Available online at www.sciencedirect.com

ScienceDirect

A SSR Linkage Map of Maize×Teosinte F$_2$ Population and Analysis of Segregation Distortion

ZHOU Jun-qing[1*], GUO Yu-qiu[1*], GAO Yu-feng[1], LI Jian-sheng[1] and YAN Jian-bing[1, 2]

[1] National Maize Improvement Center of China, China Agricultural University, Beijing 100193, P.R.China
[2] International Maize and Wheat Improvement Center (CIMMYT), Mexico D.F. 06600, Mexico

Abstract

In this study, a linkage genetic map was constructed using a F$_2$ population derived from a cross between a elite maize inbred, B73, and its progenitor, Teosinte (*Z. mays* ssp. *mexicana*), through 205 simple sequence repeat (SSR) markers and one morphological marker. By Mapmaker 3.0, polymorphic markers were clustered into 10 groups, covering 10 chromosomes of maize×teosinte, with a total length of 2 002.4 cM and an average interval of 9.7 cM. Genotyping errors were detected using R/QTL (LOD=2.0) in 109 markers referring to 176 individuals, distributed across all 10 chromosomes with a ratio 1.2%. Projected error loci were re-run and 304 out of the 460 were confirmed as errors and replaced. A new linkage map was constructed, in which markers maintained the same order but the total map length decreased to 1 947.8 cM, with an average interval of 9.4 cM between markers. In total, 25.2% (*P*<0.05) markers were identified to have segregation distortion, in which 34.6% deviated towards the pollination parent (B73), 30.8% deviated towards Teosinte, 32.7% deviated towards heterozygote and 1.9% deviated towards both parents. This map was also compared with published maize×teosinte and maize IBM map.

Key words: maize, molecular linkage map, segregation distortion, simple sequence repeat, teosinte

INTRODUCTION

Maize (*Zea mays* L. ssp. *mays*), one of the most important crops in the world, was introduced into China approximately 500 yr ago (Liu 2000). Because of the broad utilization of single hybrids during the past century, maize genetic basis was tend to more narrow. An estimated 5% or less of the available genetic variability in maize is currently used in commercial breeding programs throughout the world, with less than 1% used in the USA (Hoisington *et al*. 1999). The risks associated with a narrow genetic base in domesticated food crops have been well documented, for example,

potato late blight which led to the great Irish famine in 1845-1847 and southern corn leaf blight in 1970. Exotic germplasm containing many agricultural valuable genes is a resource for crop improvement and has been successfully exploited over the past decades (Tanksley *et al*. 1996; Doebley *et al*. 2006). Teosinte, the closest relative and probable ancestor of maize, has large genetic variation compared with maize and is considered as a potential resource for maize improvement and for the study of maize genetics and evolution (Reeves 1950; Iltis *et al*. 1980, 2000; Cohen and Galinat 1984; Harshberger 1986; Doebley and Stec 1991, 1993; Fukunaga *et al*. 2005; Briggs *et al*. 2007).

The construction of the molecular marker linkage

map is fundamental for map-based cloning of genes, comparative genomics, and marker-assisted selection. Simple sequence repeats (SSRs) is a PCR based marker and well used in lots of species (Lübberstedt *et al.* 1998). Mano *et al.* (2005a; 2007a, b) identified QTL controlling root aerenchyma formation in a maize×teosinte F_2 population. Teosinte was the donor of several QTLs associated with the increased capacity to form aerenchyma confirming the potential of teosinte genes to develop improved maize germplasm.

Segregation distortion was recognized as a potential evolutionary force (Sandler and Novitski 1957; Taylor and Ingvarsson 2003) obstructing gene flow between species and hampering introgression of interesting alleles in certain regions of the genome (Truco *et al.* 2007). A distorted allele without deleterious effects on fitness would rapidly spread to fixation; alternatively, the deleterious allele would be eliminated. This phenomenon is known as a deviation from the expected Mendelian frequencies of the observed genotype frequencies and has been reported in large-scale organisms, including plants and animals. Segregation distortion was identified with in nearly all population types, including F_2, backcross, doubled haploid, and recombinant inbred and also wide crosses, interspecific crosses, intraspecific crosses, sub-specific crosses, and interspecific backcrosses (Xu *et al.* 1997; Ky *et al.* 2000; Lu *et al.* 2002). Segregating distortion is higher in inter-specific crosses relative to intra-specific crosses (Jenczewski *et al.* 1997; Truco *et al.* 2007). In maize, Mangelsdorf and Jones (1926) first reported segregation distortion and subsequently reported by a series of research groups (Burham 1936; Wendel *et al.* 1987; Gardiner *et al.* 1993; Lu *et al.* 2002; Yan *et al.* 2003). Segregation distortion has also been reported in rice (McCouch *et al.* 1988), barley (Devaux *et al.* 1995), tomato (Paterson *et al.* 1988), and moss (Stuart *et al.* 2007).

To date, there has no systemic comparative study of a linkage map between maize and offspring of maize×teosinte in same generation and different populations. The objectives of this study were to construct a linkage map using a maize×teosinte F_2 population; examine the consistency of location of chromosomal regions across populations; and analyse segregation distortion and assess the effects of gameophtic factors (GA) on the construction of a linkage map.

MATERIALS AND METHODS

Plant materials

An elite maize inbred line, B73, was used as female parent and crossed with teosinte (*Z. mays* ssp. *mexicana*), X_{26-4}, one F_1 individual was selected and self-pollinated to produce F_2 seeds at winter nursery farm of Sanya, Hainan Province, China, in 2004. Six ears were harvested from the F_1 individual and 190 F_2 individuals and parents were grown at the Agronomy Farm of China Agricultural University, Bejing, China, in 2005.

Construction of linkage map

DNA was extracted from the parents and the F_2 individuals following the procedure described by Saghai-Maroof *et al.* (1984). A total of 550 SSR primers were selected from MaizeGDB (http://www.maizegdb.org/ssr.php) and screened for polymorphisms between the two parents. 226 polymorphic markers equally distributed across the genome were used to construct the linkage map. SSR analysis was carried out with the method described by Senior (1996). Grain color in the F_2 population was divided into two groups, yellow and white, and used as a morphological marker. A molecular linkage map was constructed using Mapmaker 3.0 (Lincoln *et al.* 1992).

Data analysis

Segregation analysis At each locus in this study, the observed segregation ratios were tested for deviation from the theoretical Mendelian ratio (1:2:1 or 3:1) with chi-square goodness-of-fit test at the 5% significant level ($P<0.05$). From the result of Chi-square test and bi-parent genotyping, the direction of distortion was determined.

R/qtl analysis Genotypic data for all the individuals were tested using the programs "cacl.genoprob" and "cacl.errorlod" integrated in the software R/qtl (Broman *et al.* 2003). The genotyping results were regarded as error if the LOD=2 (Lincoln *et al.* 1992). Those error loci and individuals were selected and re-run using the same marker. The original data were replaced by the

different new one and the linkage map was re-constructed. **Comparison of present map with published maps** Using the published IBM map as a bridge, the colinearity of four different maize×teosinte maps were compared in terms of the marker order, segregation distortion etc. (Mano *et al*. 2005b, 2007a, b) (Table 1). Published maize×teosinte linkage maps were constructed using 338 AFLP markers and 75 SSR markers for 94 F_2 individuals, 85 SSR markers for 141 F_2 individuals, and 107 SSR markers for 195 F_2 individuals.

Table 1 Number and frequency of molecular markers with segregation distortion in four maize/teosinte populations

Population name	Type	Parents	Progenies number	SSR marker	
				Total	Distorted (%)
P1	F_2	B64×Teosinte *Zea huehuetenangensis*	94	75	6 (8)
P2	F_2	B73×Teosinte *Zea luxurians*	195	107	6 (5.6)
P3	F_2	B64×Teosinte *Zea nicaraguensis*	141	85	8 (9.4)
P4	F_2	B73×Teosinte *Zea mexicana*	190	205	51 (24.9)
Total			620	472	71 (15.0)

RESULTS

Marker polymorphism

Of the 550 SSRs used to screen for polymorphisms between the two parents, 226 were identified as polymorphismic (Fig. 1) and subsequently used for screening each population. Of these markers, 205 SSRs were used in the construction of a linkage map. For 190 individuals, chromosomal percentage from maize (B73) varied from 10.6 to 96.9%, with an average of 26.7%; while chromosomal percentage from teosinte (X26-4) varied between 1.9 and 82.5%, with an average of 25.2%. Heterozygote percentage varied from 0 to 63.6% with an average of 48.2%. In the F_2 population, average allele frequencies were 74.8% from maize (B73) and 73.3% from teosinte (X26-4) and with overall genotype frequencies were 26.7% B73, 25.2% X26-4, and 48.2% heterozygous. Segregation ratios of allelic and genotypic frequencies fitted Mendelian expectations (1:1 or 1:2:1) throughout the F_2 population with the exception of 52 markers where ratios of genotypic classes deviated from the expectationed frequency in the F_2 at *P*=0.05 level (Table 2). Within these 52 markers, 18 (34.6%) were skewed towards B73, one (1.9%) skewed towards both parents, 16 (30.8%) skewed towards X26-4, and 17 (32.7%) skewed towards the F_1. These markers were identified on all 10 chromosomes, ranging from one segregated marker on chromosome 4 to 14 markers on chromosome 5.

Linkage map

A total of 205 SSRs markers and one morphological marker were mapped to 10 chromosomes. The total map length was 2 002.4 cM. The length of each linkage group, ranged from 145.2 cM on chromosome 4 to 345.1 cM on chromosome 1, with an average interval between loci of 9.7 cM. The position of SSR markers were generally consistent with those previously published in the maize IBM map (http://www.maizegdb.org/ssr.php) with the exception of a few markers (7.3%). These markers could be divided into two groups. In the first group, markers mapped to different chromosomes (4/206, 1.9%), for example, in this study *umc1782* and *umc1512* mapped to chromosomes 7 and 1, respectively, however, in the maize IBM map, they mapped to chromosomes 8 and 5, respectively. One
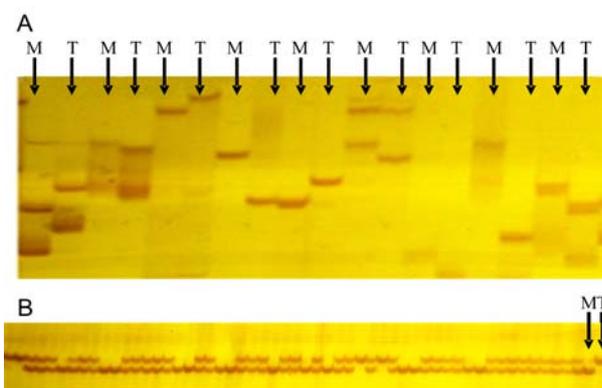

Fig. 1 A, sliver-stained polyacrylamide gel showing polymorphic PCR products from maize SSR primer between B73 and X26-4; B, sliver-stained polyacrylamide gel showing polymorphic PCR products from maize SSR primer for F_2 population from B73 and X26-4. T, teosinte; M, maize.

Table 2 SSR loci showing segregation distortion (*P*<0.05)

SSR locus	Chr.	Number of homozygotes		Number of heterozygotes	Chi-square value	Direction of skewness
		B73 allele	X26-4 allele			
umc2116**	1	134	28	19	237.1	B73
umc2149**	1	135	50	2	256.4	B73
umc2008**	3	66	39	82	10.6	B73
umc1072**	5	90	42	50	62.3	B73
umc1014**	6	73	36	77	20.2	B73
phi057*	7	61	37	92	6.3	B73
umc1433*	7	57	33	90	6.4	B73
umc0411*	7	57	31	96	7.7	B73
umc1040**	9	146	28	15	281.1	B73
bnlg1179**	1	143	43	0	293.5	B73
Yellow*	6	148	32	0	4.6	B73
bnlg1617**	6	147	33	0	324.4	B73
umc1034**	8	128	53	1	239.8	B73
umc1370**	9	157	3	2	446.9	B73
umc1733**	9	131	57	0	246.3	B73
phi050**	10	136	52	0	263.1	B73
bnlg1605**	3	132	46	0	261.1	B73
umc1518**	2	139	45	0	280.0	B73
umc2039**	4	57	58	66	13.3	B73 X26-4
umc1403*	1	36	39	111	7.1	Heterozygote
bnlg439*	1	31	47	111	8.5	Heterozygote
bnlg1866*	1	28	42	107	9.9	Heterozygote
umc1917*	1	35	40	115	8.7	Heterozygote
umc2227**	1	25	38	110	14.7	Heterozygote
umc2025*	1	42	35	110	6.3	Heterozygote
bnlg1638**	3	47	17	110	22.5	Heterozygote
umc1019**	5	20	54	105	18.3	Heterozygote
bnlg2305*	5	39	35	113	8.3	Heterozygote
umc1178*	6	39	36	109	6.4	Heterozygote
umc1887*	6	50	30	105	7.7	Heterozygote
umc2170*	6	50	32	107	6.7	Heterozygote
bnlg1136**	6	49	26	113	13.3	Heterozygote
umc2352*	8	33	47	108	6.3	Heterozygote
umc2147*	8	32	51	103	6.0	Heterozygote
umc1872*	8	32	51	105	6.4	Heterozygote
umc1360*	8	30	51	108	8.5	Heterozygote
umc1749*	2	49	59	71	8.8	X26-4
bnlg1879*	5	32	55	97	6.3	X26-4
umc1447**	5	29	70	86	19.1	X26-4
umc1591**	5	20	74	90	31.8	X26-4
umc1060**	5	28	68	92	17.1	X26-4
umc1563**	5	26	68	92	19.0	X26-4
umc1332**	5	20	72	87	30.4	X26-4
umc1512**	5	24	68	90	21.3	X26-4
umc1171**	5	23	73	90	27.1	X26-4
umc2026**	5	21	69	88	25.9	X26-4
umc2164**	5	23	69	97	22.5	X26-4
umc1155**	5	20	66	102	23.9	X26-4
umc1741**	8	36	83	67	38.3	X26-4
umc2042*	8	31	53	98	6.4	X26-4
umc2122*	10	35	59	82	7.4	X26-4
bnlg1067**	8	33	155	0	346.3	X26-4

*, significant difference at *P*<0.05; **, significant difference at *P*<0.01.

possible reason behind this difference could be multicopies of markers which map to different locations/chromosomes. In the second group, the physical position within a chromosome was different (11/206, 5.3%), for example, in this study, marker *Phi323152* was identified on chromosome 10 bin 5 whereas in IBM map, it was assigned to bin 7. This difference may be a result of recombination or inversion.

Segregation distortion

In all four populations (including three other published

maize×teosinte populations, detail in the Materials and Methods), 71 (15.0%) markers out of the 472 used SSR markers exhibited average segregation distortion. The frequency of distorted markers ranged from 5.6 to 24.9% across the four populations. Several distortion markers were identified in clusters and formed "segregation distortion hotspot" regions. In this study, 10 segregation distortion regions (SDRs) were identified on chromosomes 1, 5, 6, 7, 8, and 9, named SDR1-1, SDR1-2, SDR5-1, SDR6-1, SDR6-2, SDR7, SDR8-1, SDR8-2, SDR8-3, and SDR9-1, respectively. On chromosomes 1, 6, 7, and 9, three distortion markers were identified, respectively, skewed towards B73, which was the most among the chromosomes skewing towards B73. On chromosome 5, 11 distortion markers were identified skewer towards X26-4, which was the most among the chromosomes skewing towards X26-4. The largest SDR was located on chromosome 5 and including 11 markers. Additionally, SDR5 (located on chromosome 5), and the ga2 allele were located in the same region suggesting gametophytic factors existed in the region. SDR1-1, SDR6-2, and SDR8-3 deviated towards the heterozygote, while SDR1-2, SDR7-1, and SDR9-1 deviated towards B73. The other SDRs deviated towards B73 and heterozygote or teosinte and heterozygote. For example, marker *umc1887* in SDR6-1 skewed towards heterozygote while neighboring markers *umc1014* and *bnlg1617* skewed towards maize. Significant segregation distortion was observed within these three markers.

Genotypic error detection and re-genotyping

Using the error detection function in R/QTL software (Broman *et al*. 2003), 460 records (1.2%) were detected as genotypic errors (LOD=2), distributed across all 10 chromosomes and were associated with 109 loci

(including one morphological locus) and 176 individuals. Across all 10 chromosomes, the least genotyping errors were identified on chromosome 9 (4 markers and 18 loci), in contrast, the largest number of genotyping errors was identified on chromosome 1 (21 markers and 91 loci) (Table 3). An average of 4.2 genotyping errors (ranging from 1-25) was detected across individuals for each marker.

Re-analysis of potential genotyping error loci (with the exception of the 10 morphological markers) was performed using PCR and confirmed 304 loci were genotyped incorrectly, whilst 96 loci were correctly genotyped and 50 loci were failed to regenotype (Table 4). Genotypic data was re-adjusted accordingly and the linkage map re-constructed. All 206 markers maintained their position and order, however, the total length of the map decreased from 2 002.4 to 1 948.7 cM, with the average interval between loci shortened to 9.4 cM from 9.7 cM. With the exception of chromosome 4 which increased in length by 3.7 cM, the length of all chromosomes was reduced by 0.1 (chromosome 6) to 15.7 cM (chromosome 1).

DISCUSSION

Genotyping error detection can improve map precision

With the rapid development of molecular marker technology, many linkage maps of major crops are now used for fine mapping and map-based cloning. Linkage maps provide a powerful tool for theoretical and applied genetics research. Many potential sources of error exist in the construct of molecular maps, including during the process of DNA mixing and incorrect genotyping. In the production of tens of thousands of data points, such as in the construction of molecular

Table 3 Comparison of the length of each chromosome before and after R/qtl software detection

Item	Chromosome										T	A
	1	2	3	4	5	6	7	8	9	10		
Distance (cM) [1]	360.8	190.5	219.6	141.5	238.7	180.4	146.1	197.3	169.3	158.2	2 002	9.67
Distance (cM) [2]	345.1	187.8	211.6	145.2	227.5	180.3	144.9	193.3	165	147.1	1 948	9.41
Loci	91	20	48	60	64	39	27	43	18	50	460	46
Marker	21	8	13	12	11	8	9	14	4	9	109	10.90

[1] The length before detection of R/qtl software.
[2] The length after detection of R/qtl software.
T indicates total; A indicates average.

Table 4 Efficiency of R/qtl software detection

LOD	Truly wrong loci	Right loci	Missing loci	Efficiency (%)
2-2.5	128	22	34	85.30
2.5-3	35	21	1	62.50
3-3.5	41	20	12	67.21
3.5-4	17	8	6	68.00
4-5	53	15	4	77.94
5-6	7	2	2	77.78
>6	23	8	1	74.19
Total	304	96	60	76.00

maps, a small number of errors were inevitable, however, while the presence of errors will reduce the function of a map, this is rarely considered. Falque *et al.* (2005) reported a 1.86% error margin in data on IBM_Gnp2004 framework data set of 77 markers. Based on this error ratio through 1 000 simulations, the linkage map length of IBM_Gnp2004 framework increased 15.3%. In this study, approximately 1% of genotypic data were found to be incorrect. The identification of the errors and subsequent re-genotyping of markers allowed the refined of the linkage consecutive map.

Comparison of maize×teosinte and maize×maize maps

Through constructing the linkage map using SSR markers, we found that a large number of maize markers were transferable and suitable for mapping a maize×teosinte population. By comparing the position of SSR makers with those in IBM2, two patterns, the transfer of single markers and the transfer of groups of markers, were observed. For the transfer of single markers, markers were transferred on to the same chromosome, or, alternatively, onto different chromosomes. Groups of markers were also identified in these markers which had the same order within a chromosome, however, the interval between markers was either expanded, fixed and shrunk relative to their group in maize. This may be explained, in part, by processes of meiosis dramatic exchange which takes place on different parts of the same chromosome or on different chromosomes.

The highly transferability of maize SSR makers in constructing maize×teosinte maps and the conserved orders of markers between maize×teosinte and maize×maize maps imply that maize sequence information can be used for further study in teosite. As we know, huge elite genes are hided in teosinte (Tanksley *et al.* 1996), the wild relative of maize provides beneficial information for maize improvement using teosinte as resource.

Segregation distortion

In the four maize×teosinte population, 52 markers were common across two populations, 20 markers were common across three populations, and four markers were common across all populations, allowing a base for comparison between maps.

Numerous examples of segregation distortion have been reported in different crops and between different populations within the same crop. Segregation distortion is the result of a variety of different mechanisms including pollen-tube competition, pollen lethals, and selective fertilization. In maize, several GA genes have been reported to associate with segregation distortion, for example, ga1 (4.02), ga2 (5.05), ga7 (3.09), ga8 (9.02), and ga10 (5.00-5.09) (Coe and Polacco 1995). Previously, Lu *et al.* (2002) identified three SDRs out of a total of 18 close to the location of five known gametophytic factors in four linkage maps in maize. In this study, only two out of the 10 SDRs were detected near the locations of five known gametophytic factors confirming the hypothesis that gametophytic factors are not the only reason of segregation distortion.

Segregation distortion loci were observed on every chromosome across all four populations (Fig. 2) (Li *et al.* 2007). Chromosome 5 has the greatest number of segregation distortion loci (14) whilst chromosome 10 has the least number of segregation distortion loci (2). Several distortion loci were identified across more than one population whilst the others were specific to one population. Marker *phi014* was identified as skewed in two populations. Two, one, and 10 SDRs were identified in the B64×*hue*, B73×*lux*, and B64×*nic* populations, respectively. More SSR markers were used in the B64×*nic* populations and this may account, in part, for the higher number of SDRs observed. The percent of the segregation distortion loci varied from 5.6 to 24.9% across the four populations. In all four populations, no SDR were detected on chromosomes 3 and 10. No SDR were detected across all the four populations,
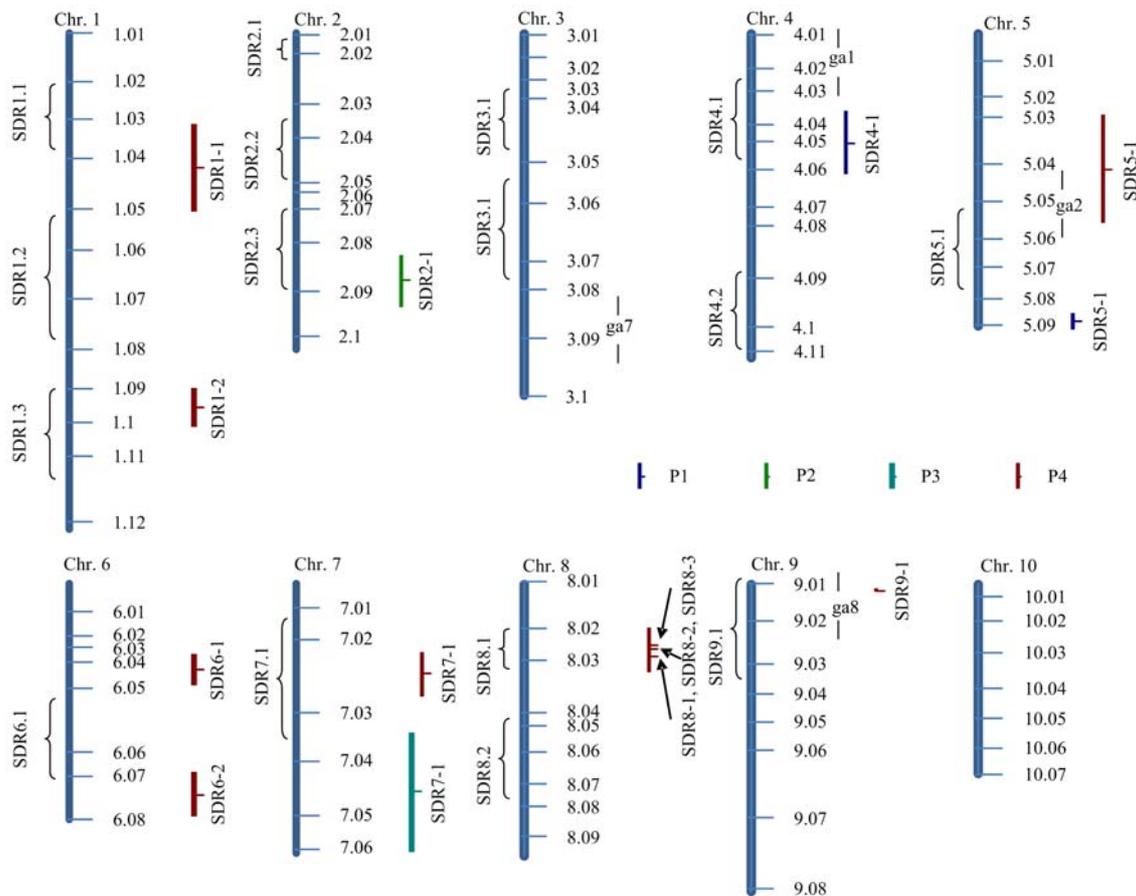
Fig. 2 Comparison of segregation distortion regions (SDRs) between maize and offspring of maize×teosinte. P1, B64×teosinte *Zea huehuetenangensis* F₂; P2, B73×teosinte *Zea luxurians* F₂; P3, B64×teosinte *Zea nicaraguensis* F₂; P4 B73×teosinte *Zea mexicana*. Marker locations are based on IBM2 2004 and an integrated bins map. Ga represents known gametophyte factors.

implying there were different mechanisms in different backgrounds.

Lu *et al*. (2002) previously identified 12 SDRs in F₂Syn3 population of maize linkage maps, 14 SDRs in a recombinant inbred population, 9 SDRs in a F₆:₇ population and 6 SDRs in a F₂ population suggesting that segregation distortion accumulated with additional generations of meiosis. But, in the same generation of meiosis for different materials, the number of SDRs was also different. For the F₂ population, in B73×teosinte there were 10 SDRs but only 6 SDRs in the maize F₂ population of Tx303×CO159 (Gardiner *et al*. 1993). The frequency of markers showing segregation distortion was 10% in the Tx303×CO159 mapping population comparing 24.9% of the B73×teosinte (*mexicana*) F₂ population. Given that this is the same generation of meiosis, additional reasons must be responsible for the observed higher frequency, for example, far-relative

cross.

By comparing maize×maize populations, nine SDRs were the same as or near the maize×teosinte population (Table 5). SDR5-1 and SDR9-1 were covered with ga2 and ga8, respectively. These results suggest that segregation distortion does not have stochastic distribution across the genome and the presence of steady heritable factors control segregation distortion. Our

Table 5 Corresponding regions of segregation distortion between maize×maize and maize×teosinte populations

Maize×Maize	Maize×Teosinte	GA[1]
SDR1.1	SDR1-1	
SDR1.2	SDR1-1	
SDR1.3	SDR1-2	
SDR5.1	SDR5-1	ga2
SDR6.1	SDR6-2	
SDR7.1	SDR7-1	
SDR8.1	SDR8-1	
SDR8.1	SDR8-3	
SDR9.1	SDR9-1	ga8

[1] GA, gametophytic factor.

results indicate that the control of segregation distortion is not only in intra-species but also in wide cross.

Acknowledgements

References

Briggs W H, McMullen M D, Gaut B S, Doebley J. 2007. Linkage mapping of domestication loci in a large maize-teosinte backcross resource. *Genetics*, **177**, 1915-1928.

Broman K W, Wu H, Sen S, Churchill G A. 2003. R/qtl: QTL mapping in experimental cross. *Bioinformatics*, **19**, 889-890.

Burnham C R. 1936. Differential fertilization in the Bt-Pr linkage group of maize. *Journal of the American Society of Agronomy*, **28**, 968-975.

Coe E H, Polacco M. 1995. Gene list and working maps. *Maize Genetics Cooperation Newsletter*, **694**, 157-191.

Cohen J I, Galinat W C. 1984. Potential use of alien germplasm for maize improvement. *Crop Science*, **24**, 1011-1015.

Devaux P, Kilian A, Kleinhofs A. 1995. Comparative mapping of the barley genome with male and female recombination-derive, doubled-haploid populations. *Molecular and General Genetics*, **249**, 600-608.

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

Doebley J, Gaut S, Smith D. 2006. The molecular genetics of crop domestication. *Cell*, **127**, 1309-1321.

Falque M, Decousset L, Dervins D, Anne-Marie J, Johann J, Jean-Pierre M, Xavier R, Nicolas R're, Celine R, Delphine S, *et al.* 2005. Linkage mapping of 1454 new maize candidate gene loci. *Genetics*, **170**, 1957-1966.

Fukunaga K, Hill J, Vigouroux Y, Matsuoka Y, Sanchez J, Liu K, Buckler E, Doebley J. 2005. Genetic diversity and population structure of teosinte. *Genetics*, **169**, 2241-2254.

Gardiner J M, Coe E H, Melia-Hancock S, Hoisington D A, Chao S. 1993. Development of a core RFLP map in maize using an immortaliazed F$_2$ population. *Genetics*, **134**, 917-930.

Harshberger J W. 1896. Fertile crosses of teosinthe and maize. *Garden and Forest*, **9**, 522-523.

Hoisington D, Khairallah M, Reeves T, Ribaut J M, Skovmand B, Taba S, Warburton M. 1999. Plant genetic resources: what can they contribute toward increased crop productivity? *Proceedings of the National Academy of Sciences of the USA*, **96**, 5937-5943.

Iltis H H, Benz B F. 2000. *Zea nicaraguensis* (Poaceae), a new teosinte from Pacific coastal Nicaragua. *Novon*, **10**, 382-390.

Iltis H H, Doebley J F. 1980. Taxonomy of *Zea* (Gramineae). II. Subspecific categories in the *Zea mays* complex and a generic synopsis. *American Journal of Botany*, **67**, 994-1004.

Jenczewski E, Gherardi M, Bonnin I, Prosperi J M, Olivieri I, Huguet T. 1997. Insight on segregation distortions in two intraspecific crosses between annual species of Medicago (Leguminosae). *Theoretical and Applied Genetics*, **94**, 682-691.

Ky C L, Barre P, Lorieux M, Thouslot P, Akaffou S, Louarn J, Charrier A, Hamon S, Noirot M. 2000. Interspecific genetic linkage map, segregation distortion and genetic conversion in coffee (*Coffea* sp.). *Theoretical and Applied Genetics*, **101**, 669-676.

Li L, Yan J B, Lei H Z, Song Z, Wu P, Xu Y B, Li J S. 2007. QTL-Finder: a bioinformatics tool for QTL integration, comparison and discovery of candidate genes across genomes and experiments. In Zhang Q F, ed., *The Abstract of Plant Genomics Conference in China VIII*. Plant Genomics Conference in China, Shanghai. pp. 56-56.

Lincoln S, Daly M J, Lander E S. 1992. *Constructing Genetic Linkage Maps With MAPMAKER/EXP*. ver. 3.0b. Whitehead Institute Technical Report, Cambridge, Massachusetts, USA.

Liu J L. 2000. *Maize Breeding*. 2nd ed. China Agriculture Press, Beijing. p. 20.

Lübberstedt T, Dussle C, Melchinger A E. 1998. Application of microsatellites from maize to teosinte and other relatives of maize. *Plant Breeding*, **117**, 447-450.

Lu H, Romero-Severson J, Brnard R. 2002. Chromosomal regions associated with segregation distortion in maize. *Theoretical and Applied Genetics*, **105**, 622-628.

Mano Y, Muraki M, Fujimori M, Takamizo T, Kindiger B. 2005a. AFLP-SSR maps of maize×teosinte and maize×maize: comparison of map length and segregation distortion. *Plant Breeding*, **124**, 432-439.

Mano Y, Muraki M, Fujimori M, Takamizo T, Kindiger B. 2005b. Identification of QTL controlling adventitious root formation during flooding condition in teosinte (*Zea mays* ssp. *Huehuetenangensis*) seedings. *Euphytica*, **142**, 33-42.

Mano Y, Omori F, Kindiger B, Takahashi H. 2007a. A linkage map of maize×teosinte *Zea luxurians* and identification of QTLs controlling root aerenchyma formation. *Molecular Breeding*, **21**, 327-337.

Mano Y, Omori F, Takamizo T, Kindiger B, Bird R M, Loaisiga C H, Takahashi H. 2007b. QTL mapping of root aerenchyma

formation in seedings of a maize×rare teosinte *Zea nicaraguensis* cross. *Plant Soil*, **295**, 103-113.

Mangelsdorf P C, Jones D F. 1926. The expression of Mendelian factors in the gametophyte of maize. *Genetics*, **11**, 423-455.

McCouch S R, Kochert G, Yu Z H, Wang Z Y, Khush G S, Coffman W R, Tanksley S D. 1988. Molecular mapping of rice chromosomes. *Theoretical and Applied Genetics*, **76**, 815-829.

Peterson A, Lander E, Hewitt J D, Peterson S, Lincoln S E, Tanksley S D. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature*, **335**, 721-726.

Reeves R G. 1950. The use of teosinte in the improvement of corn inbreds. *Agronomy Journal*, **42**, 248-251.

Saghai-Maroof M A, Soliman K M, Jorgensen R A, Allard R W. 1984. Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. *Proceedings of the National Academy of Sciences of the USA*, **81**, 8014-8018.

Sandler L, Novitski E. 1957. Meiotic drive as an evolutionary force. *American Naturalist*, **41**, 105-110.

Senior L, Chin E, Lee M, Smith J S C, Stuber C W. 1996. Simple sequence repeat markers developed from maize sequences found in the GENBAND database: map construction. *Crop Science*, **36**, 1676-1683.

Stuart M, John W, Jonathan S A. 2007. A linkage map reveals a complex basis for segregation distortion in an interpopulation cross in the moss *Ceratodon purpureus*. *Genetics*, **176**, 2489-2500.

Tanksley S D, Nelson J C. 1996. Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theoretical and Applied Genetics*, **92**, 191-203.

Taylor D R, Ingvarsson P K. 2003. Common features of segregation distortion in plants and animals. *Genetica*, **117**, 27-35.

Truco M J, Antonise R, Lavelle D, Ochoa O, Kozik A, Witsenboer H, Fort S B, Jeuken M J W, Kesseli R V, Lindhout P, *et al*. 2007. A high-density, integrated genetic linkage map of lettuce (Lactuca spp.). *Theoretical and Applied Genetics*, **115**, 735-746.

Wendel J F, Edwards M D, Stuber C W. 1987. Evidence for multilocus genetic control of preferential fertilization in maize. *Heredity*, **58**, 297-302.

Xu Y, Zhu L, Xiao J, Huang N, McCouch S R. 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.). *Molecular and General Genetics*, **253**, 535-545.

Yan J B, Tang H, Huang Y Q, Zheng Y L, Li J S. 2003. Genetic analysis of segregation distortion of molecular markers in maize F_2 population. *Acta Genetica Sinica*, **30**, 913-918.

(Managing editor WANG Ning)