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ORIGINAL PAPER

A genetic map of *Lophopyrum ponticum* chromosome 7E, harboring resistance genes to Fusarium head blight and leaf rust

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Abstract The leaf rust resistance gene *Lr19* and Fusarium head blight (FHB) resistance quantitative trait loci (QTL) derived from the wild wheatgrass *Lophopyrum ponticum* have been located on chromosome 7E. The main objectives of the present study were to develop a genetic map of chromosome 7E and map the two resistance loci using a population of 237 $F_{7:8}$ recombinant inbred lines (RILs) derived from a cross between two Thatcher-*L. ponticum* substitution lines, K11463 ($7el_1$(7D)) and K2620 ($7el_2$(7D)). 532 G-SSR, E-SSR and STS markers from wheat chromosome group 7 were screened in the parent lines. Of these, 118 markers were polymorphic, with a polymorphism frequency of 22.2%. A genetic map of *L. ponticum* chromosome 7E was constructed with 64 markers, covering 95.76 cM, with an average genetic distance of 1.47 cM between markers. The major FHB resistance locus, temporarily assigned as *FhbLoP*, was mapped to the very distal region of the long arm of chromosome 7E within a 3.71 cM interval flanked by *Xcfa2240* and *Xswes19*, which accounts for 30.46% of the phenotypic variance. *Lr19* was bracketed by *Xwmc273* and *XBE404744*, with a map distance of 1.54 and 1.43 cM from either side, respectively. The closely linked markers identified in this study will be helpful for marker-assisted introgression of the *L. ponticum*-derived *FhbLoP* and *Lr19* genes into elite cultivars of wheat, and the development of a genetic map will accelerate the map-based cloning of these two genes.

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Introduction

Lophopyrum ponticum (Podp.) Löve [syn *Thinopyrum ponticum* (Podp.) Barkw. and D. R. Dewey, syn *Elytrigia pontica* (Podp.) Holub. and syn *Agropyron elongatum* (Host) Beau.], a tertiary gene pool for carrying potentially favorable traits, have been extensively used in wheat improvement (Oliver et al. 2006). Many agronomically important genes, including *Lr19* (Prins et al. 1997), *Yp* (Knott 1980), *Sr25* (Singh et al. 2006), *Qfhs.pur-7EL* (Shen et al. 2004; Shen and Ohm 2007), and genes controlling yield and biomass (Reynolds et al. 2001; Monneveux et al. 2003), have been identified on the long arm of chromosome 7E of *L. ponticum*. The utilization of exotic germplasm has so far been impeded by the complexity of the *L. ponticum* genome (Chen et al. 1998; Zhang et al. 1996). Chromosomes from some cereals have remained well conserved during speciation, whereas others have undergone major structural rearrangements (Gale and Devos 1998; Sorrells et al. 2003). However, it is feasible to map *L. ponticum* chromosome 7E using markers developed earlier in wheat.

Fusarium head blight (FHB), also known as scab, is caused mainly by *Fusarium graminearum* Schwabe [telomorph: *Gibberella* zeae Schw. (Petch)] and is a devastating disease of wheat and barley that occurs in warm and humid regions around the world. The development of FHB-resistant cultivars is generally accepted to be the most cost-effective and environmentally benign way to minimize this infection (Parry et al. 1995). However, breeding of resistant

cultivars is difficult given the complex polygenic inheritance of FHB resistance, the large environmental effects on FHB disease expression (Bai and Shaner 1994) and the poor agronomic characteristics of resistant wheat germplasm (Mesterhazy 1995). Until now, no resistant source that can offer complete wheat resistance to FHB has been identified (Buerstmayr et al. 2003), although numerous sources of resistance have been reported (Cuthbert et al. 2006, 2007; Qi et al. 2008). A number of quantitative trait loci (QTLs) conferring FHB resistance have been identified on all wheat chromosomes except chromosome 7D (Buerstmayr et al. 2009). Shen et al. (2004) identified the resistant QTL of *FhbLoP* (syn. *Qfhs.pur-7EL*) in one Thatcher-*L. ponticum* substitution line, K2620 ($7el_2(7D)$), and later mapped it to the distal region of the long arm of chromosome $7el_2$ (Shen and Ohm 2007). However, there was a 10.4 cM interval between the identified flanking markers. To facilitate marker-assisted selection (MAS) and map-based cloning of the QTL of *FhbLoP*, delimiting the QTL to a shorter interval is crucial. Fortunately, the extensive synteny and collinearity between homoeologous linkage groups of the Triticeae have made it possible to construct a high-density molecular map of the target QTL.

Wheat leaf rust, known as brown rust, is a serious fungal disease affecting wheat that is mainly caused by the rust fungus *Puccinia triticina* Eriks. It is the most prevalent of wheat rust diseases, occurring in nearly all wheat-growing areas. The leaf rust resistance gene *Lr19*, derived from chromosome $7el_1$ of *L. ponticum*, has provided effective resistance against all or most pathotypes of leaf rust in many parts of the world (McCallum and Seto-Goh 2006; Gennaro et al. 2009). To date, several markers associated with *Lr19* have been identified (Autrique et al. 1995; Prins et al. 2001; Gupta et al. 2006; Ayala-Navarrete et al. 2007). However, sources used for mapping in previous studies were mostly wheat-*L. ponticum* translocation lines ($7DS.7el_1$) carrying *Lr19* in different wheat backgrounds. Thus, recombinant events seldom occurred between the two pairing chromosomes of wheat chromosome 7D and *L. ponticum* chromosome $7el_1$, limiting estimation of the genetic map distances around the target gene *Lr19*. As a result, these markers are not always useful for determining the presence of *Lr19* in different wheat lines.

To exploit the desirable resistance genes on chromosome 7E and utilize these genes in wheat breeding, it is necessary to develop a high-density map of the region. It has been reported that $7el_1$ and $7el_2$ pair quite regularly and are almost completely homologous (Dvorak 1975; Knott et al. 1977; Kim et al. 1993). A mapping population of recombinant inbred lines (RILs) was developed at Purdue University by single-seed descent from a cross between two Thatcher-*L. ponticum* substitution lines K11463 ($7el_1(7D)$), carrying *Lr19*, and K2620 ($7el_2(7D)$), conferring *FhbLoP* (Shen and Ohm 2007). In this study, we constructed the first genetic map of *L. ponticum* chromosome 7E, and finely mapped *FhbLoP* and *Lr19*. This new map will facilitate MAS in wheat breeding programs and map-based cloning of the two genes.

Materials and methods

Mapping population

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 for the RIL population development have been described previously by Shen and Ohm (2007). 237 $F_{7:8}$ RILs were available for the mapping of *L. ponticum* chromosome 7E and evaluation of FHB and leaf rust resistance in Taian, China. The Robertsonian translocation line KS24-2 ($7DS.7el_2L$) was used, together with the two parents, to determine the approximate location of the centromere of chromosome 7E.

Genomic DNA extraction and marker analysis

DNA samples were prepared from parents and $F_{7:8}$ seedlings of each RIL according to previously described protocols (Kong et al. 2008). PCR amplification was performed using 20 μl total volume of 1× PCR buffer, 1.5 mM $MgCl_2$, 200 μM dNTP, 0.4 μM each of forward and reverse primers, 1 unit of *Taq* polymerase and 50 ng of template DNA. The amplification profile consisted of 1 cycle at 94°C for 2 min, followed by 33 cycles of 30 s at 94°C, 45 s at 52–60°C (annealing temperature depended on the specific primers) and 50 s at 72°C, with a final extension of 10 min at 72°C. PCR products were separated in 6% non-denaturing polyacrylamide gels. Gels were then silver stained and photographed.

Disease evaluation

FHB evaluation

Type II FHB resistance evaluation was performed as described by Shen et al. (2004). Briefly, single-floret inoculation was conducted in a greenhouse for FHB type II disease evaluation of $F_{5:6}$ and $F_{6:7}$ in 2005 and 2006, respectively, at Purdue University (West Lafayette, IN, USA) and $F_{7:8}$ in 2008 at Shandong Agricultural University (Taian, China). The inoculum was a mungbean culture of the isolates of *F. graminearum*, with a concentration of $5–10 \times 10^4$ conidia/ml. At anthesis, the basal florets of the third or fourth spikelet from the tip of parental and RIL

spikes were each inoculated with 10 μl of a conidial suspension, and the inoculated spikes were covered with transparent plastic bags for 72 h to maintain high humidity. 3 weeks after inoculation, ten plants of each RIL and parent lines were evaluated for FHB response in each experiment. The mean of the ten inoculated plants was calculated and recorded as disease severity measured as the number of diseased spikelets (NDS) in the inoculated spikes.

Leaf rust evaluation

Using the parents K11463, K2620 and Thatcher as controls, the population of RILs was evaluated for leaf rust disease in the adult growth stage against the *Puccinia triticina* isolate 09-10-2 (syn. 121 R63-1), the most virulent and predominant pathotype of *P. triticina* in southeast Asia. These experiments were conducted at Shandong Agricultural University (Taian, China). Adult plants (heading stage) were spray-inoculated with a suspension of conidia spores of *P. triticina* isolate 09-10-2 per ml dH_20 plus 1 drop of Tween-20 at nightfall. 14 days after inoculation (growth condition: 24 ± 5°C, 90% relative humidity), the plants were scored for infection types (IT) according to Roelfs' (1984) methods. A scale ranging from 0 to 4 was used to describe the IT. IT values of 0 (fleck; immune), 1 (small uredinia with necrosis) and 2 (small uredinia with chlorosis) were considered as resistant, while IT values of 3 (medium-size uredinia with or without chlorosis) and 4 (large uredinia without chlorosis) were considered susceptible.

DNA marker analysis

We utilized the collinearity among homoeologous group 7 chromosomes to select markers that were mapped on wheat chromosomes 7A, 7B and 7D to map *L. ponticum* chromosome 7E. The selected markers include wheat G-SSR markers designated as GWM, GDM, WMC, BARC, CFD, CFA and PSP, and EST-derived markers, including CFE (Zhang et al. 2005), KSUM (Yu et al. 2004), SWES (Chen et al. 2005), MAG (Xue et al. 2008), STS (Ayala-Navarrete et al. 2007) and CAPS (Shen and Ohm 2007). Relevant information about these markers has been published on the GrainGenes website (http://wheat.pw.usda.gov). In addition, seven primer pairs of EST-SSR and EST-STS markers mapped to *L. ponticum* chromosome 7E were designed based on the EST sequences in wheat homoeologous group 7 (Table 1).

Data analysis

The phenotypic data obtained from the leaf rust test in the RIL populations were subjected to Chi-square (χ^2) analysis to confirm the goodness-of-fit of observed ratios to theoretical expectations. Linkage analysis was performed using MAPMAKER/Exp version 3.0b (Lincoln et al. 1993). Map distances were determined using the Kosambi mapping function (Kosambi 1944) and loci were ordered using the 'sequence' and 'compare' commands, with an LOD threshold score ≥3.0 and the maximum distance allowed between markers set to 37.5.

QTL detection and statistical analysis

FHB QTL analysis was conducted using the software QTLNetwork version 2.0 (Yang et al. 2007) based on the mixed linear regression model, with a probability into and out of the model of 0.05 and window size set at 10 cM. Significant thresholds for QTL detection were calculated for each data set using 1,000 permutations and a genome-wide error rate of 0.10 (suggestive) and 0.05 (significant).

Results

Genetic linkage map of *L. ponticum* chromosome 7E

A total of 532 primer pairs from wheat homoeologous group 7 were screened, including G-SSRs, E-SSRs and STSs. Of these, 118 primers were polymorphic between parents and were further used to analyze the population.

Table 1 EST-SSR and EST-STS primers on wheat group 7 chromosomes applied to linkage analysis of *L. ponticum* chromosome 7E

Locus	Accession number	Forward primer	Reverse primer	Specificity
XBE404744	BE404744	ACATGTTTGAAGCTGGCACA	GCGTTGACGATGACTTGTGT	$7el_1$
Xpsr680	Psr680	GCTCCACTACTTCATCATCC	TGTTTCCTCTATCACTGACTTG	$7el_1$ and $7el_2$
XBE489982	BE489982	TTTGTTTCTTGGCTGGGTTTC	CCATTCGGCCTGCTTCG	$7el_1$ and $7el_2$
XBG262436	BG262436	GGTTCACCACCAACACGG	CGAACGGCTTAGACTCCC	$7el_2$
XBE500495	BE500495	CCCCTCCCTTTCTTCGC	GGGCTGGTTCATTCCACTAA	$7el_2$
XHX2166	HX2166-1 (CJ579028)	CAGGGATGTCGGAGAAGA	GGTGACGACTCCTTTGAA	$7el_1$ and $7el_2$
XHX33	HX33 (CJ664083)	GATGATAATGACTCCCTATG	AGAATCCCTTCTGCTGACC	$7el_2$

The linkage map of *L. ponticum* chromosome 7E was constructed with 64 markers, including 38 locus-derived markers from E-SSRs/E-STSs and 26 G-SSRs. The map covered a total length of 95.76 cM, with an average marker density of 1.47 cM per locus (Fig. 1). The location of the centromere was approximately determined between EST-SSR markers *Xcfe19* and *Xksum052* after scanning two substitution lines, K2620 ($7el_2$(7D)) and K11463 ($7el_1$(7D)), as well as the Robertsonian translocation line KS24-2 (7DS.$7el_2$L), using $7el_2$-specific markers. The $7el_2$-specific band (~270 bp) amplified by *Xksum052* was present in both K2620 and KS24-2, while the $7el_2$-specific band (~300 bp) derived from *Xcfe19* was present in K2620 but not in KS24-2 (data not shown). 24 markers, including 17 G-SSR markers and 7 E-SSRs/E-STSs, were mapped on the short arm of chromosome 7E, and 40 markers consisting of 8 G-SSR markers and 32 E-SSRs/E-STSs were placed on the long arm of chromosome 7E.

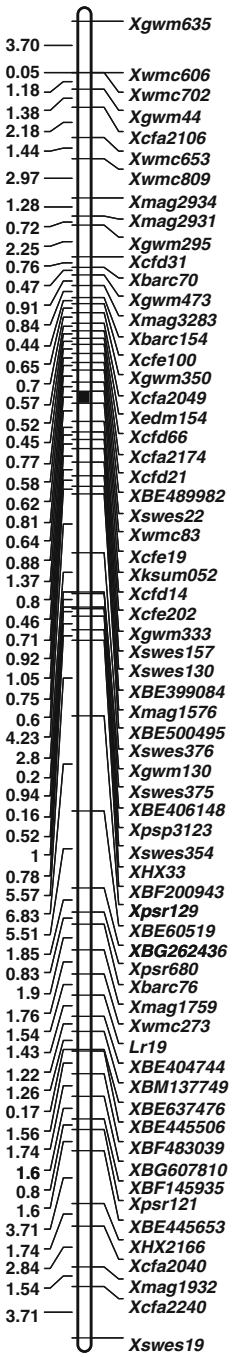

Fig. 1 Genetic map of *Lophopyrum ponticum* chromosome 7E. The short arm of the chromosome is at the *top*. *Left* approximate distances in centi-Morgans (cM). *Right* molecular markers. The *letter X* in front of each marker locus name indicates a molecular marker with unknown function. Marker loci mapped with a LOD > 3 are integrated in the framework. The *vertical short bar* indicates the approximate location of the centromere

Quantitative analysis of FHB resistance *FhbLoP*

The resistant parent, K2620, had consistently fewer NDS than the susceptible parent, K11463, and population data displayed a continuous distribution ranging from 0.5 to 13 and 0.8 to 12.5 at Indiana in 2005 and 2006, respectively, and 0.8 to 14 in 2008 at Shandong (Fig. 2). Estimated proportions of variance components relative to the phenotypic variances for FHB severity are summarized in Table 2. The values of kurtosis and skewness were less than 1 (<1) in the three environments, which suggested that the phenotype data could be utilized for QTL analysis. Approximately, 30.46% of the phenotypic variations were attributable to genotypic effects, 0.13% to G × E interaction effects, and 69.54% to residuals, indicating that FHB resistance was controlled by large residuals. The ratio V_G/V_{GE} was 234.3, suggesting that genotypic effects were more important than G × E interaction effects for this trait in the three environments. The ratio V_G/V_P, the estimated narrow sense heritability, was greater than 30.46% for FHB resistance. The small values of V_{GE}/V_P for FHB resistance (Table 2) made the detection of QTL position with significant QTL × E effects quite difficult using this population.

One major QTL for FHB resistance was detected and mapped to the very distal region of the long arm of chromosome $7el_2$, flanked by *Xcfa2240* and *Xswes19* (Fig. 3), which contributed 30.46% to the phenotypic variation over the 3 years (Table 3). The consistent effectiveness of *FhbLoP* across environments indicates that this resistance gene is an effective genetic resource that could be used for improving type II FHB resistance in wheat breeding programs.

Markers linked to *Lr19*

Leaf rust inoculations showed that leaf rust-resistant parent, K11463, was highly resistant, displaying the fleck reaction (IT = 0), while the susceptible parent K2620 produced a susceptible phenotype (IT = 4). Out of 237 RIL plants, 108 were resistant (IT = 0) and 129 susceptible (IT = 4), which fit a monogenic segregation ratio of 1:1 ($\chi^2 = 1.861$, $P > 0.10$). *Lr19* was flanked by *Xwmc273*

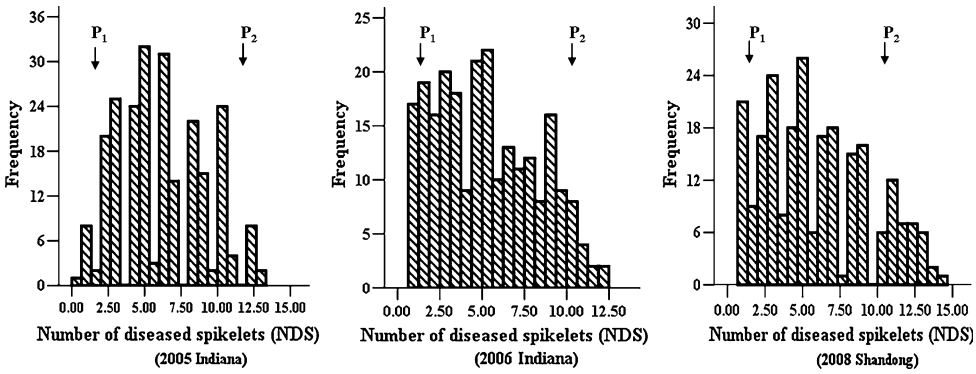

Fig. 2 Frequency distribution of FHB severity recorded as number of diseased spikelets

Table 2 Descriptive statistical values for FHB disease in the RIL population in three environments in 3 years

	Mean[a]	Min[a]	Max[a]	Kurtosis	Skewness	V_G/V_P[b]	V_E/V_P[c]	V_{GE}/V_P[d]	V_e/V_P[e]
2005 (Indiana)	5.94	0.50	13.00	−0.79	0.27	0.3068			0.6932
2006 (Indiana)	5.22	0.80	12.50	−0.90	0.36	0.3231			0.6769
2008 (Shandong)	5.88	0.80	14.00	−0.78	0.46	0.3014			0.6986
Mean	5.53	0.70	13.25	−0.84	0.41	0.3046	0.0123	0.0013	0.6954

[a] Mean, Min and Max represents mean, minimum and maximum of NDS in the RIL population

[b] V_G/V_P represents the variance of genetic main effects divided by phenotypic variance

[c] V_E/V_P represents the variance of environmental effects divided by phenotypic variance

[d] V_{GE}/V_P represents the variance of genotype-by-environment interaction effects divided by phenotypic variance

[e] V_e/V_P represents the variance of residual effects divided by phenotypic variance

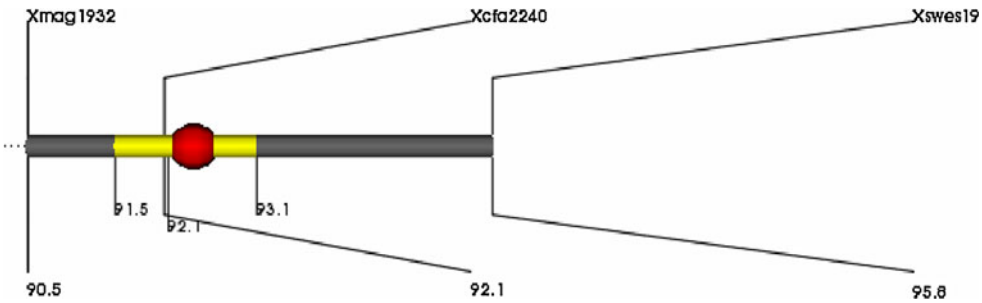

Fig. 3 Genotypic data from 237 RILs plants. Phenotypic data were derived from disease tests on $F_{5:6}$, $F_{6:7}$ and $F_{7:8}$ RIL populations with software QTLNetwork version 2.0. The *circle* represents *FhbLoP* position, and the *gray region* flanking the circle represents the support interval of QTL position

Table 3 Effects of QTLs for FHB disease in three environments in 3 years

Year/Environment	Flanking markers	Position	H^2 (%)	*P* value	$A^a \times AE_1^b$		$A \times AE_2^c$		$A \times AE_3^d$	
					AE_1	*P* value	AE_2	*P* value	AE_2	*P* value
2005 (Indiana)	*Xcfa2240-Xswes19*	92.1	30.68	0.00						
2006 (Indiana)	*Xcfa2240-Xswes19*	92.1	32.31	0.00						
2008 (Shandong)	*Xcfa2240-Xswes19*	92.1	30.14	0.00						
Multi-environments	*Xcfa2240-Xswes19*	92.1	30.46	0.00	−0.00	0.9917	0.00	0.9915	−0.00	0.9910

[a] A the estimated additive effect

[b] AE_1 the predicted additive by environment (2005 Indiana) interaction effect

[c] AE_2 the predicted additive by environment (2006 Indiana) interaction effect

[d] AE_3 the predicted additive by environment (2008 Shandong) interaction effect

and *XBE404744*, with genetic distances of 1.54 and 1.43 cM, respectively (Fig. 1).

Discussion

Genetic map of *L. ponticum* chromosome 7E

We report here the first genetic linkage map of chromosome 7E of *L. ponticum*, which was constructed using an RIL population derived from two Thatcher-*L. ponticum* substitution lines, K11463 ($7el_1$/7D) and K2620 ($7el_2$/7D). Dvorak (1975) first reported that the chromosomes of decaploid *A. elongatum* $7el_1$ and $7el_2$ were almost completely homologous, both chromosomes paired with high frequency ranging from 50 to 80% of the cells, and that the slight reduction in pairing may be due to extensive heterozygosity between these *Agropyron* chromosomes. Later, Knott et al. (1977) and Kibiridge-sebunya and Knott (1983) again found that the whole chromosomes $7el_1$ and $7el_2$ paired almost completely. Cai and Jones (1997) reported that *L. ponticum* carried strong promoters for homoeologous chromosome pairing. However, there was no direct evidence from our study that meiotic chromosome pairing between $7el_1$ and $7el_2$ was markedly influenced by meiotic pairing control genes. We have observed that 21 bivalents, including one alien bivalent, existed at metaphase I (MI) in pollen mother cells (PMCs) of RIL population $F_{7:8}$ plants by genomic in situ hybridization (GISH), which confirms that chromosome pairing is stable in the RIL population. The genetic map of chromosome 7E covered a total length 95.76 cM with 64 molecular markers, indicating that the chromosomes of $7el_1$ and $7el_2$ undergo synapsis and recombination. The map length of chromosome 7E (95.76 cM) is shorter than the consensus maps of chromosome 7A (131 cM), 7B (151 cM) and 7D (154 cM) by Somers et al. (2004), as the average genetic distance between markers on chromosome 7E (1.47 cM) is smaller than those of 7A (2.1 cM), 7B (2.2 cM) and 7D (2.2 cM).

The development of a genetic map is prerequisite for gene isolation by map-based cloning and MAS (Peng et al. 2000). Importantly, our map of chromosome 7E is enriched in E-SSRs/STSs on the long arm (32 EST-SSRs/STSs in 40 markers). Holton et al. (2002) have reported that ESTs sharing homology to candidate genes can be specifically targeted for genetic mapping and can be useful for aligning genome linkage across distantly related species for comparative analysis.

FHB QTLs and *FhbLoP*

In recent decades, the combination of severe FHB epidemics in some principal wheat growing areas and improved technology for detecting mycotoxins that pose food safety threats have contributed to a growing emphasis on FHB research (Buerstmayr et al. 2009). Bai and Shaner (1994) have reported that FHB resistance is under polygenic control and that the expression of plant resistance to the pathogen is strongly influenced by the environment. In light of this challenge, researchers have attempted to perform genetic analysis of FHB resistance through chromosomal manipulation (e.g., intervarietal genetic recombination) and via the mapping of QTL based on high-density genetic maps. *Fhb1* and *Fhb2* originated in the Asian cultivar Sumai 3 and are widely used for FHB resistance breeding. In contrast, other resources harboring QTLs for FHB resistance, such as the European cultivars Fundulea 201R (Shen et al. 2003) and Renan (Gervais et al. 2003) and the South America cultivars Frontana (Steiner et al. 2004) and Ernie (Liu et al. 2007), have not been extensively utilized. Exploiting resistance genes from species related to wheat is necessary to broaden the genetic pool of FHB resistance. The resistance gene *FhbLoP* on chromosome $7el_2$ of *L. ponticum* was reported by Shen et al. (2004) and Shen and Ohm (2007). However, the genetic distance between flanking markers *XBE445653* and *Xcfa2240* was more than 10 cM, due to the lack of informative markers. The present study finely mapped *FhbLoP* to an interval of just 3.71 cM between *Xcfa2240* and *Xswes19* on chromosome 7E. Utility of *FhbLoP* will impede by very low recombination between 7D and 7E. So, further studies will focus on developing wheat-*Lophopyrum* introgression by *ph1b* mutation and MAS to utilize *FhbLoP* QTL in wheat breeding.

Markers linked to *Lr19*

Several genes closely linked with *Lr19* have been identified with RFLP markers, including *Yp*, *Sr25*, *Sd1* and *Wsp-D1* (Prins and Marais 1998). In the present study, nine markers were very closely linked to *Lr19* and the mean interval length was only 1.74 cM/loci. These high-density markers could be used to verify other genes or traits around *Lr19* and identify introgressed *L. ponticum* 7E segments in cultivated wheat. Since *Lr19* is proximal to *FhbLoP* with several different transfers of *Lr19* (Knott 1980), we expect most of the *Lr19* sources to be terminal translocations, including Agatha-28 and Lr19-149 without *Yp* (Knott 1980; Prins et al. 1997). Therefore, it should be feasible to transfer *FhbLoP* to a wheat stock with *Lr19* using these lines and the marker details found in our study. Furthermore, several cultivars from the Centro Internacional de Mejoramiento de Maizy Trigo (CIMMYT) carrying *Lr19* derived from *L. ponticum* would be useful for increasing grain yield and biomass (Reynolds et al. 2001; Monneveux et al. 2003). Some of the recombinant RILs should combine *FhbLoP* and *Lr19* with high yield, which could be

used for marker-assisted introgression of these traits into elite cultivars of wheat. In addition, we are evaluating the phenotype of *Sr25*, which is closely linked with *Lr19*, using these RILs and by mapping *Sr25* on chromosome 7E.

In summary, the construction of a genetic map of *L. ponticum* chromosome 7E is a starting point for exploiting desired genes from 7E in cultivated species. The closely linked markers facilitate pyramiding the resistance of *Fhb-LoP* and *Lr19* in wheat with MAS and provide an important resource for map-based cloning of these two genes.

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