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Characterization of a set of chromosome single-segment substitution lines derived from two sequenced elite maize inbred lines

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Abstract

Chromosome single-segment substitution lines (SSSLs) are powerful tools for detecting and precisely mapping quantitative trait loci (QTLs) and evaluating the action of genes as single Mendelian factors. In this study, 108 SSSLs, which included 46 uniquely substituted segments, were developed from an advanced backcross procedure with the marker-assisted selection of 146 simple sequence repeat (SSR) markers using the elite maize inbred line Zheng58 as the recipient and Chang7-2 as the donor. Each SSSL contained a single substituted chromosome segment that was derived from donor strain Chang7-2 in the genetic background of the recipient Zheng58 strain. The 46 substituted segments were unevenly distributed on ten maize chromosomes, and the substituted segment length ranged from 2.7 centimorgan (cM) to 283.5 cM with an average of 66.0 cM. The total length of the 46 substitution segments was 3,035.2 cM, which covered 2,142.6 cM (31.47%) of the entire maize genome. To evaluate the potential application of these SSSLs for QTL detection, 44 SSSLs were used for the phenotypic characterization of plant height in three field trials. Twenty-nine QTLs of plant height were identified, and the percentages of additive effects varied from -8.45% to 12.86%. The results demonstrated that these SSSLs possesses large genetic variations and are excellent tools for genetically dissecting complex traits over several environments.

Keywords: maize, SSR marker, single-segment substitution line, substituted segment, plant height

Introduction

Genetic populations play a significant role in mapping and map-based cloning of quantitative trait loci (QTLs). Most genetic populations used in the past were primary mapping populations, such as $F_{2:3}$, BC_1, double haploid (DH) and recombinant inbred lines (RILs), which were used to identify the evident effects of QTLs (Ahn et al, 1993; Li et al, 1995; Yu et al, 2002). However, the differences in genetic background between individuals frequently resulted in QTL mapping deviation, leading to lower chances of fine mapping and gene cloning. With the advancement of research, secondary mapping populations (Yano, 2001; Xi and Wu, 2006), such as chromosome segment substitution lines (CSSLs) (Kubo et al, 2002), introgression lines (ILs) (Eshed et al, 1992), near-isogenic lines (NILs) (Xia and Zheng, 2002) and backcross recombinant inbred lines (BCRILs) (Monforte and Tanksley, 2000), have been used increasingly.

An ideal substitution line should only contain one isolated chromosomal substituted segment of the donor genotype in the recurrent parent genetic background (Howell et al, 1996). These substitution lines enable the detection of beneficial donor alleles, which are separated from the undesirable portions of the donor genotype and are valuable for the accurate assessment and mapping of QTLs, thus improving the study of quantitative traits in replicated environments (Cermakova et al, 1999). Therefore, it is necessary to construct chromosome single-segment substitution lines (SSSLs) that only contain one substituted donor segment in a simplified genetic background.

SSSLs and similar populations have been constructed in tomato (Eshed and Zamir, 1994; Bernacchi et al, 1998) and rice (Xi et al, 2006; Talukdar and Zhang, 2007). 118 single-segment introgression lines (SSILs) of maize (*Zea mays* L) were developed with two elite inbred lines, 87-1 and Zong3, as the recurrent parents, and a waxy corn line, Hengbai522, as the donor (Wang et al, 2007). By means of marker-assisted backcrossing, a set of 89 NILs of maize was created by Szalma et al (2007), and Salvi et al (2011) produced an introgression library including 75 lines using the extremely early-flowering maize variety Gaspé Flint and the elite line B73 as donor and recipient genotypes, respectively, and utilized that collection to investigate the genetic basis of flowering time and related traits of adaptive and agronomic importance in maize.

Twenty-four QTLs for plant height and its components on the substituted segments of 52 SSSLs in rice were identified (He et al, 2005). Nine QTLs for

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plant height and 15 QTLs for ear height were detected by Bai et al (2010) using 98 Z3HBILs near-isogenic ingression lines in maize. Li et al (2008) identified and fine-mapped a new locus, *S-d*, that confers the partial pollen sterility of intersubspecific F_1 hybrids in rice, to a 67-kb interval using secondary segregation NIL populations. Wan et al (2008) fine-mapped a single recessive gene, *gw-5*, which controls both grain width and the length-to-width ratio in rice. *gw-5* was finally narrowed down to a 49.7-kb genomic region by using 6,781 individual CSSL plants. The qPGWC-7 QTL, which controls grain chalkiness, was fine-mapped to a 44-kb DNA fragment using F_2 segregation CSSL populations in rice (Zhou et al, 2009). The fw2.2 is a quantitative trait locus key to the evolution of tomato fruit size, and it was cloned by Frary et al (2000) using ingression lines containing one segment from the donor. Krieger et al (2010) analyzed the function of the *single flower truss* (*SFT*) flowering gene, which drives heterosis for tomato yield using isogenic mutant heterozygotes. Using SSSLs, Wang et al (2008b) reported the isolation and functional analysis of the *grain incomplete filling 1* (*GIF1*) rice gene, which encodes a cell wall invertase that is required for carbon partitioning during early grain filling. Liu et al (2009) analyzed the dynamic expression of nine QTLs for tiller number using SSSLs in rice. Liu et al (2008) studied QTLs with additive effects and additive-by-environment interaction effects on rice panicle number with the use of SSSLs.

In this study, Zheng58 and Chang7-2, two representative Chinese maize inbred lines with available whole-genome sequences (Lai et al, 2010), were selected as basic materials to construct the Chang7-2 SSSLs in the Zheng58 genetic background using backcrossing and molecular marker-assisted selection. A one-year and three-environment plant height QTL analysis was performed to assess the potential value of these SSSLs and to provide reference information for studies on similar maize populations.

Materials and Methods

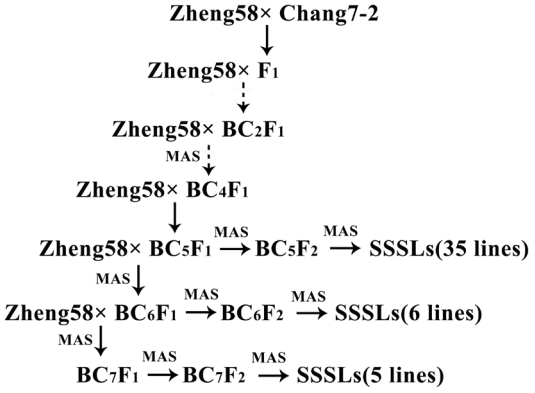

Figure 1 - Experimental scheme of single-segment substitution line construction.

Parental materials and SSSL construction methodology

Zheng58, a parent inbred line of the commercial maize hybrid, Zhengdan958, was used as the recipient, and Chang7-2, the other parent inbred line of Zhengdan958, was used as the donor to construct maize chromosome SSSLs using a combination of crossing, backcrossing and molecular marker-assisted selection (MAS) (Figure 1). A mini-scale DNA extraction was performed according to the procedure described by Zhang and Xi (2007). SSR detection was performed using the method described by Wang et al (2009).

Substituted segment length calculation

The substituted segment length was estimated based on graphical genotypes (Young and Tanksley, 1989;). A chromosome segment that is flanked by two donor type markers (DD) is considered a 100% donor type, a chromosome segment that is flanked by two recipient type markers (RR) is considered a 0% donor type and a chromosome segment that is flanked by one donor and one recipient type marker (DR) is considered a 50% donor type. The sum of the DD length and the two DR lengths was considered as the estimated length of a chromosome substituted segment. The length of the donor-substituted segments was calculated based on the marker's location on the maize SSR linkage map, IBM2 2008 Neighbors (http://www.maizegdb.org).

Field experiments and plant height QTL analysis of SSSL

Forty-four homozygous SSSLs and the recurrent parental inbred line, Zheng58, were used as the experimental materials to conduct QTL analysis. These materials were planted in single, alternating rows with a 4-m row length. The parental line, Zheng58, was planted in multiple repeats as the field experimental control. In 2010, these 45 homozygous inbred lines were planted in the following three environments: Zhengzhou (34°82'N, 113°62'E; three replicates) and Puyang (35°45'N, 115°54'E; one replicate) in Henan province, Sanya (18°25'N, 109°50'E; two replicates) in Hainan province, China; regular field management was maintained. Twelve mature individuals from each row were selected for plant height (PH) measurement.

QTL analysis was performed using the method described by Liu et al (2004). The combined Zheng 58 observation value from multiple plots was used as the control. The differences between the SSSL and Zheng58 values were compared using t-test, with $P < 0.001$ as the significance threshold for the existence of a QTL on the substituted segment. The QTL nomenclature followed the principles described by McCouch et al (1997). The substitution mapping method (Paterson et al, 1990) was used for QTL fine-mapping of the SSSL overlapping segments. The additive effect values and additive effect percentages of each QTL were estimated according to the method previously described by Eshed and Zamir (1995). The

additive effect (A) was half of the difference between each SSSL and Zheng58, and the additive effect percentages (A%) was calculated from the additive effect divided by the mean of Zheng58.

Results

SSSL Construction

Based on the high-density SSR molecular marker linkage map of IBM2 2008 neighbors (http://www.maizegdb.org), 472 pairs of SSR primers were selected to screen for polymorphisms in accordance with the equidistance principle. Among these primers, 146 pairs (30.93%) showed polymorphisms between the parental lines, with 9-19 pairs of SSR markers on each chromosome and an average distance of 46.6 cM between markers. Marker-assisted selection (MAS) and backcross procedures were used to construct SSSL populations.

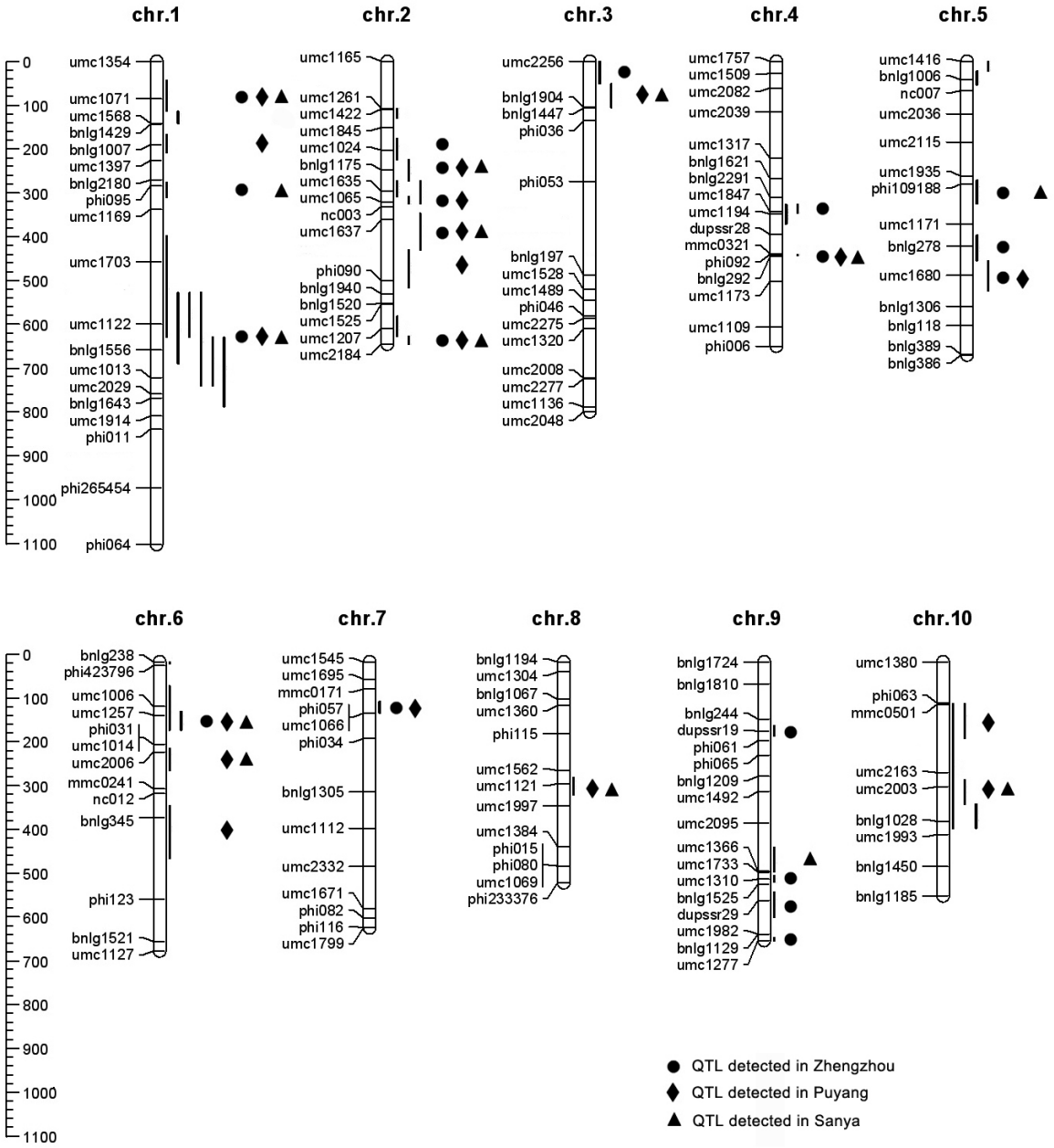

Figure 2 - Location of the 46 chromosome substituted segments in the SSSLs and QTLs of plant height. All markers in this figure were used in this study. The bars to the right of the chromosomes represent the 46 unique substituted segments in the SSSLs. The length of the substituted segments was calculated based on the marker's location on the maize SSR linkage map, IBM2 2008 Neighbors. The dots, diamonds and triangles to the right of the substituted segment denote the plant height QTLs that were identified in Zhengzhou, Puyang and Sanya, respectively.

Table 1 - Coverage of 46 substituted segments in SSSLs on maize chromosomes.

Chromosome	Chr.1	Chr.2	Chr.3	Chr.4	Chr.5	Chr.6	Chr.7	Chr.8	Chr.9	Chr.10	Total
Number of substituted segments	10	10	2	3	5	5	1	1	5	4	46
Total length of substituted segments (cM)	1154.1	456.5	104.9	65.9	236.1	318.7	27.1	39.8	158.7	473.2	3035.2
Coverage length of substituted segments (cM)	566.9	402.8	104.9	47.2	236.1	275.5	27.1	39.8	158.7	283.5	2142.6
Percent coverage (%)	51.40	62.46	13.12	7.25	35.25	41.75	4.47	7.91	24.96	53.06	31.47

In our experiment, the maize inbred line Zheng58 was used as the female parent and crossed with Chang7-2 to generate F_1. F_1 was then used as the male parent and backcrossed with Zheng58, generating BC_1F_1. Ten plants of BC_1F_1 were selected to backcross with Zheng58, of which two were selected. The selected BC_2F_1 seeds were planted in two experiment plots, and 100 individual plants were selected for a simultaneous genome-wide SSR molecular marker screening and backcrossed with Zheng58. Thirty-seven plants were picked based on the presence of fewer donor segments in the individual plants. The plants were also selected to include as wide genome coverage as possible with all the substituted segments in the different individual plants. The selected BC_3F_1 seeds were then planted in 37 rows, ten plants from each row were selected to trace the chromosome substituted segments of Chang7-2 through molecular marker detection. A total of 98 plants were selected according to their SSR marker genotypes. The selected BC_4F_1 seeds were then planted in 98 rows for continuous backcrossing. The backcrossed seeds from the same row of BC_4F_1 were equally mixed to plant BC_5F_1 in rows, and 60 BC_5F_1 plants with 1-2 substituted segments were selected for selfing based on molecular marker genotypes. The 38 BC_5F_1 plants with three or more donor segments were backcrossed again with Zheng58 (Figure 1). Similarly, for generations of BC_6F_1 and BC_7F_1, individual plants with 1-2 substituted segments were self-crossed, according to the molecular marker genotype results, to obtain homozygote for the substituted segments; whereas plants with three or more donor-substituted segments were backcrossed again with Zheng58, decreasing the number of donor segments in the individual plants. The following results were obtained through selfing and molecular marker testing: 84 homozygous SSSLs from 60 BC_5F_2 plants with 35 unique substituted segments; 9 homozygous SSSLs from 25 BC_6F_2 plants containing 6 unique substituted

Table 2 - Location and additive effects of plant height QTLs identified in different environments.

	QTL position			$\bar{X}\pm$SE (cm)			A(%)[b]		
QTL	Linkage marker	Bin	Interval(cM)[a]	Zhengzhou	Puyang	Sanya	Zhengzhou	Puyang	Sanya
qPH1-1	umc1071	1.01	70.9	124.89 ± 0.95	126.67 ± 1.67	115.79 ± 1.95	-3.75	-2.79	4.43
qPH1-2	bnlg1007	1.02	41.5	-	142.42 ± 1.38	-	-	3.08	-
qPH1-3	phi095	1.03	33.5	126.92 ± 1.51	-	116.04 ± 1.12	-3.00	-	4.55
qPH1-4	umc1122	1.07	100.8	155.15 ± 1.25	159.25 ± 1.95	133.79 ± 1.99	7.45	9.35	12.86
qPH2-1	umc1024	2.04	48.7	125.81 ± 0.96	-	-	-3.41	-	-
qPH2-2	bnlg1175	2.04	47.4	128.19 ± 1.31	125.33 ± 1.72	114.96 ± 1.25	-2.53	-3.29	4.04
qPH2-3	umc1065	2.05	17.2	144.42 ± 1.08	147.58 ± 1.95	-	3.48	5.00	-
qPH2-4	umc1637	2.07	84.6	147.69 ± 1.18	149.00 ± 1.77	120.75 ± 2.00	4.69	5.53	6.76
qPH2-5	phi090	2.08	84.4	-	125.92 ± 1.94	-	-	-3.07	-
qPH2-6	umc2184	2.09	17.2	122.52 ± 1.18	120.00 ± 2.41	97.65 ± 2.57	-4.63	-5.28	-4.10
qPH3-1	umc2256	3.01	53.0	128.81 ± 0.92	-	-	-2.30	-	-
qPH3-2	bnlg1904	3.04	53.0	-	146.25 ± 2.94	116.33 ± 1.45	-	4.51	4.68
qPH4-1	umc1847	4.07	18.7	115.92 ± 0.93	-	-	-3.37	-	-
qPH4-2	phi092	4.08	2.7	116.79 ± 1.32	124.83 ± 1.50	99.83 ± 1.91	-6.75	-3.48	-3.07
qPH5-1	phi109188	5.03	54.4	127.53 ± 0.97	-	114.50 ± 2.10	-2.77	-	3.82
qPH5-2	bnlg278	5.05	58.6	127.94 ± 1.35	-	-	-2.62	-	-
qPH5-3	umc1680	5.06	69.0	122.91 ± 1.52	122.50 ± 4.67	-	-4.49	-4.35	-
qPH6-1	umc1257	6.02	43.3	114.17 ± 0.85	111.50 ± 2.33	96.88 ± 1.24	-7.72	-8.45	-4.46
qPH6-2	umc2006	6.04	50.6	-	124.83 ± 3.29	122.58 ± 1.89	-	-3.48	7.62
qPH6-3	bnlg345	6.05	120.4	-	145.58 ± 1.12	-	-	4.26	-
qPH7-1	phi057	7.01	27.1	122.67 ± 1.22	141.60 ± 1.98	-	-4.57	2.61	-
qPH8-1	umc1121	8.05	39.8	-	148.5 ± 1.92	114.63 ± 1.32	-	5.34	3.88
qPH9-1	dupssr19	9.02	24.6	120.91 ± 1.18	-	-	-5.23	-	-
qPH9-2	umc1366	9.06	56.7	-	141.50 ± 2.84	-	-	2.74	-
qPH9-3	umc1310	9.06	13.4	128.58 ± 1.15	-	-	-2.38	-	-
qPH9-4	dupssr29	9.07	57.1	126.03 ± 1.02	-	-	-3.33	-	-
qPH9-5	umc1277	9.07	7.0	127.91 ± 1.24	-	-	-2.63	-	-
qPH10-1	mmc0501	10	79.8	-	142.92 ± 1.41	-	-	3.26	-
qPH10-2	umc2003	10	55.5	-	126.67 ± 2.12	96.42 ± 1.61	-	-2.79	-4.68

[a]The QTL interval was calculated based on the marker's location on the maize SSR linkage map, IBM2 2008 Neighbors.
[b]A%: the additive effect percentage, $A\% = (PH_{SSSL} - PH_{zheng58})/(2 \times PH_{zheng58}) \times 100\%$. Positive values for the additive effect indicate that the Chang7-2 alleles increase plant height(PH)

segments; and 15 homozygous SSSLs from 27 BC_7F_2 plants containing 5 unique substituted segments. Thus, 108 SSSLs, including 46 unique types, were obtained in this experiment, and each SSSL only contained one substituted segment from Chang7-2 in the genetic background of Zheng58 (Figure 2).

Genomic characterization of these SSSLs

The 46 unique substituted segments in SSSLs were distributed on the ten maize chromosomes, ranging from one on chromosomes 7 and 8 to ten on chromosomes 1 and 2, with an average of 4.6 on each chromosome. The average length of the substituted segments per chromosome was 303.5 cM, ranging from 27.1 cM on chromosome 7 to 1154.1 cM on chromosome 1. The coverage length of the 46 substituted segments in the maize genome was 2,142.6 cM (31.47%). The percent coverage of substituted segments on each chromosome varied from 4.47% on chromosome 7 to 62.46% on chromosome 2 (Table 1, Figure 2).

The lengths of the 46 substituted segments in the SSSLs ranged from 2.7 cM to 283.5 cM, with a total length of 3,035.2 cM and an average length of 66.0 cM. Thirty-seven substituted segments were < 90.0 cM, accounting for 80.44% of the total segments. Three substituted segments were > 210.0 cM, accounting for 6.52% of the total segments.

SSSL-based QTL analysis of plant height

To assess the potential values of these SSSLs in QTL analysis, we investigated the phenotypic values of 44 SSSLs in three environments (Zhengzhou, Puyang and Sanya). Phenotypic variations in the recurrent parent line, Zheng58, were not significant between Zhengzhou and Puyang, at an average height of 134.59 ± 1.43 cm; However, an average height of 106.37 ± 1.90 cm was observed in Sanya. The plant height for the 44 SSSLs ranged from 89.48 ± 1.84 cm to 161.50 ± 1.00 cm, with an average of 123.16 ± 0.28 cm. The distribution of plant height for the SSSLs was concentrated between 120.00 cm and 145.00 cm in Zhengzhou and Puyang, whereas the phenotypic value distribution in Sanya was between 95.00 cm and 120.00 cm. A visualization of the phenotypic differences between each SSSL line and Zheng58 is pro-

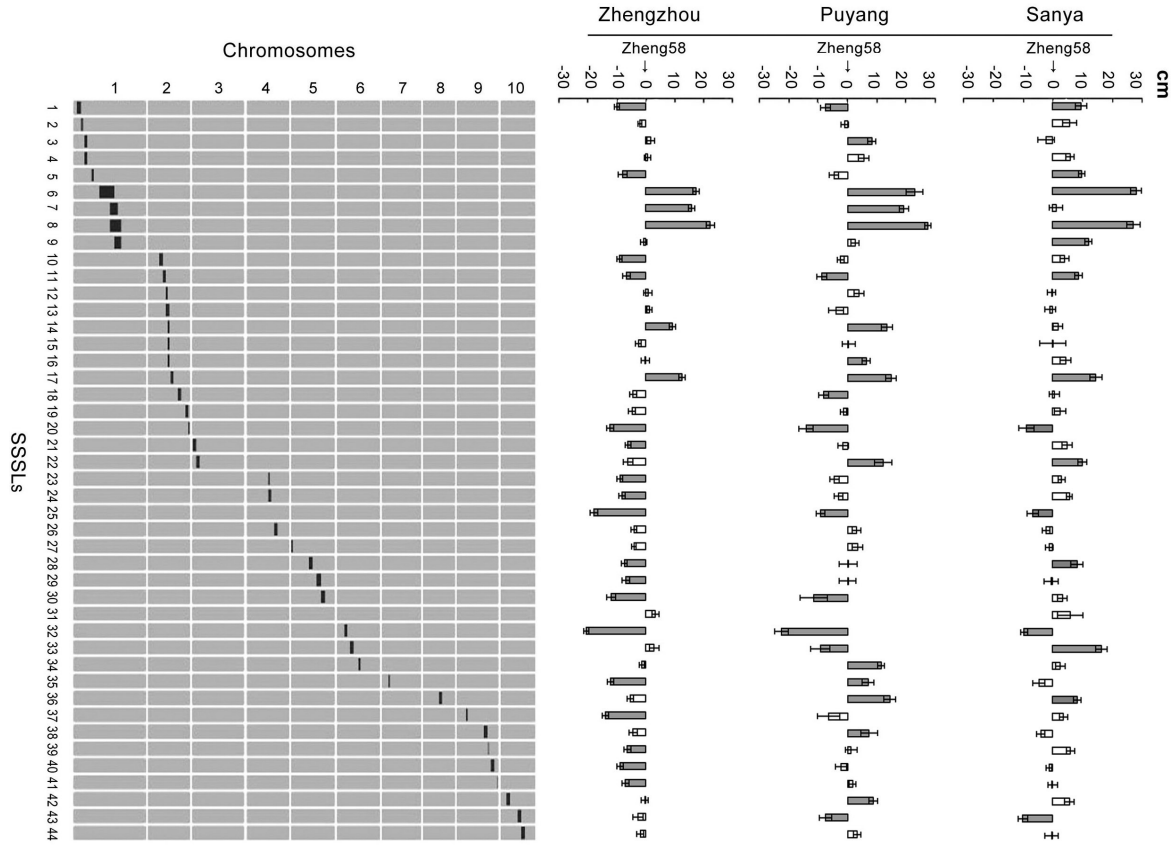

Figure 3 - Graphical genotype and QTL effect. (A) Graphical genotype of the Zheng58 × Chang7-2 single-segment substitution lines (SSSLs). SSSLs are represented horizontally and chromosome positions (polymorphic SSR markers as reported in Figure 2) are indicated vertically. Black rectangles indicate homozygous chromosome substitution segment derived from Chang7-2, grey rectangles represent homozygous genetic background of Zheng58, respectively. (B) Phenotypic differences of plant height (PH) between each SSSL line and Zheng58 in three environments (Zhengzhou, Puyang and Sanya), represented as horizontally columns. Black columns indicate SSSL lines significantly different from Zheng58 ($P < 0.001$). Units are 'cm' for plant height.

vided in Figure 3. The results of the t-test showed that the plant heights of 23, 22 and 15 SSSLs from the Zhengzhou, Puyang and Sanya sites, respectively, were significantly different ($P < 0.001$) from that of the recurrent parent Zheng58 (Figure 3) .

QTL analysis revealed that 29 plant height QTLs were found in 34 SSSLs (Figure 2). Twenty plant height QTLs were identified from 23 SSSLs at the Zhengzhou site, 19 QTLs from 22 SSSLs at the Puyang site, and 13 QTLs from 15 SSSLs were identified at the Sanya site. The additive effect percentages of the 29 QTLs ranged from -8.45% to 12.86%. Among the 29 QTLs, seven were repetitively detected at all three experimental sites (Table 2). These seven plant height QTLs were distributed on chromosomes 1, 2, 4 and 6. Among them, the gene effect directions of five QTLs were stably expressed at all the experimental sites, whereas qPH1-1 and qPH2-2 showed different gene effect directions at the Sanya site. These two plant height QTL might be sensitive to photoperiod.

Discussion

A total of 108 homozygous maize SSSLs with 46 unique substituted segments were obtained in this study using molecular MAS of 146 SSR markers. Zheng58 was the recipient, and Chang7-2 was the donor strain. These 46 substituted segments covered 2,142.6 cM of the entire maize genome, with 31.47% coverage. QTL analysis of maize plant height using these SSSLs demonstrated that these SSSLs have great genetic variations and are excellent tools for genetically dissecting complex traits over several environments.

A large mapping population, consisting of 128 CSSLs, was derived from the crossing and backcrossing of two sequenced rice cultivars, using 9311, an elite indica cultivar, as the recipient and Nipponbare, a japonica cultivar, as the donor. Based on 254 PCR-based molecular markers, it was found that these CSSLs contain 142 substituted segments with an average of 1.11 substituted segments per CSSL. Based on 7.68 million high-quality SNPs, these CSSLs were found to contain 259 substituted segments with an average of 2.02 substituted segments per CSSL (Xu et al, 2010). Similarly, the 108 chromosome SSSLs obtained in our research were based on the genotype of 146 SSR markers. As the number of markers increased, some individual SSSLs might be found to contain background segments from the donor. The 'SSSL' that contained two or more substituted segments from the donor could form new SSSLs through further backcrossing with the recurrent parent in combination with MAS.

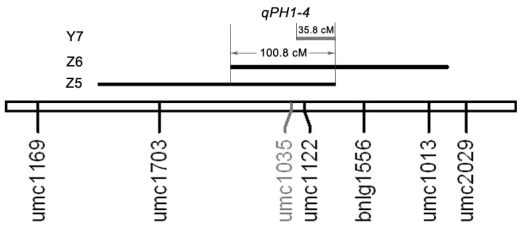

Figure 4 - Substitution mapping of plant height QTLs in the contig of chromosome 1.

Xi et al (2006) developed a mapping population consisting of 217 SSSLs using *Oryza sativa* L 'Hua-Jing-Xian74', an elite Indica cultivar as the recipient, and six other strains as the donors. The substituted segments from each individual donor covered 23.0% to 45.1% of the entire rice genome. Two maize mapping populations of link-up single-segment ingression lines were developed by Wang et al (2007) using three to four advanced backcross cycles with 87-1 and Zong3 as recurrent parents and Hengbai522 as the donor. The substituted segments that were introduced into the two different genetic backgrounds covered 48.9% and 79.2% of the maize genome respectively. In our study, the 46 unique substituted segments in the obtained SSSLs covered 31.47% of the maize genome, and some genomic regions were uncovered. These missing donor segments can be supplemented by lines that carry multiple segments or from the early backcrossing generations.

In the present study, the 44 SSSLs that were used for plant height QTL analysis exhibited two overlapping substituted segments in the Bin1.05-1.08 region. QTLs with positive effects on plant height were identified on the substituted segments Z5 and Z6. Therefore, QTL qPH1-4, which controls plant height on substituted segments Z5 and Z6, was mapped to the overlapping region of these two segments between the SSR markers umc1703 and bnlg1556, with a genetic distance of 100.8 cM (Figure 4). In addition, plant height QTL analyses with another set of SSSLs (i.e., inbred line 87-1, recipient; Zong3, donor) that was established by our group showed that a plant height QTL was detected on substituted segment Y7, with an additive effect percentage of -12.31%. The QTL was located between the SSR markers umc1035 and bnlg1556, with a genetic distance of 35.8 cM, and it has been fine mapped using a F_2 segregation population derived from the crossing of Y7 and recipient parent (data not published). Thus, the plant height QTL qPH1-4 mapped in this study may be located between SSR markers umc1035 and bnlg1556 (Figure 4).

A total of 314 plant height QTL in maize were found out by searching the MaizeGDB database (http://www.maizegdb.org/cgi-bin/qtl_loci_summary_table.cgi). In our study, seven plant height QTLs, qPH1-1, qPH1-4, qPH2-2, qPH2-4, qPH2-6, qPH4-2 and qPH6-1 were detected in all the environments and mapped in the Bin1.01, 1.07, 2.04, 2.07, 2.09, 4.08 and 6.02 regions respectively. The six QTL locations were similar to those from previous results. Using IL populations, Guo et al (2009) identified

plant height QTLs in the Bin1.01 region near the SSR marker bnlg1014, which explained 8.7% of the phenotypic variance. The Ph1-1, ph1b and ph1-2 plant height QTLs were mapped in the Bin1.07 region using different $F_{2:3}$ populations (Sibov et al, 2003; Yan et al, 2003a, b; Lan and Chu, 2005). Tang et al (2007a, b) identified a stable maize plant height QTL in the Bin1.07 region using immortalized F_2 and RIL populations. Using IL populations of HB522 in the genetic background of Zong3, Bai et al (2010) identified plant height QTLs near the SSR marker umc1245 in the Bin1.07 region, which explaineed 15.2% of the phenotypic variance. The plant height QTL Ph2 was detected between the SSR markers umc1845 and bnlg0166 in the Bin2.04 region, using $F_{2:3}$ populations (Sibov et al, 2003). Tang et al (2007b) identified the plant height QTL qPH2 between the SSR markers umc2372 and umc1497, in the Bin2.07 region, using RIL populations; these QTLs explained 9.11% of the phenotypic variance. Guo et al (2009) detected plant height QTLs near the SSR markers umc1256 and umc1551, in the Bin2.09 region, using IL populations. Zhang et al (2007) and Guo et al (2009) found plant height QTLs in the Bin4.08 region using $F_{2:4}$ and IL populations. In the Bin6.02 region, the plant height QTL qPH6-1 found in this study may be a newly identified QTL. Of all the plant height QTLs that were detected in this study, qPH6-1 displayed the greatest negative effect.

The additive effect percentage of qPH1-1 and qPH2-2 for plant height were positive in Sanya but negative in Zhengzhou and Puyan (Table 2). This difference in the additive effect percentage between short-day (Sanya) and long-day (Zhengzhou and Puyang) environments indicate that qPH1-1 and qPH2-2 might be involved in photoperiod sensitivity. Several QTLs have been determined for photoperiod sensitivity, including PLHT1.47f, PLHT2.70f and qPH2 (Briggs et al, 2007; Wang et al, 2008a). Based on their chromosomal positions, it has been suggested that qPH1-1 and qPH2-2 are the same loci as the QTLs, PLHT1.47f, PLHT2.70f and qPH2, respectively (Coles et al, 2010).

As typical representatives of Chinese maize inbred lines, the completely sequenced genomes of Zheng58 and Chang7-2, with their large numbers of SNP and indel polymorphism markers and conserved sequences(Lai et al, 2010), can provide a good foundation for further fine-mapping of functional and major QTLs identified in these SSSLs.

Acknowledgements

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