GMR Genetics and Molecular Research
Online Journal
ISSN:1676-5680

High segregation distortion in maize B73 x teosinte crosses

G. Wang, Q.Q. He, Z.K. Xu and R.T. Song

Shanghai Key Laboratory of Bio-Energy Crop, School of Life Sciences, Shanghai University, Shanghai, P.R. China

Corresponding author: R.T. Song
E-mail: rentaosong@staff.shu.edu.cn

Genet. Mol. Res. 11 (1): 693-706 (2012)
Received August 16, 2011
Accepted January 19, 2012
Published March 19, 2012
DOI http://dx.doi.org/10.4238/2012.March.19.3

ABSTRACT. Two genetic linkage maps of cultivated maize inbred lines and teosinte species were constructed. One population comprised 81 F_2 individuals derived from a cross between maize inbred line B73 and *Zea mays* ssp *parviglumis*, while the second consisted of 63 backcross individuals from a cross of maize inbred line B73 with *Z. mays* ssp *diploperennis*. In the B73 x *Z. mays* ssp *parviglumis* F_2 population, 172 simple sequence repeat (SSR) markers were mapped to 10 chromosomes, which covered 2210.8 cM. In the B73 x *Z. mays* ssp *diploperennis* backcross population, 258 SSR markers were mapped to 10 chromosomes, covering 1357.7 cM. Comparison of the two maps revealed that the total map length of *Z. mays* ssp *diploperennis* covers 1357.7 cM, which is about 61.4% of that of *Z. mays* ssp *parviglumis* (2210.8 cM). Extensive segregation distortion regions were found on chromosomes 1, 2, 3, 5, 6, 7, and 10 in the B73 x *Z. mays* ssp *parviglumis* F_2 population and on chromosomes 1-5 and 8-10 in the B73 x *Z. mays* ssp *parviglumis* backcross population. Segregation distortion analysis confirmed that the segregation distortion ratio in the interspecific population B73 x *Z. mays* ssp *diploperennis* was higher than in B73 x *Z. mays* ssp *parviglumis*. We found that the recombination distances are highly variable in these genetic crosses between cultivated and wild species of maize.

Key words: Maize; Teosinte; Genetic linkage map; Shrinkage; Segregation distortion

INTRODUCTION

Maize (*Zea mays* L.) is an important food and forage crop planted worldwide. Recently, maize breeding for high yield, robust quality, and disease resistance has become stagnant owing to the narrow genetic background of the maize germplasm. Therefore, exploring varieties of the germplasm for excellent potential gene sources is becoming more and more imperative.

Teosinte, the closest wild relative of maize, has been considered and used as a germplasm resource for maize improvement to provide disease resistance and various favorable agronomic traits (Cohen and Galinat, 1984). Because maize and teosinte have the same number of diploid chromosomes (2N = 2X = 20; with the exception of *Zea perennis*, a tetraploid perennial teosinte), the fertile F_1 hybrids can be easily acquired by crossing maize and teosinte. The gene flow moves from teosinte to maize via introgressive hybridization. During the introgression, the chromosome fragment of teosinte introgresses into the maize chromosome through repeated backcrosses (BC). The objective of BC breeding is to increase the recipient genome content and decrease the donor genome content by repeated BC to the recipient line. Two problems come to light during this process: foreground and background selection. A series of theoretical and practical studies indicate that a molecular marker can resolve these problems. The linkage maps show the genetic linkage relationship among different molecular markers, and these markers can be used for genome-wide scanning. Combined with a physical map, molecular marker analysis can confirm that a chromosome fragment introgressed from donor to recipient. Genetic maps provide important information for detailed genetic analysis of qualitative and quantitative traits and have proven to be important tools for plant improvement (Doerge, 2002).

During linkage map construction, recombination frequency and segregation distortion are notable. Recombination frequency is a measure of genetic linkage and is used in the creation of a genetic linkage map. Recombination rates are different among different parent combinations. The map length of an interspecific hybrid has been recognized as being shorter than that of an intraspecific hybrid (Doebley and Stec, 1991, 1993). Variability in recombination rates in maize was first reported in 1918 by Bregger and later confirmed using molecular markers (Tulsieram et al., 1992). Segregation distortion was first reported in maize by Mangelsdorf and Jones (1926) based on a linkage between the gametophyte factor Ga1 and the Su allele for starchy endosperm. At present, segregation distortion has been reported in rice (Harushima et al., 1996; Xu et al., 1997; Matsushita et al., 2003), maize (Lu et al., 2002; Sibov et al., 2003; Yan et al., 2003), barley (Konishi et al., 1992), grain sorghum (Pereira et al., 1994), and tomato (Paterson et al., 1991), among other crops. Segregation distortion may be related to the genetic background of the biparents. The segregation distortion ratio in interspecific populations is confirmed to be higher than that in intraspecific populations, that is, segregation distortion is prone to occur in interspecific populations. Further studies on segregation distortion in plants will enhance our understanding of deviant gene segregation during the introgression of target genes from wild species to cultivars.

In this study, we constructed two genetic linkage maps of maize x teosinte. One population comprised 81 F_2 individuals of maize inbred line B73 x *Z. mays* ssp *parviglumis*, and the other consisted of 63 BC individuals of B73 x *Z. mays* ssp *diploperennis*. The analysis of the genetic linkage maps provided potential clues about the recombination frequency and segregation distortion of different genetic background combinations of maize and teosinte.

MATERIAL AND METHODS

Material

Maize inbred line B73 was used as the maize parental line for genetic population construction. *Zea mays* ssp *parviglumis* (PI 384061, abbreviated as *parviglumis*) and *Z. mays* ssp *diploperennis* (PI 441931, abbreviated as *diploperennis*) were used as teosinte lines. B73 and *parviglumis* were used to develop an F_2 mapping population. The F_1 was generated from the cross between B73 and *diploperennis*, and F_1 plants were then used as female parents and B73 as the male parents in the genetic cross B73 x F_1, to generate the BC population. *Zea mays* ssp *parviglumis* and *diploperennis* were planted in the greenhouse of Shanghai University. B73, F_2, and BC populations were planted in the spring of 2008 in the experimental field on the Shanghai University campus. Eighty-two F_2 individuals and 63 BC individuals were randomly selected as the mapping population.

The genomic DNA of the parents (B73, *Z. mays* ssp *parviglumis*, and *Z. mays* ssp *diploperennis*) and 81 F_2 and 63 BC progeny were extracted for simple sequence repeat (SSR) analysis using the cetyltrimethylammonium bromide method (Murray and Thompson, 1980).

Analysis of SSR markers

On the principle of bin site uniform distribution, SSR primers were selected from the maize genetics and genomics database (http://www.maizegdb.org) published by the University of Missouri and were synthesized by the Shanghai Sango Biological Engineering Technology & Services Co., Ltd. The polymorphic primers between B73 and *parviglumis* were used to analyze the F_2 population, and the polymorphic primers between B73 and *diploperennis* were used to analyze the BC population.

A polymerase chain reaction (PCR) system with a total volume of 10 µL was made with the following: 20 ng template DNA, 10 pM each primer, 200 µM dinucleotide triphosphates, 1X buffer, 1.6 mM $MgCl_2$, and 0.5 U Taq DNA polymerase. The PCR process included 5 min at 94°C followed by 30 cycles of 35 s at 94°C, 40 s at 56°C, and 1 min at 72°C, and a final extension for 5 min at 72°C. The electrophoretic separation of the PCR products was carried out with 8% polyacrylamide gel and 1X Tris-borate-ethylenediaminetetraacetic acid electrophoretic buffer under the constant power of 80 W followed by ethidium bromide staining.

Genotypic statistics

Each locus of the F_2 progeny samples had three banding patterns. The patterns from B73 and *parviglumis* were labeled 1 and 2, respectively, a heterozygous pattern was marked with 3, and a deletion with 0. Each locus of the BC progeny samples had two banding patterns. The patterns from B73 were labeled 1, the heterozygous pattern was labeled 3, and a deletion was marked with 0.

Linkage analysis

A linkage analysis was made by using Mapmaker/EXP 3.0b (Lander et al., 1987) and

setting threshold of log of odds (LOD) ≥4.0, the recombinant rates were converted into map distances (cM) with the Kosambi function, and a linkage map was constructed using the mapping commands (Lander et al., 1987).

SSR marker segregation analysis

Segregation of each marker in the two populations was tested for goodness of fit to the expected 1:2:1 (B73 x *Z. mays* ssp *parviglumis* F_2 population) and 1:1 (B73 x *Z. mays* ssp *diploperennis* BC population) Mendelian segregation ratios using the χ^2 analysis.

RESULTS AND DISCUSSION

Polymorphism analysis

A total of 713 SSR makers were screened between B73 and *parviglumis*, resulting in 220 (30.9%) polymorphic markers. The polymorphic markers were then applied to the F_2 population analysis. A total of 320 polymorphic markers were identified from 873 tested SSR markers between B73 and *diploperennis*, and the polymorphic ratio was 36.6%. These markers were used to analyze the BC population.

In this study, B73 and *parviglumis* are different subspecies of the *Z. mays* species; however, B73 and *diploperennis* are different species of the genus *Zea.* The SSR analysis showed that the polymorphic ratio between B73 and *diploperennis* was higher than that between B73 and *parviglumis*. The result implied that the sequence divergence between B73 and *parviglumis* was less than that of B73 and *diploperennis.* Accordingly, *parviglumis* is considered to be more closely related to maize than are other types of teosinte (Doebley et al., 1984) based on the relative genetic distances calculated from allozyme frequencies.

Map construction

According to the segregation data of the 220 polymorphic SSR markers, a genetic linkage map of B73 x *parviglumis* was constructed, which included 11 linkage groups (10 chromosomes) and 172 SSR markers and spanned 2210.8 cM (Figure 1). The longest linkage group was 327.3 cM; the shortest was 76.1 cM. The average genetic distance between two neighboring loci was 12.8 cM, and the distribution of markers on the chromosomes was relatively even, without crowding in any region.

The 320 polymorphic markers were used for analyzing the BC population (B73 x *diploperennis*). In the segregation analysis among the individual plants, 258 markers were mapped into 10 linkage groups, which spanned 1357.7 cM with an average genetic distance between neighboring markers of 5.3 cM (Figure 2). The longest distance was 198.1 cM; the shortest was 76.1 cM. Notably, the genetic distance between adjacent markers was 0 cM in some regions.

Molecular linkage maps have been constructed for some maize x teosinte crosses, including *Z. mays* ssp x *parviglumis* (Doebley and Stec, 1993; Lauter and Doebley, 2002; Briggs et al., 2007), *Z. mays* ssp x *mexicana* (Doebley and Stec, 1991), *Z. mays* ssp x *huehuetenangensis* (Mano et al., 2005a,b), *Z. luxurians* (Omori and Mano, 2007; Mano et al., 2008)

and *Z. mays* ssp x *nicaraguensis* (Mano et al., 2007; Mano et al., 2009), and a *diploperennis* x *parviglumis* cross (Westerbergh and Doebley, 2002). These linkage maps were constructed with various molecular markers (such as restriction fragment length polymorphism, amplified fragment length polymorphism, SSR, single-nucleotide polymorphism, and indels) based on the genetic population (F_2 or BC mainly). Previously, two maps were constructed based on the population of *Z. mays* ssp x *parviglumis* (Doebley and Stec, 1993; Briggs et al., 2007), but no maps have been constructed based on the population of *Z. mays* ssp x *diploperennis*. The population size, number of markers, and average distance of adjacent markers of B73 x *parviglumis* are inferior to those of the W22 x *parviglumis* map constructed by Briggs et al. (2007); however, as a base map, the B73 x *parviglumis* map could resolve the genetic linkage relationship among markers. These markers can be used for genome-wide scanning during introgressive hybridization.

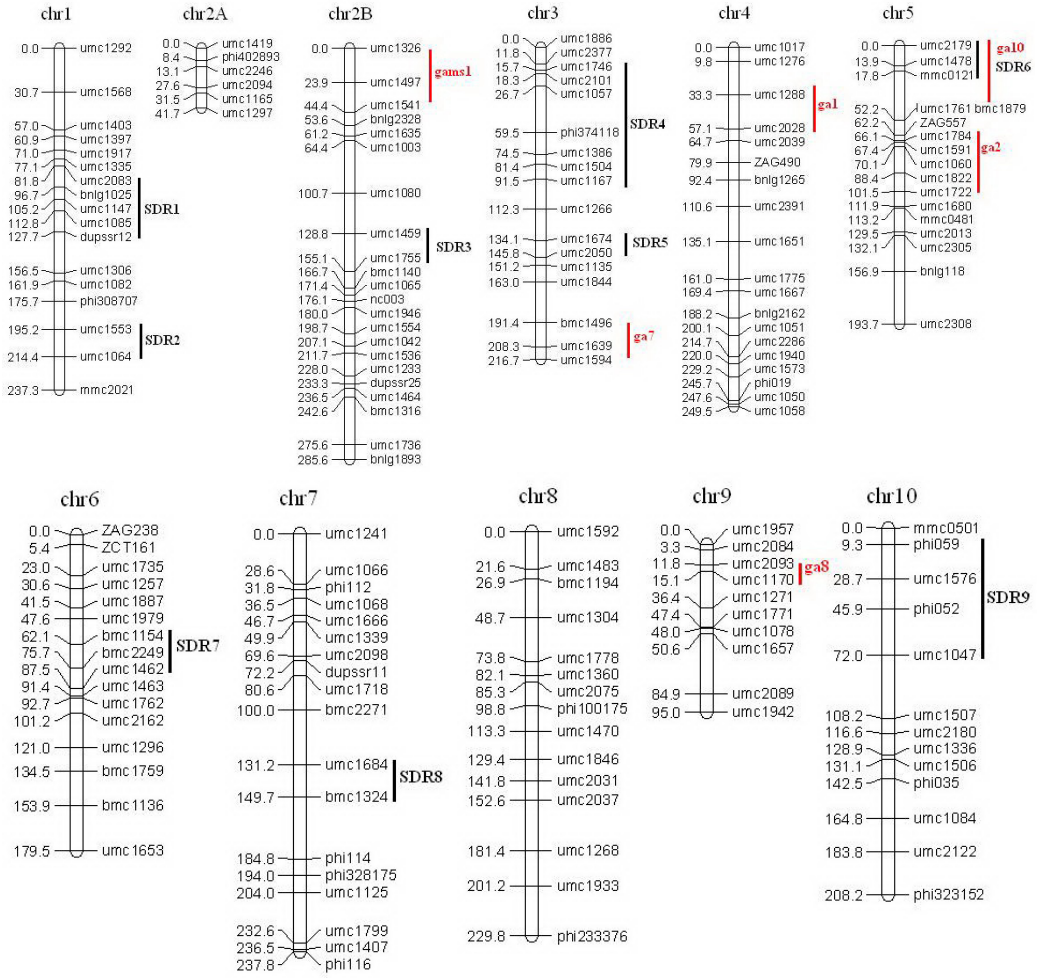

Figure 1. Genetic linkage map of B73 x *Zea mays* ssp *parviglumis* with SSR markers and the SDR distribution. SDR = Segregation distortion region; ga and gams = gametophytic factors.

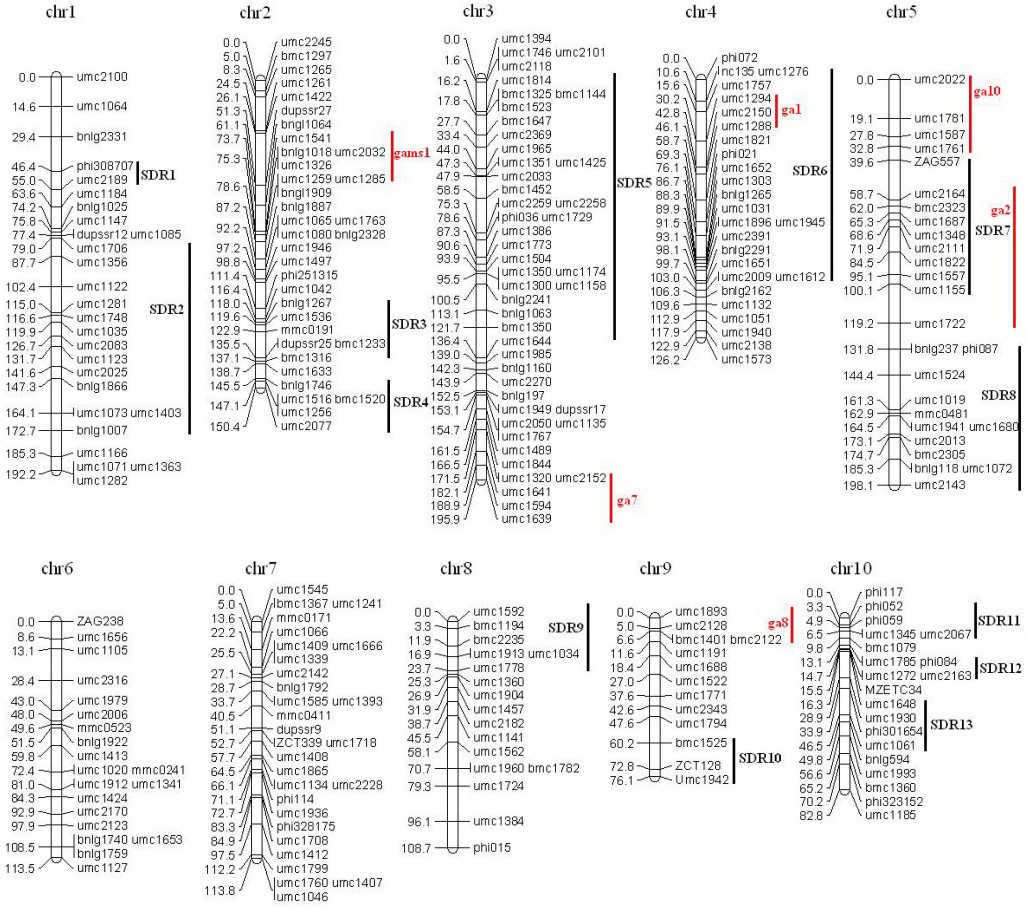

Figure 2. Genetic linkage map of B73 x *Zea mays* ssp *diploperennis* with SSR markers and the SDR distribution. SDR = Segregation distortion region; ga and gams = gametophytic factors.

Recombination frequency variability and recombination shrinkage

Comparing the genetic length of each chromosome of our two linkage maps, we found that the genetic lengths of the chromosomes of B73 x *parviglumis* were longer than those of B73 x *diploperennis* (except that of chromosome 5; Table 1). The length of chromosome 10 of the B73 x *diploperennis* linkage map was only 39.7% the length of chromosome 10 of B73 x *parviglumis*. The total map length of B73 x *diploperennis* covered 1357.7 cM, approximately 61.4% that of B73 x *parviglumis* (2210.8 cM). The data suggested that the recombination distances were variable among different genetic background combinations. The genetic distances of all adjacent common markers of the B73 x *diploperennis* map were shorter than those of the B73 x *parviglumis* map. Compared with those of B73 x *parviglumis*, the genetic distances of bnlg1025-umc1147, umc1147-umc1085, umc1085-dupssr12, umc2025-umc1135, umc2305-bnlg118, and umc1778-umc1360 of B73 x *diploperennis* were shrunken dramatically (Table

2). When we compared the B73 x *diploperennis* map with the SSR map of intermated B73 x Mo17 (IBM) population (www.maizegdb.org), we found that the recombination shrinkage in the B73 x *diploperennis* map was ubiquitous. For example, the genetic distances of all adjacent common markers, such as umc1386-umc1773, umc2050-umc1135, umc1135-umc1767, umc1767-umc1489, and umc2152-umc1641 on chromosome 3 were shrunken (Table 3). The phenomenon of recombination shrinkage was obvious in the B73 x *diploperennis* linkage map.

Table 1. Comparison of linkage map length between B73 x *Zea mays* ssp *parviglumis* and B73 x *Z. mays* ssp *diploperennis*.

		Chr. 1	Chr. 2	Chr. 3	Chr. 4	Chr. 5	Chr. 6	Chr. 7	Chr. 8	Chr. 9	Chr. 10	Total
Total map length	B73 x *Z. mays* ssp *parviglumis*	237.3	327.3	216.7	249.5	193.7	179.5	237.8	229.8	95.0	208.2	2210.8
	B73 x *Z. mays* ssp *diploperennis*	192.2	150.4	195.9	126.2	198.1	113.5	113.8	108.7	76.1	82.8	1357.7
Average distance	B73 x *Z. mays* ssp *parviglumis*	13.8	11.7	12.7	12.5	11.3	10.9	13.8	15.3	9.8	16.8	12.8
	B73 x *Z. mays* ssp *diploperennis*	7.1	4.3	4.4	4.8	7.6	5.7	3.9	6.4	5.9	4.1	5.3

Table 2. Genetic distances of adjacent common markers of B73 x *Zea mays* ssp *parviglumis* and B73 x *Z. mays* ssp *diploperennis* map.

Marker	Genetic distance (cM)		Chromosome
	B73 x *Z. mays* ssp *parviglumis*	B73 x *Z. mays* ssp *diploperennis*	
bnlg1025-umc1147	8.5	1.6	chr. 1
umc1147-umc1085	7.6	1.6	chr. 1
umc1085-dupssr12	14.9	0.0	chr. 1
umc1746-umc2101	2.6	0.0	chr. 3
umc1386-umc1506	6.9	6.6	chr. 3
umc2025-umc1135	5.4	0.0	chr. 3
umc1135-umc1844	11.8	11.8	chr. 3
umc1639-umc1594	8.4	7.0	chr. 3
umc1761-ZAG557	10.0	6.8	chr. 5
mmc0481-umc2305	1.3	1.6	chr. 5
umc2305-bnlg118	24.8	10.6	chr. 5
umc1666-umc1339	3.2	0.0	chr. 7
umc1799-umc1407	3.9	1.6	chr. 7
umc1778-umc1360	8.3	1.6	chr. 8

Table 3. Genetic distances of adjacent common markers on chromosome 3 of B73 x *Zea mays* ssp *diploperennis* and SSR map of intermated B73 x Mo17 (IBM) population.

	umc1386-umc1773	umc2050-umc1135	umc1135-umc1767	umc1767-umc1489	umc2152-umc1641
B73 x *Z. mays* ssp *diploperennis*	3.3 cM	0.0 cM	0.0 cM	6.8 cM	6.8 cM
SSR IBM map	6.8 cM	1.5 cM	1.4 cM	17.6 cM	15.2 cM

Previous research has found that the recombination levels in maize-teosinte hybrids are equivalent to those in maize-maize hybrids, indicating that the maize and teosinte genomes are similar (Emerson and Beadle, 1932). Contrastingly, Coe et al. (1990) have confirmed that the recombination between adjacent molecular markers in a maize-teosinte F_2 population often appears smaller than that between the same markers in a maize-maize F_2 population. A reduction of map length has been previously recognized in interspecific or wide cross-hybridizations of plants, including maize-teosinte crosses (Doebley and Stec, 1991, 1993; Williams et al., 1995). Recombination frequencies were different among different parental combinations.

It has been recognized that the map length of an interspecific hybrid is shorter than that of an intraspecific hybrid. In *Z. mays* maps, recombination decreases progressively in the following order: maize x maize > maize x *Z. mays* ssp *parviglumis* > maize x *Z. mays* ssp *mexicana* in the F_2 generation (Doebley and Stec, 1991, 1993). Comparison of the two map lengths convinced us that the map length of an interspecific hybrid (B73 x *diploperennis*) is shorter than that of an intraspecific hybrid (B73 x *parviglumis*).

The maize mapping studies suggest that the recombination rate heterogeneity among genetic backgrounds is under polygenic control. A study by Tulsieram et al. (1992) suggested that cis-factors potentially influence recombination rates. The first explanation for recombination shrinkage was based on the assumption that base-sequence homology determines where crossing-over will occur (Borts and Haber, 1987). Based on the theory of homologous recombination, we can deduce that genetic crossovers are more likely to occur between sequence-identical homologues in homozygous regions than between sequence-divergent strands in heterozygous regions (Williams et al., 1995). The analysis of the *a1* gene suggests that sequence divergence can convert both a transcribed gene hot spot and an untranscribed gene hot spot into average spots or cold spots (Yao and Schnable, 2005). Compared with that of the B73 x *parviglumis* linkage map, the map length of B73 x *diploperennis* is obviously shrunken. The greater sequence divergence uncovered through SSR analysis may be one reason for the recombination shrinkage in the B73 x *diploperennis* linkage map.

Earlier studies have proven that recombination shrinkage increases the quantity of DNA and number of genes transmitted as a unit, reducing the precision at which individual genes (or traits) can be selected for. Reduced recombination in such regions may contribute greatly to maintaining trait associations by "linkage drag" or "genetic hitchhiking" (Birky Jr. and Walsh, 1988). Linkage drag will be a barrier to using exotic maize germplasm in maize breeding programs. From this perspective, *parviglumis* is better than *diploperennis* as a donor in BC breeding of maize.

Segregation distortion

Forty-eight (21.8%) of 220 SSR markers in the B73 x *parviglumis* map indicated distorted segregation (Table 4). Nine segregation distortion regions (SDRs) were identified, distributed on all seven chromosomes except chromosomes 4, 8, and 9 (Figure 2). In B73 x *diploperennis*, 144 (45.0%) polymorphic SSR markers showed aberrant segregation ratios (Table 5). A total of 116 (80.6%) markers were located in putative SDRs. Thirteen SDRs were identified, distributed on eight chromosomes of maize except chromosome 6 and 7. The SDRs were unevenly distributed over 10 chromosomes. Chromosomes 3, 4, 8, and 9 had one SDR. Chromosomes 1, 2, and 5 had two SDRs, and chromosome 10 had three SDRs. In a comparison of the two maps, SDR2, SDR3, SDR4, SDR5, and SDR9 of B73 x *parviglumis* overlapped with SDR1, SDR3, SDR5, SDR11, and SDR12 of B73 x *diploperennis*.

Segregation distortion has frequently been found during the construction of genetic linkage maps. Segregation distortion for molecular markers in populations derived from wide crosses involving crop plants and their wild relatives is a common phenomenon (Doebley and Stec, 1991; Harushima et al., 1996). In tomato, Paterson et al. (1991) reported that 48 of 70 (68%) markers at 21 distinct regions had distorted ratios in a cross with a related wild species. In rice, Xu et al. (1997) found chromosomal regions associated with marker-segregation distortion in six segregating populations. Bonierbale et al. (1988) has reported segregation distortion

for eight regions in a cross between potato and a related species. In maize, Wendel et al. (1987) have observed that 11 of 17 (65%) segregating allozyme loci showed significant segregation distortion in an F_2 population. Gardiner et al. (1993) detected chromosomal regions associated with segregation distortion on chromosomes 1, 2, 3, and 5. In 2002, Lu et al. detected a total of 18 regions associated with segregation distortion on all of 10 maize chromosomes. In this study, 8 and 13 SDRs were detected in the B73 x *parviglumis* and B73 x *diploperennis* linkage maps, respectively. The B73 x *diploperennis* linkage map displayed more SDRs and SDR markers than the B73 x *parviglumis* map did. Population type (BC) and size (63 individuals) of the B73 x *diploperennis* map explain the higher segregation distortion. In addition, the result shows indirectly that segregation distortion is prone to happen in interspecific populations.

Table 4. Chi-square test for segregation distortion of markers in B73 x *Zea mays* ssp *parviglumis* F_2 population.

Marker	Chromosome bin	Genotype				P value	Chromosome location (Y/N)
		B73	*parviglumis*	Heterozygote	Deletion		
Umc2083	1.05-1.06	15	14	52	0	0.0377	Y
Umc1988	1.06	15	14	52	0	0.0337	N
Bnlg1025	1.07	13	13	55	0	0.0056	Y
Dupssr12	1.08	10	13	58	0	**	Y
Umc1085	1.08	10	25	46	0	0.0295	Y
Umc2047	1.09	68	0	13	0	**	N
Umc1064	1.11	29	13	39	0	0.0401	Y
Umc1553	1.11	30	16	35	0	0.0421	Y
Umc1459	2.05	12	13	55	1	0.0038	Y
Umc1755	2.06	34	17	30	0	0.0019	Y
Umc2129	2.07	38	0	43	0	**	N
Umc1633	2.08	66	0	11	4	**	N
umc1746	3.00	22	0	59	0	**	N
Umc2101	3.00	28	12	41	0	0.0421	Y
Umc1746	3.00	29	13	39	0	0.0401	Y
Umc1886	3.01	21	9	51	0	0.0111	Y
Umc1057	3.02	29	10	42	0	0.0110	Y
phi374118	3.02	29	0	52	0	**	Y
Umc1386	3.04	24	0	56	1	**	Y
Umc1504	3.04	24	6	51	0	0.0021	Y
Umc1167	3.05	26	10	45	0	0.0257	Y
Umc1674	3.06	31	16	34	0	0.0219	Y
Umc2050	3.07	26	11	44	0	0.0459	Y
Umc2152	3.09	28	9	39	5	0.0097	N
Umc1329	4.06	34	18	29	0	0.0016	N
Umc2139	4.09	67	0	14	0	**	N
Umc2179	5.01	13	16	52	0	0.0342	Y
Mmc0121	5.01-5.02	15	7	59	0	**	Y
Umc1462	6.05	21	11	49	0	0.0489	Y
Bmc1154	6.05	26	11	44	0	0.0459	Y
Umc2170	6.06	64	0	16	1	**	N
Umc1545	7.00	71	0	10	0	**	N
Umc1068	7.02	15	13	53	0	0.0201	Y
Umc1684	7.03	32	7	42	0	**	Y
Umc1324	7.03	44	0	37	0	**	Y
phi420701	8.00	39	0	42	0	**	N
phi100175	8.03	21	11	49	0	0.0489	Y
Umc1268	8.07	30	27	24	0	0.0011	Y
phi233376	8.09	19	10	52	0	0.014	Y
Umc1596	9.01	67	0	14	0	**	N
phi052	10.02	27	0	54	0	**	Y
Umc1576	10.02	27	9	45	0	0.0111	Y
phi059	10.02	15	8	56	2	**	Y
Umc1047	10.03	35	0	46	0	**	Y
phi323152	10.05	23	8	50	0	0.0067	Y
phi035	10.06	18	0	63	0	**	Y

**$P < 0.001$.

Table 5. Chi-square test for segregation distortion of markers in B73 x *Zea mays* ssp *diploperennis* BC population.

Marker	Chromosome bin	Genotype			P value	Chromosome location (Y/N)
		B73	Heterozygote	Deletion		
Phi308707	1.10	41	22	0	0.016	Y
Umc2189	1.10	40	23	0	0.003	Y
Umc1147	1.07	40	23	0	0.032	Y
Umc1706	1.07	40	22	1	0.023	Y
Umc1356	1.07	40	21	2	0.016	Y
Umc1122	1.07/1.06	45	17	1	**	Y
Umc1281	1.06	42	21	0	0.008	Y
Umc1748	1.06	43	20	0	0.003	Y
Umc1035	1.06	41	22	0	0.016	Y
Umc1123	1.06	42	21	0	0.008	Y
Umc2083	1.05-1.06	43	20	0	0.003	Y
Umc2025	1.05	43	19	1	0.002	Y
Bnlg1866	1.03	45	18	0	**	Y
Umc1073	1.03	42	21	0	0.008	Y
Umc1403	1.03	42	21	0	0.008	Y
Bnlg1007	1.02	43	20	0	0.003	Y
Umc1071	1.01	40	23	0	0.032	Y
Umc1363	1.01	40	23	0	0.032	Y
Umc1282	1.01	40	23	0	0.032	Y
Bnlg1887	2.06	23	40	0	0.032	Y
Bnlg1267	2.07/2.08	20	41	2	0.007	Y
Umc1536	2.07/2.08	19	44	0	0.001	Y
mmc0191	2.07/2.08	19	43	2	0.002	Y
dupssr25	2.08	12	51	0	**	Y
Bmc1233	2.08	12	51	0	**	Y
Bmc1316	2.08	11	52	0	**	Y
Bnlg1746	2.08	6	56	1	**	Y
Umc1516	2.08	5	58	0	**	Y
Bmc1520	2.09	5	58	0	**	Y
Umc1256	2.09	5	58	0	**	Y
Umc2077	2.09	5	58	0	**	Y
Umc1394	3.01	40	23	0	0.032	Y
Umc1814	3.02	43	20	0	0.003	Y
Bmc1144	3.02	44	19	0	0.001	Y
Bmc1325	3.02/3.03	44	19	0	0.001	Y
Bmc1523	3.02/3.03	44	19	0	0.001	Y
Bmc1647	3.02	44	15	1	**	Y
Umc2369	3.03	44	16	3	**	Y
Umc1965	3.04	41	22	0	0.016	Y
Umc1351	3.04	42	20	1	0.005	Y
Umc1425	3.04	42	20	1	0.005	Y
Umc2033	3.04	44	19	0	0.001	Y
Bmc1452	3.04	40	23	0	0.032	Y
Umc2259	3.03	45	18	0	**	Y
Umc2258	3.03	45	18	0	**	Y
phi036	3.04	43	20	0	0.003	Y
Umc1729	3.04	43	20	0	0.003	Y
Umc1386	3.04	43	15	5	**	Y
Umc1773	3.04	44	19	0	0.001	Y
Umc1504	3.04	44	19	0	0.001	Y
Umc1350	6.07	45	18	0	**	Y
Umc1174	3.05	45	18	0	**	Y
Umc1300	3.05	45	18	0	**	Y
Umc1158	3.05	45	18	0	**	Y
Bnlg2241	3.06	44	19	0	0.001	Y
Bnlg1063	3.06	41	22	0	0.016	Y
Bmc1350	3.08/8.07	42	21	0	0.008	Y
Umc1644	3.06	39	23	1	0.043	Y
nc135	4.01	44	19	0	0.001	Y
Umc1276	4.01	44	19	0	0.001	Y
Umc1757	4.01	45	18	0	**	Y

Continued on next page

Table 5. Continued.

Marker	Chromosome bin	Genotype			P value	Chromosome location (Y/N)
		B73	Heterozygote	Deletion		
Umc1294	4.02	49	14	0	**	Y
Umc2150	4.02	46	17	0	**	Y
Umc1288	4.02	44	19	0	0.001	Y
Umc1821	4.03/4.04	40	22	1	0.023	Y
phi021	4.03	43	18	2	0.001	Y
Umc1652	4.04	43	20	0	0.003	Y
Umc1303	4.05	45	18	0	**	Y
Bnlg1265	4.05	44	19	0	0.001	Y
Umc1031	4.05	45	16	2	**	Y
Umc1896	4.05	46	17	0	**	Y
Umc1945	4.06	46	17	0	**	Y
Umc2391	4.06	45	18	0	**	Y
Bnlg2291	4.06	42	20	1	0.005	Y
Umc1651	4.07	43	18	2	0.001	Y
Umc2009	4.08	41	22	0	0.016	Y
zag557	5.03	41	22	0	0.016	Y
Umc2164	5.05	43	19	1	0.002	Y
Bmc2323	5.04	43	20	0	0.003	Y
Umc1687	5.05	43	20	0	0.003	Y
Umc1348	5.05	40	22	1	0.023	Y
Umc2111	5.05	41	20	2	0.007	Y
Umc1822	5.05	42	21	0	0.008	Y
Umc1557a	5.03	40	23	0	0.032	Y
Umc1155	5.05	43	19	1	0.002	Y
Bnlg1237	5.05/5.06	42	21	0	0.008	Y
phi087	5.06	42	21	0	0.008	Y
Umc1524	5.06	48	15	0	**	Y
Umc1019	5.06	40	23	0	0.032	Y
mmc0481	5.06	41	22	0	0.016	Y
Umc1941	5.06	42	21	0	0.008	Y
Umc1680	5.06	42	21	0	0.008	Y
Umc2013	5.07	45	18	0	**	Y
Bmc2305	5.07	46	17	0	**	Y
Bnlg118	5.07	27	35	1	0.001	Y
Umc1072	5.07	44	19	0	0.001	Y
Umc2143	5.08	43	19	1	0.002	Y
Umc1592	8.01	42	21	0	0.008	Y
Bmc1194	8.01/8.02	42	21	0	0.008	Y
Bmc2235	8.02	41	22	0	0.016	Y
Umc1913	8.02	40	23	0	0.032	Y
Umc1034	8.02/8.03	40	23	0	0.032	Y
Umc1778	8.03	40	23	0	0.032	Y
Umc1904	8.03	40	23	0	0.032	Y
Umc1562	8.05	40	23	0	0.032	Y
Umc1724	8.06	42	21	0	0.008	Y
Bmc1525	9.07	39	23	1	0.043	Y
zct128	9.07	40	23	0	0.032	Y
Umc1942	9.07	40	23	0	0.032	Y
phi052	10.02	39	23	1	0.043	Y
phi059	10.02	40	23	0	0.032	Y
Umc1345	10.03	41	22	0	0.016	Y
Umc2067	10.03	41	22	0	0.016	Y
Umc1785	10.03	39	22	2	0.031	Y
phi084	10.04	41	22	0	0.016	Y
Umc1272	10.04	42	21	0	0.008	Y
Umc2163	10.04	42	21	0	0.008	Y
Umc1648	10.04	43	20	0	0.003	Y
Umc1930	10.04	42	21	0	0.008	Y
phi301654	10.04	43	20	0	0.003	Y
Umc1061	10.06	40	23	0	0.032	Y
umc1993	10.06	40	23	0	0.032	Y

**P < 0.001.

In many plant species, the most commonly reported genetic factors associated with distorted segregation ratio occur at the gamete and zygote level. In maize, the most commonly reported genetic factors associated with distorted segregation ratio are gametophytic factors (*ga*; Mangelsdorf and Jones, 1926; Burnham, 1936; Jain, 1967; Neuffer et al., 1997). In maize, four of 14 SDRs detected in the linkage map of an elite hybrid (Zong x 87-1) were located in regions in which gamete genes were reported (Yan et al., 2003); only three of 18 SDRs were detected close to the locations of five known *ga* factors (Lu et al., 2002). In the B73 x *parviglumis* linkage map, SDR3 was located near the *gams1* allele, SDR5 was located near the *ga7* allele, and SDR6 overlapped with the *ga10* allele (Table 6; see Figure 1). In the B73 x *diploperennis* linkage map, SDR3 was located near the *gams1* allele, SDR6 overlapped with the *ga1* allele, and SDR7 overlapped with the *ga2* allele near the *ga10* allele (see Table 6; see Figure 2). These SDRs could reasonably be attributed to the presence of *ga* factors in the linkage group. The locations of other SDRs detected in both linkage maps in our studies nearly overlap with previously identified SDRs (Lu et al., 2002; Yan et al., 2003; see Table 6). Nevertheless, these SDRs had no correlation with the *ga* factors and lack a clear explanation. The results suggest that there may be other genetic reasons for segregation distortion.

Table 6. Segregation distortion regions (SDRs) distribution.

Lu. et al. (2002)	Location (bin)	Yan et al. (2003)	Location (bin)	*parviglumis*	Location	*diploperennis*	Location	Gametophytic factors location
SDR1.1	1.02-1.04	SDR1-1	1.03-1.04	SDR1	1.05-1.07	SDR2	1.10	
SDR1.2	1.05-1.08	SDR1-2	1.06-1.08		1.07-1.08	SDR1	1.02-1.07	
SDR1.3	1.09-1.11			SDR2	1.11			
SDR2.1	2.01-2.02							
SDR2.2	2.03-2.05			SDR3	2.05-2.06			gams1 (Bin2.04)
SDR2.3	2.07-2.09	SDR2-1	2.06-2.08			SDR3	2.07-2.08	
						SDR4	2.08-2.09	
SDR3.1	3.04-3.05	SDR3-1	3.05-3.05	SDR4	3.00-3.05	SDR5	3.02-3.06	
SDR3.2	3.06-3.07	SDR3-2	3.05-3.05	SDR5	3.06-3.07			ga7 (Bin3.09)
SDR4.1	4.02-4.05	SDR4-1	4.05-4.06			SDR6	4.01-4.08	ga1 (Bin4.02)
SDR4.2	4.09-4.11	SDR4-2	4.05-4.06					
SDR5.1	5.05-5.07	SDR5-1	5.03-5.04	SDR6	5.01-5.02	SDR7	5.03-5.05	ga10 (Bin5.00-5.02)
						SDR8	5.06-5.08	ga2 (Bin5.04-5.05)
SDR6.1	6.05-6.07	SDR6-1	6.01					ga*-GFS1994 (chr6)
		SDR6-2	6.04-6.05	SDR7	6.05			
SDR7.1	7.01-7.03	SDR7-1	7.00-7.01	SDR8	7.03			
		SDR7-2	7.02					
SDR8.1	8.02-8.03					SDR9	8.01-8.03	
SDR8.2	8.05-8.08							
SDR9.1	9.01-9.04	SDR9-1	9.02			SDR10	9.07	ga8 (Bin9.02)
								ga*-94-764 (chr9)
SDR10.1	10.02-10.04	SDR10-1	10.01-10.02	SDR9	10.01-10.03	SDR11	10.02-10.03	
						SDR12	10.03-10.04	
SDR10.2	10.06-10.07					SDR13	10.04-10.06	
								gams2 (unknown)

ACKNOWLEDGMENTS

Research supported by the National Natural Science Foundation of China (#30700472 and #31171559) and the Ministry of Science and Technology of China (#2006AA10Z148, #2006AA10A107, and #2009CB118400).

REFERENCES

Birky CW Jr and Walsh JB (1988). Effects of linkage on rates of molecular evolution. *Proc. Natl. Acad. Sci. U. S. A.* 85: 6414-6418.

Bonierbale MW, Plaisted RL and Tanksley SD (1988). RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. *Genetics* 120: 1095-1103.

Borts RH and Haber JE (1987). Meiotic recombination in yeast: alteration by multiple heterozygosities. *Science* 237: 1459-1465.

Bregger J (1918). Linkage in maize: the C aleurone factor and waxy endosperm. *Am. Nat.* 52: 57-61.

Briggs WH, McMullen MD, Gaut BS and Doebley JD (2007). Advance QTL mapping in a RIL resource for positional cloning of maize domestication genes. *Genetics* 177: 1915-1928.

Burnham CR (1936). Differential fertilization in the *Bt-Pr* linkage group of maize. *J. Am. Soc. Agron.* 28: 968-975.

Coe EH, Hoisincton DA and Neuffer MG (1990). Linkage Map of Corn (*Zea mays* L.). In: Genetic Maps (O'Brienc SJ, ed.). Spring Harbor Laboratory, Cold Spring Harbor, 639-667.

Cohen JI and Galinat WC (1984). Potential use of alien germplasm for maize improvement. *Crop Sci.* 24: 1011-1015.

Doebley J and Stec A (1991). Genetic analysis of the morphological differences between maize and teosinte. *Genetics* 129: 285-295.

Doebley J and Stec A (1993). Inheritance of the morphological differences between maize and teosinte: comparison of results for two F_2 populations. *Genetics* 134: 559-570.

Doebley J, Goodman MM and Stuber CW (1984). Isoenzymatic variation in *Zea* (Gramineae). *Syst. Boatany* 9: 203-218.

Doerge RW (2002). Mapping and analysis of quantitative trait loci in experimental populations. *Nat. Rev. Genet.* 3: 43-52.

Emerson RA and Beadle GW (1932). Studies of *Euchlaena* and its hybrids with *Zea*: crossing over between the chromosomes of *Euchlana* and those of *Zea*. *Z. indukt Abstamm-u. VererbLehre* 62: 305-315.

Gardiner JM, Coe EH, Melia-Hancock S, Hoisington DA, et al. (1993). Development of a core RFLP map in maize using an immortalized F_2 population. *Genetics* 134: 917-930.

Harushima Y, Kurata N, Yano M, Nagamura Y, et al. (1996). Detection of segregation distortions in an *indica-japonica* rice cross using a high-resolution molecular map. *Theor. Appl. Genet.* 92: 145-150.

Jain SK (1967). Population dynamics of a gametophyte factor controlling selective fertilization. *Genetica* 38: 485-503.

Konishi T, Yano Y and Abe K (1992). Geographic distribution of alleles at the Ga2 locus for segregation distortion in barley. *Theor. Appl. Genet.* 85: 419-422.

Lander ES, Green P, Abrahamson J, Barlow A, et al. (1987). MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics* 1: 174-181.

Lauter N and Doebley JD (2002). Evidence for genetic variation for phenotypically invariant traits in teosinte. *Maize Genet. Newslett.* 76: 54-55.

Lu H, Romero-Severson J and Bernardo R (2002). Chromosomal regions associated with segregation distortion in maize. *Theor. Appl. Genet.* 105: 622-628.

Mangelsdorf PC and Jones DF (1926). The expression of Mendelian factors in the gametophyte of maize. *Genetics* 11: 423-455.

Mano Y, Muraki M, Fujimori M, Takamizo T, et al. (2005a). AFLP-SSR maps of maize x teosinte and maize X maize: comparison of map length and segregation distortion. *Plant Breed.* 124: 432-439.

Mano Y, Muraki M, Fujimori M, Takamizo T, et al. (2005b). Identification of QTL controlling adventitious root formation during flooding conditions in teosinte (*Zea mays* ssp. *huehuetenangensis*) seedlings. *Euphytica* 142: 33-42.

Mano Y, Omori F, Takamizo T, Kindiger B, et al. (2007). QTL mapping of root aerenchyma formation in seedlings of a maize x rare teosinte "*Zea nicaraguensis*" cross. *Plant Soil* 295: 103-113.

Mano Y, Omori F, Kindiger B and Takahashi H (2008). A linkage map of maize x teosinte *Zea luxurians* and identification of QTLs controlling root aerenchyma formation. *Mol. Breed.* 21: 327-337.

Mano Y, Omori F, Loaisiga CH and Bird R McK (2009). QTL mapping of above-ground adventitious roots during flooding in maize x teosinte "*Zea nicaraguensis*" backcross population. *Plant Root* 3: 3-9.

Matsushita S, Iseki T, Fukuta Y, Araki E, et al. (2003). Characterization of segregation distortion on chromosome 3 induced in wide hybridization between *indica* and *japonica* type rice varieties. *Euphytica* 134: 27-32.

Murray MG and Thompson WF (1980). Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Res.* 8: 4321-4325.

Neuffer MG, Coe EH and Wessler SR (1997). Mutants of Maize. Cold Spring Harbor Laboratory Press, Cold Spring Harbor.

Omori F and Mano Y (2007). QTL mapping of root angle in F_2 populations from maize 'B73' X teosinte '*Zea luxurians*'.

Plant Root 1: 57-65.
Paterson AH, Damon S, Hewitt JD, Zamir D, et al. (1991). Mendelian factors underlying quantitative traits in tomato: comparison across species, generations, and environments. *Genetics* 127: 181-197.
Pereira MG, Lee M, Bramel-Cox P, Woodman W, et al. (1994). Construction of an RFLP map in sorghum and comparative mapping in maize. *Genome* 37: 236-243.
Sibov ST, de Souza CLJ, Garcia AA, Garcia AF, et al. (2003). Molecular mapping in tropical maize (*Zea mays* L.) using microsatellite markers. 1. Map construction and localization of loci showing distorted segregation. *Hereditas* 139: 96-106.
Tulsieram L, Compton WA, Morris R, Thomas-Compton M, et al. (1992). Analysis of genetic recombination in maize populations using molecular markers. *Theor. Appl. Genet.* 84: 65-72.
Wendel JF, Edwards MD and Stuber CW (1987). Evidence for multilocus genetic control of preferential fertilisation in maize. *Heredity* 58: 297-301.
Westerbergh A and Doebley J (2002). Morphological traits defining species differences in wild relatives of maize are controlled by multiple quantitative trait loci. *Evolution* 56: 273-283.
Williams CG, Goodman MM and Stuber CW (1995). Comparative recombination distances among *Zea mays* L. inbreds, wide crosses and interspecific hybrids. *Genetics* 141: 1573-1581.
Xu Y, Zhu L, Xiao J, Huang N, et al. (1997). Chromosomal regions associated with segregation distortion of molecular markers in F_2, backcross, doubled haploid, and recombinant inbred populations in rice (*Oryza sativa* L.). *Mol. Gen. Genet.* 253: 535-545.
Yan JB, Tang H, Huang YQ, Zheng YL, et al. (2003). Genetic analysis of segregation distortion of molecular markers in maize F_2 population. *Yi Chuan Xue Bao* 30: 913-918.
Yao H and Schnable PS (2005). Cis-effects on meiotic recombination across distinct a1-sh2 intervals in a common *Zea* genetic background. *Genetics* 170: 1929-1944.

