 10, and 15) were associated with PH, of which two QTLs associated with PH on Chr 6 were linked to Satt202 (R^2 = 23.3%) and Satt100 (R^2 = 20.0%) in each of the J x S and I x S populations. These QTLs positioned near the major flowering gene *E1* had the largest effect accounting for more than 20% of phenotypic variations in both populations. Additionally, two PH QTLs were mapped on Chr 10 with Satt153 and Chr 15 with Satt212 only in the J x S population and their phenotypic variations were explained as 10.9 and 12.0%, respectively. One QTL associated with NNMS was mapped on Chr 2 with Satt041 only in J x S and the other NNPP QTL was located on Chr 6 with Satt100 in both populations. The 11.2 and 20.5% of the NNMS phenotypic variations were explained in each population.

Table 2. Phenotypic correlation coefficients between flowering traits and yield traits in two RIL populations derived from Jinpumkong 2 x SS2-2 and Iksannamulkong x SS2-2

Traits	DF	DM
	Jinpumkong 2 x SS2-2	
PH (cm)	0.62**	0.56**
NNMS	0.74**	0.59**
PNPP	0.49**	0.41**
SNPP	-0.24*	-0.28**
SW (g)	-0.26*	-0.10
SYPP (g/plant)	0.35**	0.26*
	Iksannamulkong x SS2-2	
PH (cm)	0.78**	0.69**
NNMS	0.85**	0.76**
PNPP	0.52**	0.51**
SNPP	-0.40**	-0.29**
SW (g)	-0.25**	-0.03
SYPP (g/plant)	0.23**	0.35**

[†] The same abbreviations for traits were used as Table 1.

* and ** denote significance at 0.05 and 0.01 probability level, respectively.

Five significant QTLs associated with SW were identified on four chromosomes (Chrs 1, 14, 15, and 20); two individual QTLs with SW were identified on Chr 14 with Satt577 and Chr 15 with Satt212 in the J x S population and three other individual QTLs were identified on Chrs 1, 14, and 20 with Satt147, Satt066, and Satt354 only in the I x S population, explaining 7.8, 10.4, and 8.5% of phenotypic variations, respectively (Table 3).

Seven QTLs associated with PNPP, SNPP, and SYPP were identified on five different chromosomes (Chrs 1, 6, 8, 10, and 19), which included two QTLs for PNPP, three QTLs for SNPP, and two QTLs for SYPP (Table 3). Among them, one QTL for PNPP with Satt100 was also located on the same loci associated with PH and NNMS in our study, representing 12.9% of phenotypic variation. The other QTL for PNPP with Satt390 was located on Chr 8 in the I x S population and accounted for phenotypic variation of 19.2%. This PNPP QTL was also involved in a SYPP QTL with phenotypic variation of 16.6%. Two QTLs associated with SNPP were identified on Chrs 1 and 19 with Satt439 and Satt388 only in the J x S population and these two individual QTLs were shown as 13.9 and 15.9% of phenotypic variations. The other QTL for SNPP was located on Chr 10 with Sat_108, with the locus also present in the same position as a SYPP QTL in the present study, and these SNPP and SYPP

Table 3. QTL analysis for yield traits of two mapping populations by ANOVA ($P < 0.01$)

Traits†	SSR	Chr	Position (cM)‡	RIL populations				Reported QTLs	Related Marker	Map position (cM)	References
				J x S		I x S					
				P value	R^2 (%)	*P* value	R^2 (%)				
PH (cm)	Satt100	6	109.98	-	-	<0.0001	20.0	*Pl ht 18-4*	Satt134	112.8	Wang et al. 2004
	Satt202	6	121.96	<0.0001	23.3	-	-	*Pl ht 3-2*	Satt079	117.9	Mansur et al. 1996
	Satt153	10	114.02	0.0076	10.9	-	-	*Pl ht 18-2*	Satt592	100.4	Wang et al. 2004
	Satt212	15	24.25	0.0051	12.0	-	-	*Pl ht 18-5*	Satt575	3.3	Wang et al. 2004
NNMS	Satt041	2	89.19	0.0009	12.3	-	-	-	-	-	-
	Satt100	6	109.98	0.007	11.2	<0.0001	20.5	*qNN-2*	Satt376-Satt286	95.1-97.7	Li et al. 2010
PNPP	Satt100	6	109.98	-	-	0.0006	12.9	*qNN-3*	Satt376-Satt286	113.5-113.8	Li et al. 2010
	Satt390	8	8.2	-	-	<0.0001	19.2	-	-	-	-
SNPP	Satt439	1	62.84	0.0027	13.9	-	-	-	-	-	-
	Sat_108	10	121.13	-	-	0.0049	9.7	-	-	-	-
	Satt388	19	21.61	0.0009	15.9	-	-	*qSN-1*	Satt495-Sst_113	0.0-63.5	Zhao et al. 2008
SW (g)	Satt147	1	103.46	-	-	0.003	7.8	*Sd wt 7-2*	Sat_036	75.3	Orf et al. 1999
	Satt577	14	1.64	0.0088	11.3	-	-	-	-	-	-
	Satt066	14	68.29	-	-	0.003	10.4	*Sd wt 13-2*	Satt304	65.6	Hoeck et al. 2003
	Satt212	15	24.25	0.0092	11.3	-	-	*Sd wt 11-2*	A069_2	24.3	Lee et al. 2001
	Satt354	20	44.89	-	-	0.0083	8.5	*Sd wt 9-1*	A515-1	44.0	Sebolt et al. 2000
SYPP (g/plant)	Satt390	8	8.02	-	-	<0.0001	16.6	-	-	-	-
	Sat_108	10	121.13	-	-	0.0007	13.0	-	-	-	-

†The same abbreviations for traits were used as Table 1.

‡ Estimated position (cM) was inferred from the publically-available USDA map (Choi et al. 2007) and reported flowering QTLs were represented within 50 cM.

QTLs accounting for 9.7 and 13.0% of phenotypic variation. These results suggested biological correlation of SYPP with PNPP and SNPP that PNPP and SNPP were the major component factors of seed yield and their genetic elements might directly influence soybean yield with relatively large effects. Furthermore, the flowering and yield QTLs were clustered on one or more genomic regions of the soybean genome.

Discussion

Generally, most of the quantitative traits were shown to be heritable and their heritability values were influenced by genotype and environment interactions (Showkat and Tyagi 2010). Quantitative traits are governed by both major and minor genes contributing large and small additive or their interaction effects. In the present study, we used two different soybean populations of J x S and I x S for identifying QTLs with six yield-related traits and observed correlations between flowering/maturity and yield-related traits. DF and DM showed population-specificity in two populations in our previous study (Liu et al. 2010). Highly significant positive correlations were observed among DF and DM with PH, NNMS, PNPP, and Seed yield. The significant negative correlations were shown among DF with SNPP and SW in two populations, whereas no significant correlation was observed between DM and SW (Table 2). Similar results were also reported by Malik et al. (2007) and Showkat and Tyagi (2010). Seed yeild positively correlated with DF and DM, PH, PNPP, SW, leaf area, and number of braches per plant. Panthee et al. (2007) also reported low heritability between DF and Seed yield (0.20), and no significant correlation was found between DM and SW. However, in the present study, DF and DM were found to have a lower correlation with SYPP ranging from 0.23* - 0.35**, but DF QTLs were not linked to any QTL with SYPP in our populations (Fig. 1). However, DF QTLs with other yield-related traits, such as PH and NNMS, were identified on the same loci on Chr 6 in both populations and the QTL for PNPP was also located in this region in the I x S population.

(Fig. 1) Our data revealed that DF had positive and direct effects on PH, PNPP, and NNMS and their correlation coefficients ranged from 0.52** - 0.85**. This suggests that completion of DF followed by days to pod initiation was also important selection criteria. Therefore, the characters showing a positive correlation could be effectively utilized in crop improvement programs and in the development of new high-yielding soybean varieties.

DF is considered to be an important adaptive trait because crops have to grow in different environments and photoperiodic regions. In a previous study (Liu et al. 2010), highly significant QTLs for DF were detected on Chr 6 with Satt100 and Chr 19 with Satt373 which closely linked to flowering gene loci *E1* and *E3* (Funatsuki et al. 2005). Especially, Satt100 on Chr 6 could be considered an interesting genomic region for agronomic traits in soybean. Three QTLs, *FT 2-1* with Satt100, *Pod mat 8-1* with Satt365, and *Photo ins 2-1* with P029_1, have been reported in this region (Funatsuki et al. 2005; Orf et al. 1999; Tasma et al. 2001) and the PH QTL, *Pl ht 18-4* with Satt134, the *qNN-2* QTL with Satt376-Satt286, and the *qPN-3* QTL with Satt460-Satt079 were linked to these regions (Li et al. 2010; Wang et al. 2004). Moreover, this region also included *Sd yld 1-1* with R079_1 and *Sd wt 15-1* with Satt277 (Hyten et al. 2004; Mansur et al. 1993). Hence, as one QTL could influence at least five agronomic traits in our study, it indicated pleiotropism is common for most of the QTLs and a variety of traits co-localize and correlate with each other.

The two SYPP QTLs associated with Satt390 and Sat_108

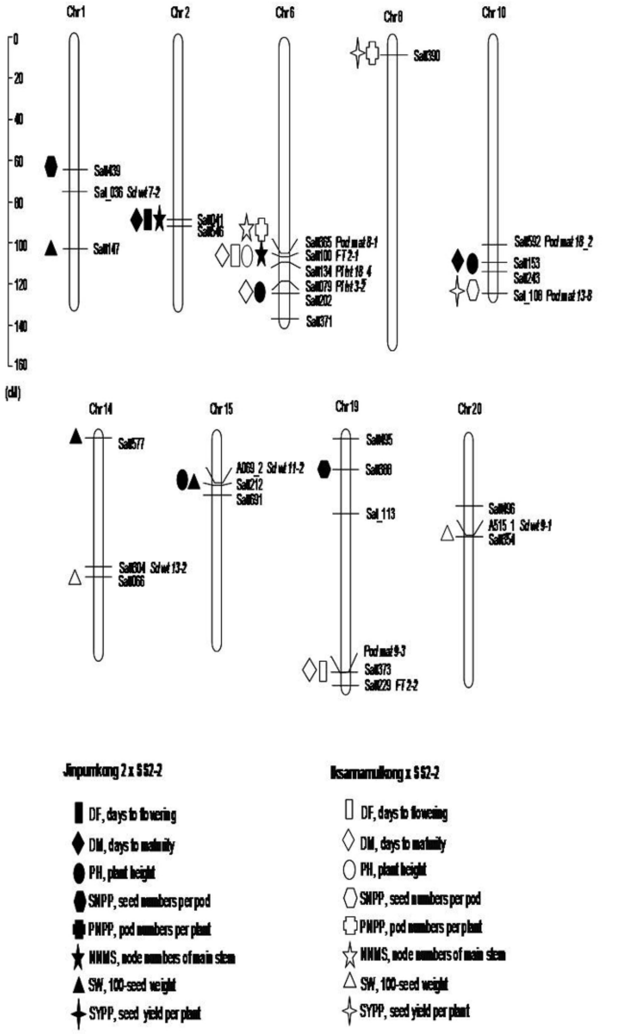

Fig. 1. Locations of six yield-related traits QTLs with DF and DM on the genetic linkage map across two different populations derived from Jinpumkong 2 x SS2-2 and Iksannamulkong x SS2-2. The map distance (cM) and marker order are in agreement with the soybean linkage map (Choi et al. 2007).

are novel since they do not match those that have already been reported on Chrs 8 and 10. However, the *Sd wt 4-5* QTL near 42.2 cM away from the T153_1 marker on Chr 8 and three pod maturity QTLs (*Pod mat 13-8* with Sat_108, *Pod mat 14-2* with Satt592, and *Pod mat 15-2* with Satt567), one QTL, *Fflr 8-2* with 138GA26, and one QTL, *Pl ht 18-2* with Satt592, located near the loci Sat_108 on Chr 10 have been reported (Maughan et al. 1996; Specht et al. 2001; Wang et al. 2004; Yamanaka et al. 2001). Moreover, highly significant correlation coefficients among these traits were also presented in this study. Yield is the complex terminal outcome of growth processes, which are controlled by diverse and interrelated developmental networks and signaling pathways. These results were in agreement with Ariyo (1995). It was reported that they most likely had a more complex relationship with each other, which could not be explained by a linear relationship, although some characters were correlated.

In this research, 18 QTLs were identified with two RIL populations derived from the crosses of J x S and I x S. Five QTLs for DF, DM, PH, PNPP, and NNMS co-located at the same genomic region on Chr 6, and two other SYPP QTLs that also concurrently influenced SNPP and SW were mapped on Chrs 8 and 10, respectively. Our findings may be useful for facilitating the selection of yield-related traits via MAS. Additionally, in order to obtain a more complete and accurate picture of QTLs associated with various traits, QTLs detected in different populations should be analyzed compared to those found in other studies.

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