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Microsatellite Mapping of a Leaf Rust Resistance Gene Transferred to Common Wheat from *Triticum timopheevii*

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A leaf rust resistance gene transferred from the tetraploid wheat *Triticum timopheevii* (Zhuk.) Zhuk. (genomic composition: A^tA^tGG) into common wheat *Triticum aestivum* L. conditioned resistance at the seedling and adult plant stages in the introgression line 'line 842-2'. To determine chromosome location and to map the resistance gene an F_2 population from a cross between 'line 842-2' and susceptible wheat cultivar 'Skala' was developed and screened against leaf rust pathotype 77 (*Puccinia triticina* Erikss.). Microsatellite markers detected introgressions of the *T. timopheevii* genome on chromosomes 1A, 2A, 2B, 5B and 6B of 'line 842-2'. Linkage analysis revealed an association between leaf rust resistance and microsatellite markers located on chromosome 5B. The markers *Xgwm880* and *Xgwm1257* were closely linked to the resistance gene with genetic distances of 7.7 cM and 10.4 cM, respectively. Infection type tests with three leaf rust isolates resulted in different patterns of infection types of 'line 842-2' and 'Thatcher' near-isogenic line with the *Lr18* gene on chromosome 5B. The data corroborated the hypothesis of the diversity of the resistance coming from *T. timopheevii*. The resistance gene of the introgression 'line 842-2' seems to be different than *Lr18* and therefore it was designated *LrTt2*.

Keywords: chromosome localization, introgression lines, leaf rust resistance, microsatellite markers, *Puccinia triticina*, *Triticum timopheevii*

Introduction

Leaf rust, caused by the fungus *Puccinia triticina* Erikss., is an important disease of hexaploid wheat (*Triticum aestivum* L.) throughout the world, causing yield losses of 30 to 50% in epidemic years (Roelfs et al. 1992; Sayre et al. 1998). The most reliable and ecologically safest method for disease control is breeding and growing of resistant cultivars. It is known that the effectiveness of resistance genes deployed in wheat cultivars can change over the years. Many wild relatives of wheat carry high levels of resistance to different dis-

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eases. However, the transfer of these genes from the related species can result in the loss of valuable agronomic characters. It is important to develop stable introgression lines of common wheat with expression of the resistance from the wild species, while retaining common wheat characteristics to be used as donor sources in breeding programs.

Earlier, a set of introgression lines derived from *T. aestivum* × *T. timopheevii* crosses was developed in the background of different cultivars of common wheat. The lines carry high levels of resistance to leaf and stem rusts transferred from the tetraploid species *Triticum timopheevii* ssp. *viticulosum* (Budashkina and Kalinina 2001). Cytological and molecular analysis demonstrated that the introgression lines have different patterns of chromosomal location and sizes of introgressed fragments of the *T. timopheevii* genome (Badaeva et al. 1991; Leonova et al. 2002).

Molecular markers are efficient tools for identification of alien introgressions in hybrid genomes and several marker types (RAPD, RFLP, AFLP, SSR) are available for genome analysis of cereals (Collard et al. 2005). Among them microsatellites, or SSR markers have been shown to be informative due to their high level of polymorphism, codominance and chromosome specificity (Röder et al. 1995; Prasad et al. 2000).

Recently the gene *LrTt1* determining seedling resistance to leaf rust that originated from *T. timopheevii* ssp. *viticulosum* was mapped on chromosome 2A using microsatellite markers (Leonova et al. 2004). Studies of common wheat hybrids containing *T. timopheevii* and *T. araraticum* introgressions and resistant to leaf rust indicated that wheats of the Timopheevi group probably contain additional and presently unknown pathogen resistance genes (Badaeva et al. 2000; Laikova et al. 2004). In this investigation, the leaf rust resistance was evaluated in the *T. aestivum* × *T. timopheevii* introgression sister line ‘line 842-2’ at the seedling and adult plant stages. Microsatellite markers were used to determine the genetic map location of the resistance gene.

Materials and Methods

Plant materials

The leaf rust resistant introgression line 842-2 (‘line 842-2’) was obtained from the cross between *T. aestivum* cv. ‘Saratovskaya 29’ (‘S29’) and *T. timopheevii* ssp. *viticulosum*. The F_1 was backcrossed to ‘S29’ and selection was performed for cytologically stable resistant plants in the BC_1F_4–BC_1F_7 generations. The line was selfed for several generations (BC_1F_{18}). ‘Line 842-2’ carried resistance to leaf rust flora prevalent in the Russian Federation (Budashkina and Kalinina 2001). The introgression line was crossed with the susceptible wheat cultivar ‘Skala’ to obtain an F_2 population. The F_2 individuals were used to derive F_3 families. The 148 F_3 families were used for genetic mapping of leaf rust resistance. ‘Thatcher’ near-isogenic line ‘RL6009’ with the *Lr18* gene was used for leaf rust resistance test with different rust isolates.

Evaluation of leaf rust resistance

The leaf rust resistance at the seedling stage was tested under greenhouse condition. Up to 25 seeds of 'line 842-2' and parental cultivars were planted in plastic pots filled with vermiculite. Seedlings 7–9 days old were inoculated using a suspension of urediniospores of race 77 of *P. triticina* according to the method of Roelfs et al. (1992). The inoculated plants were incubated at a temperature between 15 and 25 °C with a 14-hour photoperiod and more than 85% relative humidity. Leaf rust infection types (ITs) of seedlings were scored 10 to 14 days after inoculation according to the Mains and Jackson scale (1926). The adult plant resistance was estimated in the 1998–2000 and 2002–2004 growing seasons under natural infection with native population of the leaf rust pathogen prevalent in West Siberian region of Russia. In the mapping population, the adult plant leaf rust phenotyping was performed at two locations of the Novosibirsk region during 2004–2006. In field experiments, 15 to 20 plants of each F_2-derived F_3 family along with the parents were grown in a 0.5 m row, surrounded by a 1 m border of leaf rust susceptible wheat cultivar for disease spread. The F_3 plants were artificially inoculated between boot and early heading stages by a suspension of urediniospores consisting mainly of pathotype 77 of *P. triticina*. ITs at adult plant stage were evaluated 14 days after inoculation when rust was fully developed on the susceptible wheat cultivar using 0–4 immune scale: 0 – immune, no visible symptoms; 1 – resistant, necrotic flecks with or without pustules; 2 – moderately resistant, small pustules with necrotic and chlorotic areas; 3 – susceptible, moderate size pustules without necrosis or chlorosis; 4 – highly susceptible, large pustules without necrosis and chlorosis (Mains and Jackson 1926).

Phenotyping in the climate chamber

A total of thirty seeds of both 'line 842-2' carrying the resistance from *T. timopheevii* and the 'Thatcher' near-isogenic line 'RL6009' characterized by the *Lr18* resistance gene, respectively, were grown for 14 days in pots with soil. Segments cut from the middle part of the primary leaves were transferred with the adaxial side up to Petri dishes with 1.5% agar. Three isolates known to be virulent against the *Lr18* resistance gene were used separately for the inoculation to assess the resistance reaction of the lines (Table 1). The success of the inoculation was checked with leaf samples of the susceptible wheat cultivar 'Monopol' distributed in each Petri dish.

After inoculation the plant material was kept for 24 h in a chamber with complete darkness, a temperature of 16°C and nearly 100% humidity followed by 10 days with 24h light, same temperature and ambient humidity. The development of the leaf rust fungus was scored from 0 (no symptoms) to 6 (well-developed pustules). The control wheat cultivar 'Monopol' was scored with 5 or 6 in all Petri dishes.

DNA extraction and microsatellite analysis

Genomic DNA was extracted from young leaves of individual plants according to a modified procedure of Plaschke et al. (1995). Microsatellite markers (GWM, GDM) previously mapped on the chromosomes of common wheat, were used for genetic mapping (Röder et

al. 1998; Röder, unpublished data; Pestsova et al. 2000). Several microsatellites were provided by M. Ganal, TraitGenetics GmbH, Gatersleben. Procedures for microsatellite analysis, gel electrophoresis and the protocol for polymerase chain reaction (PCR) were described in Röder et al. (1998). PCR fragments were detected and analysed on automated laser fluorescence sequencer (ALFexpress, Amersham Biosciences) using the short gel cassette. The fragment sizes were calculated using the computer program Fragment Analyser 1.02 by comparison with internal and external size standards.

The genetic linkage map was constructed using the Mapmaker program version 3.0b with Kosambi mapping function (Lander et al. 1987). The threshold of log likelihood ratio (LOD) was = 3.0. A Chi-square test for goodness of fit was used to test for deviation of the observed data from the theoretically expected segregation.

Results

At the adult plant stage, the introgression line 842-2 was either immune or resistant to the field population of leaf rust (IT = 0-1), whereas the recipient cultivar 'Saratovskaya 29' was highly susceptible (IT = 4). Disease resistance tests performed in different weather conditions during 6 years (1998–2000, 2002–2004) showed that 'line 842-2' expressed high and stable level of adult plant resistance. Seedlings of 'line 842-2' were slightly susceptible to leaf rust when compared with adult plants displaying resistance or moderate resistance (IT = 1–2). Individual F_1 plants developed from the cross of 'line 842-2' with cv. 'Skala' were resistant indicating that adult plant resistance carried by 'line 842-2' was dominant. Of 148 families in the F_2-derived F_3 population 41 families were non-segregating resistant, 64 segregating and 43 non-segregating susceptible. Chi-squared analysis of data conformed to the 1:2:1 ($\chi^2 = 2.8$, $P > 0.25$) ratio suggesting the single gene control of leaf rust resistance in 'line 842-2'. The gene was tentatively designated as *LrTt2*.

Before genotyping the F_2 mapping population the parental lines 'line 842-2', 'S29', 'Skala' and *T. timopheevii* were screened with microsatellite markers to determine parental polymorphisms. In total, 350 GWM and GDM markers covering all 21 chromosomes of *T. aestivum* were tested. The choice of microsatellite markers was based on previous analysis of *T. aestivum* × *T. timopheevii* introgression lines and on the construction of a linkage maps for *T. timopheevii* (Leonova et al. 2002; Salina et al. 2006). A high level of parental polymorphism (85%) was observed. Comparative analysis detected the presence of *T. timopheevii* fragments on chromosomes 1A, 2A, 2B, 5B and 6B of 'line 842-2' (Fig. 1). On chromosomes 1A and 6B, the introgression of the *T. timopheevii* genome apparently replaced complete chromosomal arms. The short and part of the long arm up to marker *Xgwm1070* were substituted on chromosome 2B, whereas on chromosome 2A the proximal part of the short arm including the centromeric region ranging from *Xgwm95* to *Xgwm312* was replaced. On chromosome 5B there was a substitution of the region of the long arm distal to the marker *Xgwm777*.

To determine any linkage of the resistance gene with microsatellite markers chromosomes with introgressive fragments were analyzed with polymorphic SSR primers. The F_2 mapping population was genotyped with 55 markers of which 21 were previously mapped

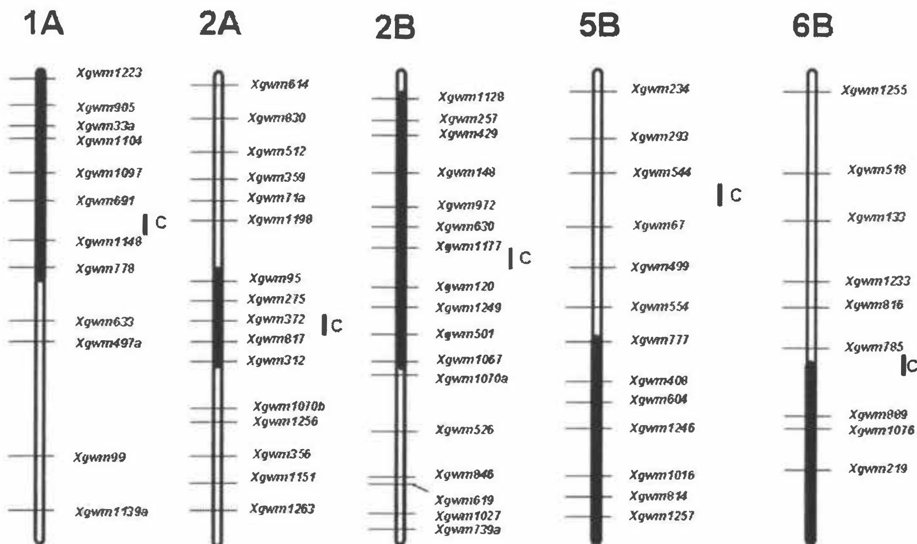

Figure 1. Schematic presentation of localization of the *Triticum timopheevii* genome in introgression 'line 842-2'. Fragments of the *Triticum timopheevii* genome are denoted with black bars. Markers used in the analysis are indicated right to the chromosome. C indicates centromere position

in the *T. timopheevii* genome (Salina et al. 2006). Linkage analysis by the MAPMAKER program revealed the association of *LrTt2* with microsatellite markers belonging to chromosome 5B. A genetic map involving *LrTt2* and eleven polymorphic microsatellite markers covered 51.4 cM (Fig. 2). The order of the microsatellite loci on the introgressive fragment of chromosome 5B in 'line 842-2' was similar to the chromosome map of 5B of the ITMI population described by Röder et al. (1998, unpublished data). However, genetic distances between markers were different because of a possible reduction of recombination rate that often occurs in distant crosses. The gene *LrTt2* determining resistance of 'line 842-2' was localized between markers *Xgwm880* (7.7 cM) and *Xgwm1257* (10.4 cM) (Fig. 2). Comparative analysis of PCR fragment sizes for three microsatellite markers (GWM1246, GWM1257 and GWM814) showed that DNA of resistant plants amplified fragments typical for *T. timopheevii* demonstrating that *LrTt2* was derived from chromosome 5G.

To clarify the relationship between *LrTt2* and the known resistance gene *Lr18* mapped on wheat chromosome 5BL (McIntosh et al. 1983) 'line 842-2' with the 'Thatcher' near-isogenic line 'RL6009' containing gene *Lr18* were tested with three isolates of *P. triticina*. The results showed that 'line 842-2' displayed a lower infection type than 'Thatcher' line 'RL6009' (Table 1).

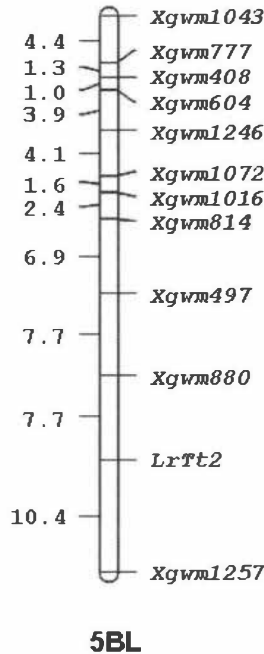

Figure 2. A genetic map of the *LrTt2* region on chromosome 5B. The microsatellite marker names are indicated on the right side. Genetic distances are given in centi Morgans on the left side

Table 1. Development of leaf rust uredinia in 'line 842-2' carrying the resistance from *T. timopheevii* and the 'Thatcher' near-isogenic line 'RL6009' characterized by the *Lr18* resistance gene against three leaf rust isolates virulent for *Lr18*

Line	Scoring of the leaf rust reaction* against		
	Isolate 1 7147661074**	Isolate 3 7747660174	Isolate 9 263701675
'RL6009'	4.5	5.1	4.6
'line 842-2'	2.3	3.0	2.2

* mean of ten plants per line and isolate

** designation of virulence in isolates according to Gilmour (1973) octal notation

Additional study of 'RL6009' with a set of GWM markers located on chromosome 5B indicated that 'Thatcher' near-isogenic line differed from 'line 842-2' both in translocation breakpoint and in the length of the PCR fragments amplifying with markers GWM814 and GWM1257 (Table 2).

Table 2. Length of PCR fragments amplified with chromosome 5B markers in 'line 842-2', 'RL6009' and wheat cultivars 'S29' and 'Thatcher'

Marker	Fragment size (base pairs)	
	'line842-2'/'S29'	'RL6009'/'Thatcher'
GWM234	246/246	244/244
GWM540	124/124	124/124
GWM499	133/133	null/null
GWM777	110/110	108/108
GWM408	null/182	180/180
GWM604	null/113	118/118
GWM1246	223/236	232/232
GWM1072	180/195	180/195
GWM814	120/145	126/145
GWM1257	263/246	260/262

Discussion

Despite the high potential of *T. timopheevii* as a donor of resistance genes, the species has been insufficiently used in breeding of common wheat. So far, two leaf rust resistance genes transferred into the common wheat from the *T. timopheevii* genome are known. One of them, *Lr18,* was transferred to the long arm of chromosome 5B and is associated with a *T. timopheevii* derived telomeric band on the chromosome arm 5BL (McIntosh et al. 2008). The second, *Lr50* was transferred from wild species *T. timopheevii* ssp. *armeniacum* to the long arm of chromosome 2B and is linked with the microsatellite markers *Xgwm382* and *Xgdm87* (Brown-Gudiera et al. 2003). However, the literature and our own data suggest that the *T. timopheevii* accessions may carry other disease resistance genes, including genes for resistance to leaf rust and powdery mildew (Järve et al. 2000; Leonova et al. 2007; Murphy et al. 2007). In previous work, gene *LrTt1,* determining seedling resistance in introgression 'line 842', was tightly linked with microsatellite marker *Xgwm817* on chromosome 2A (Leonova et al. 2004). In the present study, *LrTt2* was localized on chromosome 5B of another introgression 'line 842-2'. The introgression 'line 842' and 'line 842-2' are sister lines based on the same susceptible bread wheat cultivar 'Saratovskaya 29' and *T. timopheevii* parents. In spite of the common origin, the lines differ with respect to the number of introgressions transferred from the *T. timopheevii* genome; two introgressions in 'line 842' and five in 'line 842-2'. The segregation for adult plant leaf rust response among 148 F_3 families derived from a cross of 'line 842-2' with 'Skala' indicated the presence of a single dominant gene in 'line 842-2'. However, it may be supposed that 'line 842-2' contains more than one leaf rust resistance gene with minor effect on resistance.

The use of microsatellite markers proved to be efficient for mapping genes in various cereal species, genotyping cultivars, and analyzing hybrid genomes (Collard et al. 2005). Genetic maps of wheat saturated with different types of molecular markers allow for a more precise determination of the translocation regions in hybrids of common wheat containing alien chromosomal translocations as compared to cytogenetical methods. The data on integration of microsatellite markers specific for hexaploid wheat into chromosomal

maps of other cereal species, such as *T. dicoccoides, T. timopheevii* and *S. cereale* are also very important (Korzun et al. 1999; Khlestkina et al. 2004; Salina et al. 2006). Considering previously mapped microsatellite markers, it appears that *LrTt2* gene originates from chromosome 5G in *T. timopheevii*. The microsatellite marker *Xgwm1257* linked with *LrTt2* and amplifying a fragment specific for *T. timopheevii* may be used to transfer the resistance gene from the introgression 'line 842-2' into other wheat cultivars, however, due to loose linkage rust response tests would also be needed.

According to the literature, the localization of the *T. timopheevii* derived gene *Lr18* on the long arm of chromosome 5B was performed by genetic and cytological techniques (McIntosh et al. 1983, 2008). Considering the origin and chromosomal location it was possible to assume that *LrTt2* may be the same gene or a novel allele of *Lr18*. However, differences in infection type in the seedling test performed under controlled temperature condition indicate that *LrTt2* is probably not the same as *Lr18*. Accordingly, the results of microsatellite genotyping and race specificity tests emphasize the difference of the genetic constitution of 'line 842-2' and 'RL6009' and suppose that *LrTt2* may represent a new locus that has its origin from the 5G chromosome of *T. timopheevii*.

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