RESEARCH NOTE

A genetic analysis of segregation distortion revealed by molecular markers in *Lophopyrum ponticum* chromosome 7E

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Introduction

Segregation distortion can be defined as deviations from normal Mendelian segregation (Sandler *et al.* 1958). It is a common phenomenon found in most genetic mapping studies in many species (Faris *et al*. 1998). *Lophopyrum ponticum* (also syn. *Agropyron elongatum* (Host) Beau.) has been one of the most important perennial *Triticeae* germplasm sources for wheat improvement (Oliver *et al.* 2006). Chromosome 7E of *L. ponticum* is crucial because it is the carrier of a number of elite agronomic traits (Zhang *et al.* 2011). However, there is still no report about molecular markers showing segregation distortion region of *L. ponticum* chromosome 7E.

Segregation distortion caused by preferential transmission may be affected by genetic background. Kong *et al.* (2008) reported that a segment of the *Thinopyrum intermedium* chromosome 7E present in the translocation line P98134 was preferentially transmitted through male gametes under different genetic background conditions. However, the transmission frequency of *T. intermedium* 7E segment present in another wheat *T. intermedium* translocation line, P961341, varied with different genetic backgrounds. Similarly, studies on the translocations involving *T. ponticum* chromosome $7el_1$ indicated that *Thinopyrum* chromosome $7el_1$ was transmitted normally in Thatcher and China Spring wheat backgrounds (McIntosh *et al.* 1976). However, high levels of distortion were observed when chromosome $7el_1$ was transferred in other genetic backgrounds (McIntosh *et al.* 1995). Both $7el_1$ and $7el_2$, are gametocidal chromosomes (Kibirige-Sebunya and Knott 1983; Prins *et al.* 1996). Gametocidal chromosomes cause abortion of gametes lacking the gametocidal chromosome, which results in partial sterility and exclusive transmission of these chromosomes (Endo 1990). We report for the first time since Kibirige-Sebunya and Knott (1983) the result of preferential transmission between homologous chromosomes $7el_1$ and $7el_2$ revealed by molecular markers under the Thatcher genetic background.

We previously constructed the first genetic linkage map of *L. ponticum* chromosome 7E (Zhang *et al.* 2011). According to Zhang *et al.* (2011), the genetic map of chromosome 7E covers a total length of 95.76 cM, including the two genes *FhbLoP* and *Lr19* that have been fine mapped to the distal long arm of chromosome 7E. The centromere of chromosome 7E is located approximately between the EST-SSR markers *Xcfe19* and *Xksum052* (Zhang *et al.* 2011). The development of 7E map will allow us to investigate the loci showing distorted segregation. This study intends to show chromosome regions with distorted segregation, identify the genetic factors involved in the segregation distortion, discuss the possible transmission patterns of $7el_1$ and $7el_2$ under the Thatcher genetic background and evaluate the *L. ponticum* 7E map to facilitate alien segment introgression by marker-assisted selection.

Materials and methods

Plant materials and population development

Thatcher *L. ponticum* substitution lines, K11463 ($7el_1$(7D)) and K2620 ($7el_2$(7D)) were used as parents to develop a population of recombinant inbred lines (RILs). The details of RIL population development were described previously by Shen and Ohm (2007). In this study, 237 $F_{7:8}$ RILs were used to survey the distorted markers of the *L. ponticum* chromosome 7E.

Data analysis

At each locus, the allele from the female parent (K11463) was denoted 'a', whereas the allele from the male parent

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(K2620) was assigned as 'b'. The expected allelic ratio in the RIL populations was 1:1 (a:b). The segregation fit of each locus to 1:1 ratio was examined using the chi-square test. A region with at least three adjacent loci showing significant segregation distortion ($P < 0.05$) was defined as the segregation distorted region (SDR) (Paillard *et al.* 2003). The chromosome locations of SDR were based on the genetic map of chromosome 7E, which was recently described by Zhang *et al.* (2011).

Results

Analysis of markers with segregation distortion

Segregation analysis was based on 64 molecular markers, including 26 G-SSR and 38 E-SSR/E-STS markers located on the *L. ponticum* chromosome 7E. Among these 64 molecular markers, 20 (31.25%) showed normal 1:1 segregation, whereas 44 (68.75%) were significantly deviated from the expected normal segregation ratio ($P < 0.05$). Among 26 G-SSR markers, 21 (80.77%), including gwm, wmc, barc, cfd, cfa and psp, showed distorted segregation towards $7el_2$ from the male genotype at a significant level ($P < 0.05$; table 1). Interestingly, 23 (60.53%) out of 38 EST-derived markers were segregated distortedly at a significant level ($P < 0.05$; table 2), and showed a biased manner favourable to $7el_2$ from the male genotype. Surprisingly, all markers examined displayed a uniparental segregation distortion of chromosome $7el_2$ inherited from the male parent K2620, rather than that of chromosome $7el_1$ from the female parent K11463 (tables 1 and 2). Among all the EST-derived markers, *Xswes354* exhibited the highest extent (91.8%, table 2) of deviation toward $7el_2$ from K2620, whereas the *Xpsp3123* marker within the G-SSR group showed the highest extent of deviation (72.6%; table 1) biased towards $7el_2$ from K2620.

Table 1. Chi-square test for segregation distortion of G-SSRs in a RIL population derived from K11463/K2620.

Markers	Genotype a	Genotype b	Genotype -	X^2	Direction of distortion
Xgwm333	83	150	4	19.8^g	K2620
Xpsp3123	51	180	6	72.6^g	K2620
Xwmc83	83	146	8	17.8^f	K2620
Xcfd31	87	144	6	14.5^e	K2620
Xcfd66	87	144	6	14.5^e	K2620
Xgwm130	89	147	1	14.7^e	K2620
Xcfd21	90	145	2	13.4^d	K2620
Xgwm350	92	141	4	10.8^d	K2620
Xwmc809	88	136	13	10.7^d	K2620
Xbarc154	95	136	6	7.7^b	K2620
Xcfa2049	95	136	6	7.7^b	K2620
Xcfa2106	96	137	4	7.7^b	K2620
Xcfd14	98	135	4	6.3^b	K2620
Xgwm295	95	139	3	8.8^b	K2620
Xgwm44	94	138	5	8.8^b	K2620
Xgwm473	95	137	5	8.1^b	K2620
Xwmc606	95	135	7	7.4^b	K2620
Xwmc653	93	136	8	8.5^b	K2620
Xwmc702	87	128	22	8.3^b	K2620
Xbarc70	100	133	4	5.1^a	K2620
Xcfa2174	98	130	9	5^a	K2620

$^aP < 0.05$, $^bP < 0.01$, $^cP < 0.005$, $^dP < 0.001$, $^eP < 0.0005$, $^fP < 0.0001$ and $^gP < 0.00001$. a, Genotype of K11463; b, genotype of K2620; -, deficient.

Table 2. Chi-square test for segregation distortion of EST-derived markers in a RIL population derived from K11463/K2620.

Markers	Genotype a	Genotype b	Genotype -	χ^2	Direction of distortion
Xmag1576	82	147	8	18.9^g	K2620
XBE399084	72	155	10	30.9^g	K2620
XBE406148	33	156	48	80.6^g	K2620
XBE605194	33	156	48	80.6^g	K2620
XBF200943	60	172	5	54.6^g	K2620
Xcfe19	77	143	17	20.3^g	K2620
Xcfe202	80	147	10	20.3^g	K2620
Xswes157	78	150	9	23.2^g	K2620
Xswes22	83	149	5	19.3^g	K2620
Xswes354	45	192	0	91.8^g	K2620
Xksum052	88	146	3	14.9^e	K2620
XBE489982	88	139	10	11.9^d	K2620
XBE500495	88	139	10	11.9^d	K2620
XBG262436	53	97	87	13.2^d	K2620
Xedm154	91	144	2	12.4^d	K2620
Xpsr129	73	118	46	11^d	K2620
Xmag2931	92	140	5	10.4^c	K2620
Xswes375	90	136	11	9.8^c	K2620
Xswes376	94	142	1	10.2^c	K2620
Xmag1759	95	131	11	6.2^b	K2620
Xmag3283	93	135	9	8.2^b	K2620
Xswes130	98	138	1	7.3^b	K2620
Xcfe100	102	134	1	4.8^a	K2620

$^aP < 0.05$, $^bP < 0.01$, $^cP < 0.005$, $^dP < 0.001$, $^eP < 0.0005$, $^fP < 0.0001$ and $^gP < 0.00001$. a, Genotype of K11463; b, genotype of K2620; -, deficient.

Segregation distortion region

Studies on 44 marker loci segregation patterns indicated that the distorted segregations were not random events ($P < 0.05$). Figure 1 demonstrated that 43 distorted markers ($P < 0.05$) were clustered into three special regions on chromosome 7E. These regions were designated as SDR1, SDR2 and SDR3, which consist of 6, 33 and 4 markers, respectively. The SDR regions covered about 55.48 cM, which includes nearly half of the long arm (34.28/68.87 cM) and almost the whole short arm (21.2/26.9 cM). The SDR2 region is extended from the short arm through the centromere of chromosome 7E.

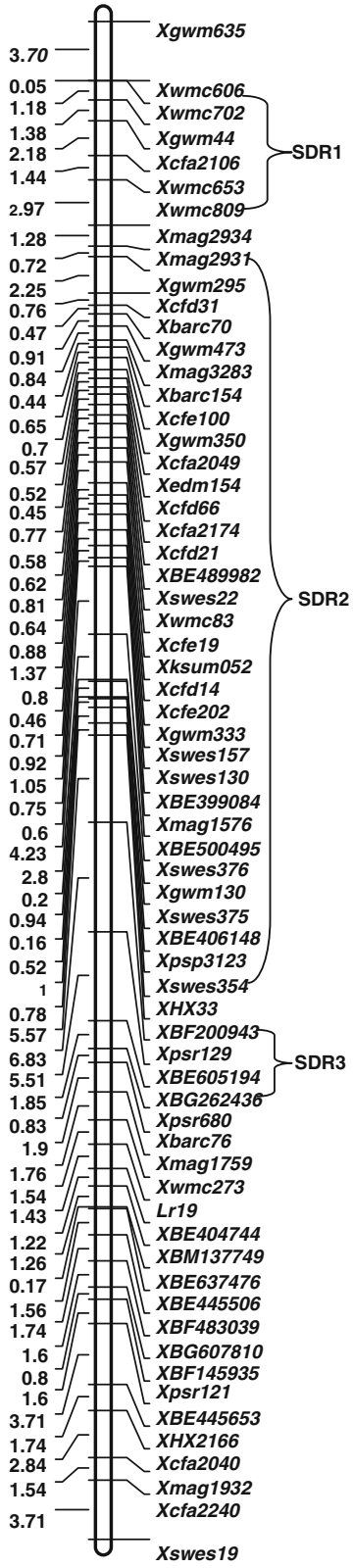

Figure 1. Genetic map of the *L. ponticum* chromosome 7E. The short arm of the chromosome is at the top. Map distances (cM) and marker names are shown on the left and right sides of each chromosome, respectively. The maps represent regions of segregation distortion, which include markers showing significant deviations from the expected segregation ratios at the significant level ($P < 0.05$).

Discussion

Previously, we demonstrated that the leaf-rust evaluation data gained from the RIL populations fitted a monogenic segregation ratio of 1:1, suggesting the goodness of fit of observed ratios to theoretical expectations. We also showed that the phenotypic data of the *Fusarium* head blight (FHB) disease agreed with a normal distribution, indicating that the FHB of RIL populations was controlled by quantitative trait loci (QTL) (Zhang *et al.* 2011). Moreover, the SDR clusters detected in this study are distant from the regions that harbour *FhbLop* and *Lr19*. The markers that closely linked to *FhbLop* and *Lr19* showed normal 1:1 segregation, which was in agreement with the phenotypic data of *FhbLop* and *Lr19*. The results mentioned above indicate that segregation distortion does not affect the QTL analysis of *FhbLop* and *Lr19*. Therefore, we conclude that the markers closely linked to *Lr19* and *FhbLoP* are practicable for marker-assisted selection (MAS) in alien segment introgression.

In comparison with other types of mapping populations, RIL populations that were derived from single seed descent had undergone several rounds of meiosis and natural selection during the inbreeding process, resulting in a high proportion of distorted markers (Singh *et al.* 2007). Accordingly, the present study indicates that it is not unusual that the distorted frequency is as high as 69% (44 out of 64 markers). The proportion of distorted markers skewed towards one of the parental genotypes varied with populations (Tekeoglu *et al.* 2002; Singh *et al.* 2007). An extreme example of all markers displaying the preferential distorted segregation favouring the female parent in a F_2 cotton population has been demonstrated by Li *et al.* (2007). We report for the first time an opposite extreme example; all the distorted markers favour the chromosome $7el_2$ of the male parent K2620. Other studies have also demonstrated that distorted segregation occurs frequently in RIL populations, as revealed by different types of markers such as AFLP, SSR, RFLP and RAPD (Haussmann *et al.* 2002). These data strongly suggest that segregation distortion is not due to marker types. Our study indicates that some interior genetic factors might account for the direction of distorted markers and segregation.

Aberrant segregation ratios in plants may arise from a variety of genetic causes. For e.g., the most commonly reported genetic factors associated with the distorted segregation ratio in *L. ponticum* were *Sd-1* and *Sd-2*, both located on chromosome $7el_1$ (Prins and Marais 1999). It is believed that *Sd-1* is proximal to *Xpsr129* (Prins *et al.* 1996). When both *Sd-1* and *Sd-2* act together, preferential transmission of *Lr19* occurs. However, in the absence of *Sd-1*, *Sd-2* generally results in reduced transmission of *Lr19* alone (Prins and Marais 1999; Marais *et al.* 2010). Our study shows that the SDR3 region covers four markers, including *Xpsr129*, *XBE60159*, *XBF200843* and *XBG262436*, and that this region is located on the long arm of chromosome 7E. However, we do not believe that the segregation distortion on chromosome 7E is the result of *Sd-1* located in the

neighbouring region of marker *Xpsr129*, due to the fact that the K11463 accession carries the *Sd-1* gene. This would result in a preferential distorted segregation favouring the female K11463 instead of the male K2620. Moreover, it would be impossible for *Sd-2* to cause such segregation distortion due to the presence of *Sd-1*. Therefore, we propose that the K2620 used in the present study might contain a gametocidal gene, resulting in distortion in favour of the male parent K2620. In addition, preferential selection of chromosome $7el_2$ was observed through the male in the RIL populations, indicating that the gametocidal effect of $7el_2$ was likely stronger than that of $7el_1$ in a Thatcher genetic background. Alternatively, the gametocidal effect of $7el_2$ might be dominant over that of $7el_1$ when both of them are present in the Thatcher genetic background.

Segregation distortion may arise from genetic and environmental causes, and the relative contribution of each of these factors may differ in different populations (Xu *et al.* 1997). Thus, we could not draw a thorough conclusion from the RIL population. In order to investigate the mechanisms of segregation distortion, it is necessary to develop different populations (e.g. doubled haploid, F_2 and backcross) and methods (e.g. cytological and molecular biological techniques).

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