Triticum aestivum – Triticum timopheevii Introgression Lines as a Source of Pathogen Resistance Genes

I.N. LEONOVA[1], E.B. BUDASHKINA[1], N.P. KALININA[1], M.S. RÖDER[2], A. BÖRNER[2] and E.A. SALINA[1]

[1]Institute of Cytology and Genetics SB RAS, Novosibirsk, Russia; [2]Leibniz Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany; e-mail: leonova@bionet.nsc.ru

Abstract: A collection of introgression lines was obtained from crosses of common wheat (*Triticum aestivum* L.) cultivars with tetraploid wheat *Triticum timopheevii* (Zhuk.). Evaluation of resistance to fungal diseases revealed the lines with resistance to leaf and stem rusts, powdery mildew, spot blotch, and loose smut, the most widespread in Siberian region of Russia. Localization of the *T. timopheevii* genome fragments by means of microsatellite markers determined higher frequency of substitutions and translocations on chromosomes 1A, 2A, 2B, 5A, 5B and 6B. Molecular mapping of the loci determining leaf rust resistance revealed two independent loci on chromosomes 5B and 2A. The major locus on 5BS.5BL-5GL translocated chromosome accounting 64% of the phenotypic variance of the trait was found to be closely linked to microsatellite markers *Xgwm814* and *Xgwm1257*. The other, minor locus, controlling 11% of the trait was mapped next to *Xgwm312* on chromosome 2A. Microsatellite markers located near these genes may be used for controlling the transfer of valuable traits in new wheat cultivars.

Keywords: introgression lines; leaf rust; microsatellite markers; powdery mildew; stem rust; *T. timopheevii*

Spring wheat is one of the important cereal crop cultivated in West Siberian region of the Russian Federation. Wheat production in West Siberia amounts more than 30% of annual Russia's spring wheat production. The most widespread and harmful diseases in Siberia are leaf rust, powdery mildew, stem rust, spot blotch, leaf blotch, and loose smut. The host resistance is one of the reliable and ecologically safest methods for disease control. It is known that the effectiveness of resistance genes deployed in wheat cultivars can change over the years. Therefore, search for new donors of resistance, including polygenic genotypes, is an urgent task. Many wild relatives of wheat carry high levels of resistance to different diseases. However, the direct transfer of the target genes from the related species into the genome of common wheat is complicated by genome incompatibility and cytological instability of early hybrid generations. Thus, 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 programmes.

Tetraploid wheat *Triticum timopheevii* Zhuk. ($2n$ = 28, genome composition A^tA^tGG) is an excellent sources of disease resistance particularly against rust pathogens. Attempts to use *T. timopheevii* as a source of pathogen resistance genes were undertaken earlier. Up to date, two leaf rust resistance genes (*Lr18* and *Lr50*), three genes for resistance to stem rust (*Sr36*, *Sr37*, *Sr40*)

and three genes for resistance to powdery mildew (*Pm6*, *Pm27*, *Pm37*) were transferred into the common wheat from the *T. timopheevii* genome (McIntosh *et al*. 2008). However, wheats of the Timopheevi group may carry other unknown genes determining resistance to fungal diseases.

At present, characterization and analysis of cereal hybrid genomes is often performed with the use of molecular markers. Among different types of markers (RAPD, RFLP, SSR, ALFP, and SNP), SSR markers, or microsatellites, are the most informative for the analysis of hybrid forms because of higher polymorphism level, codominant inheritance, chromosome specificity and transferability between cultivated and wild species. Microsatellite markers have been effectively used in analysis of genetic diversity of cereals, construction of molecular-genetic maps, as well as for mapping of genes and quantitative trait loci (Plaschke *et al*. 1995; Stachel *et al*. 2000; Landjeva *et al.* 2006; Salina *et al*. 2006).

In present communication, we report the data on creation of the *T. aestivum – T. timopheevii* introgression lines, evaluation of the lines for resistance to fungal diseases at seedling and adult plant stages and detection of loci associated with resistance to leaf rust.

MATERIAL AND METHODS

Plant material. Introgression lines were obtained from the cross between five common wheat cultivars: Saratovskaya 29 (S29), Skala (Sk), Irtishanka 10 (Irt10), Tcelinnaya 20 (Tcel20) and Novosibirskaya 67 (N67) with tetraploid wheat *T. timopheevii* ssp. *viticulosum*. Sterile F_1 hybrids were backcrossed once to initial wheat cultivar with subsequent self-pollination of BC_1F_1 and following generations in the condition of isolation. In the BC_1F_4–BC_1F_7 generations selection was performed for cytologically stable ($2n = 42$) resistant plants, which served as a basis for development of introgression lines.

Evaluation of resistance to fungal pathogens. Resistance to leaf and stem rusts at the seedling stage was tested under greenhouse condition. Seedlings 7–9 day old inoculated with suspension of *P. triticina* and *P. graminis* were incubated at a temperature between 15°C and 25°C with a 14-hour photoperiod, illumination of 10 000–15 000 lx, and 70–80% relative humidity. Infection types (ITs) of seedlings were scored 10 to 14 days after inoculation on a scale 0–4 according to Roelfs *et al*. (1992). Seedling test for powdery mildew resistance was carried out as described by Paderina *et al*. (1995). The adult plant resistance to leaf rust, stem rust, powdery mildew, spot blotch and loose smut was estimated under natural infection with native populations of pathogen prevalent in Russian Federation. Field experiments were performed as described by Zaharenko *et al*. (2000).

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 (*Xgwm*, *Xgdm*, *Xbarc*, and *Xwmc*) previously mapped on the chromosomes of common wheat, were used for genetic mapping (Sourdille *et al*. 2004; Ganal & Röder 2007). Procedures for microsatellite analysis, gel electrophoresis and the protocol for polymerase chain reaction (PCR) were described by 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 maps were constructed using the Mapmaker program version 3.0b with Kosambi mapping function at LOD (log likelihood ratio) ≥ 3.0 (Lander *et al*. 1987). Quantitative trait loci (QTL) were detected using MapManagerQTX version b20 software (Manly *et al*. 2001). Regression analysis was used for finding associations between phenotypic and genotypic data.

RESULTS AND DISCUSSION

In West Siberia leaf rust caused by *Puccinia triticina* Erikss. is a major fungal disease, widespread in all territory of the region. Therefore, the basic accent has been made on creation of lines resistant to leaf rust. The West Siberian population of leaf rust is represented by physiological races overcoming 28 known *Lr* resistance genes. Virulence to *Lr1*, *2c*, *3a*, *3bg*, *10*, *11*, *14a*, *17*, *18*, *20*, *21*, *23*, *32*, *33*, *36*, *39*, *40*, and *B* occurs with higher frequency (72–100%). Much lower frequency (17–66%) was observed for virulence to *Lr2b*, *3ka*, *15*, *16*, *19*, *25*, *26*, *27 + 31*, *44*, and *Lr46*. Adult plant reaction types of the *T. aestivum – T. timopheevii* introgression lines were estimated during 10 years under different weather conditions. On the basis

of the obtained results about 70 lines have been selected with resistance to the native population of leaf rust. Among the lines 65% displayed immune or resistant reaction type, others showed moderate resistance (Table 1). The highest number of the lines with immune or resistant reaction types was registered for the lines obtained on the basis of wheat cultivars Saratovskaya 29 and Irtishanka 10. In addition, all selected lines were tested to a local bulk of urediniospores for reaction at the seedling stage. This survey showed that all the lines resistant to leaf rust at adult plant stage also exhibited resistance at seedling stage.

Under field conditions, diseases can be caused by different pathogens, therefore, it is important to develop varieties possessing resistance to more than one disease. The introgression lines were screened under field condition for resistance to other fungal diseases, widely-distributed in West Siberian region. Among the lines there were found three lines with good resistance level to stem rust, twenty lines resistant to powdery mildew, five lines resistant to spot blotch and 16 lines with loose smut resistance. Three lines obtained on the basis of Saratovskaya 29 cultivar and one line on the basis of cultivar Skala were found to possess complex resistance to various fungal diseases (Table 1).

Molecular analysis of *T. aestivum – T. timopheevii* introgression lines was performed with the help of microsatellite markers. In total, 340 GWM and 10 GDM (Ganal & Röder 2007), 10 BARC (http://www.scabuza.org.research_bio.html) and 8 WMC (Gupta *et al*. 2002) primer pairs mapped to the chromosomes of the *T. aestivum* and *T. timopheevii* genomes were used to estimate polymorphism between parental wheat cultivar and *T. timopheevii*. On average, we used six to eight markers for each of chromosomes 1B, 3B, 4A, 4B, 6A, 7A, 7B, and all chromosomes of the D genome, and 15–22 markers for chromosomes 1A, 2A, 2B, 5A, 5B, and 6B. Each primer pairs revealed 1–4 loci in the five parental common wheat cultivars, 2.5 alleles per locus on the average. Intervarietal polymorphism detected in our study was not very high but polymorphism involving null alleles (absence amplification in the *T. timopheevii* genome) was observed for 70–90% of markers, depending on the genome, the highest polymorphism being found for markers of the A genome. Fourteen out of 46 primer pairs (30%) mapped on the chromosomes of the D genome amplified fragments in *T. timopheevii*. Three of them (gwm608, gwm205, and gdm84) were located to the *T. timopheevii* chromosomes (4G, 5G, and 1G, respectively), the chromosomal localization of the others is unknown thus far (Salina *et al*. 2006). The absence of amplification of microsatellite markers in *T. aestivum – T. timopheevii* introgression lines can be explained as substitutions or translocations, as well as by deletions in chromosomes of the *T. aestivum*. In our study, the absence of PCR products for certain markers of chromosome 1B, which differs from its homologue 1G by a high level of rearrangements (Salina *et al.* 2006), can be considered as deletion at the marker location site on chromosome 1B. This suggestion is supported by the data of Badaeva *et al*. (2000) obtained in analysis of 47 *T. aestivum – T. timopheevii* introgression lines by means of C-banding technique.

To determine the chromosomal location of the *T. timopheevii* genome in the introgression lines, 285 polymorphic markers were used, including those not producing PCR fragments in

Table 1. The number of the *T. aestivum – T. timopheevii* introgression lines resistant to different fungal diseases

Wheat cultivar	Total No.	Disease					
		Leaf rust (*Puccinia triticina*)		Stem rust (*Puccinia graminis*)	Powdery mildew (*Blumeria graminis*)	Spot blotch (*Bipolaris sorokiniana*)	Loose smut (*Ustilago tritici*)
		R	MR				
S29	28	25	3	3	5	3	5
Sk	7	2	5	1	4	1	3
Irt 10	14	10	4	0	5	0	3
Tcel 20	7	3	4	0	3	1	2
N67	12	5	7	0	3	0	3
Σ	68	48	23	4	20	5	16

R – resistant, MR – moderate resistant

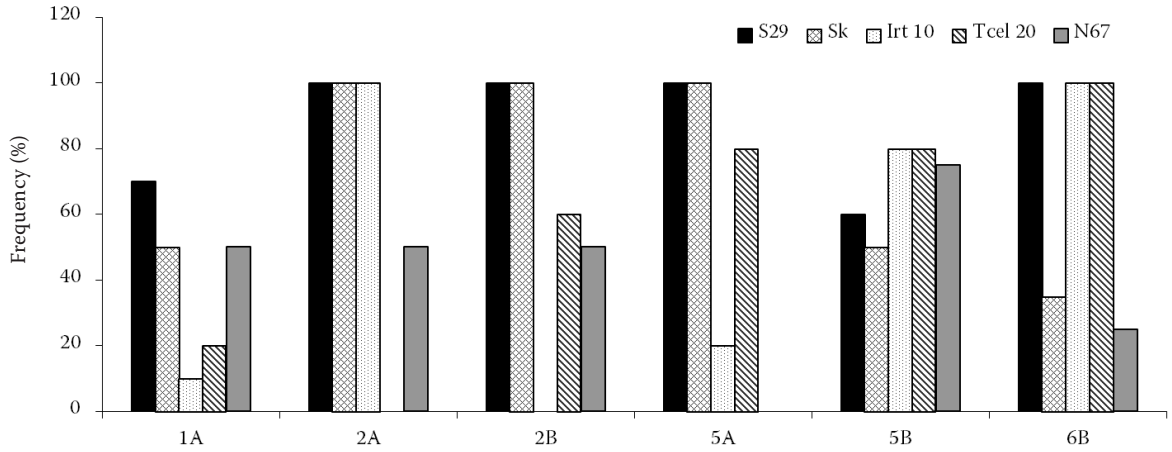

Figure 1. Frequency of substitutions and translocations on chromosomes 1A, 2A, 2B, 5A, 5B, and 6B in *T. aestivum* – *T. timopheevii* introgression lines obtained on the basis of different wheat cultivars

T. timopheevii. On the basis of the obtained data, the chromosomes containing substitutions and translocations, were divided into two groups. The first group included chromosomes 1A, 2A, 2B, 5A, 5B, and 6B in which introgressions occurred with high frequency (Figure 1). The second group included chromosomes 1B, 3A, 3B, 4B, and 7A with lower substitution and translocation level (Table 2). Microsatellite analysis did not reveal substitutions or translocations in chromosomes 4A, 6A, and 7B in all investigated introgression lines. Analysis with microsatellite markers specific to the D genome suggested introgression of *T. timopheevii* fragments into D chromosomes of four lines: the 5D, 6D, and 7D chromosomes of the lines derived from Saratovskaya 29 and the 7D chromosome of the line derived from Tcelinnaya 20. Intervarietal differences were observed both for chromosomal localization of introgression fragments and the number of introgressions. It was shown that the number of the fragments varied from three to eight, the greatest number was found in the lines obtained on the basis of cultivar Saratovskaya 29 (5.3 on the average) followed by Skala (4.8), Tcelinnaya 20 (4.2), Irtishanka (3.7), and Novosibirskaya 67 (3.0).

Three introgression lines (ILs) differing in the number and chromosomal location of the *T. timopheevii* genome fragments were selected for mapping of loci associated with resistance to leaf rust. IL-1 possessed three fragments in chromosomes 2A, 2B, and 5A; IL-2 was found to have five introgressions in chromosomes 1A, 2A, 2B, 5B, and 6B; seven introgressions in chromosomes 1A, 2A, 2B, 5A, 5B, 6B, and 4B were determined in the genome of IL-3. The lines were crossed with susceptible cultivar Skala for developing F_2 mapping populations. The leaf rust reaction was estimated in F_3 populations at the seedling and adult plant stages.

For genotyping individual plants from the F_2 mapping populations, we used 104 polymorphic microsatellite markers of which 37 markers were previously mapped in the *T. timopheevii* genome (Table 3). Linkage groups constructed for chromosomes containing introgressions indicated that the order of the microsatellite loci in introgression lines IL-1, IL-2,

Table 2. Frequency of substitutions and translocations in chromosomes 1B, 3A, 3B, 4A, 4B, 6A, 7A, and 7B in *T. aestivum* – *T. timopheevii* introgression lines (in %)

Cultivar	Chromosome							
	1B	3A	3B	4A	4B	6A	7A	7B
S29	15	10	30	0	25	0	0	0
Sk	10	0	0	0	0	0	0	0
Irt 10	25	0	15	0	10	0	0	0
Tcel 20	10	0	0	0	15	0	0	0
N67	15	0	0	0	0	0	40	0

Table 3. The list of microsatellite markers used for mapping of leaf rust resistance loci in the introgression lines IL-1, IL-2, and IL-3

Chromosome	Marker
1A	gwm33*, 99*, 633*, 691, 752, 905, 1097, 1139*, 1148, barc263*, wmc24*
2A	gwm71, 95, 275, 296, 312, 359, 372*, 382, 497a*, 515, 614*, 636*, 726*, 846, 830, 1036*, 1054a*, 1070*, 1198, 1256*
2B	gwm120, 133a*, 148, 257, 429, 501, 526, 619, 630, 739, 785a*, 972, 1027, 1067*, 1128, 1177*, 1249, 1300*
4B	gwm165, 513, 495, 736a*, 898, 910, 925, 930, 935, 940, 946
5A	gwm126*, 129, 205a*, 291*, 293, 304, 617, 666, 736b, 982*, 995*, 1171
5B	gwm118, 205b*, 234, 371*, 408, 497b*, 499*, 540, 604, 639*, 777, 810, 814*, 880, 1016, 1043, 1054b, 1072, 1246*, 1257*
6B	gwm219, 133c, 518*, 608, 790*, 785b, 816, 889*, 1076, 1199, 1233, 1255

*Markers mapped to the genome of *T. timopheevii* (Salina *et al.* 2006)

and IL-3 is in agreement with that of the chromosome 1A, 2A, 2B, 4B, 5A, 5B, and 6B maps described for the ITMI wheat population (Ganal & Röder 2007; http://wheat.pw.usda.gov).

Chromosomal localization of QTLs associated with leaf rust resistance of IL-2 and IL-3 carrying five and seven introgression fragments, respectively, revealed three loci *QLr.icg-5B*, *QLr.icg-2A* and *QLr.icg-1A* located on chromosomes 5B, 2A, and 1A, respectively. The major locus on chromosome 5B was mapped to the marker interval *Xgwm408-Xgwm1257* and accounted for 64% of the expression of the trait, on the average (Table 4). The locus on chromosome 2A was located in the marker interval *Xgwm71b-Xgwm312*. This locus controlled 11% of the phenotypic expression of the trait and originated from chromosome $2A^t$. The third, minor locus was mapped on the long arm of chromosome 1A, with a maximum near *Xgwm633*. Regression analysis detected three microsatellite markers on chromosome 5B with a high probability linked to the resistance to leaf rust: *Xgwm1072*, *Xgwm814*, and *Xgwm1257*. These markers were used as a background in composite interval mapping (CIM). The results of CIM showed that QTL on chromosome 5B did not affect the expression of the locus mapped to chromosome 2A and substantially inhibited the expression of minor locus on chromosome 1A. This indicates that the loci *QLr.icg-5B* and *QLr.icg-2A* act independently, and they together control the trait by 75%.

The more precise localization of resistance gene on chromosome 2A was performed by means of mapping population developed on the base IL-1 containing three introgression fragments in chromosomes 2A, 2B, and 5A. The leaf rust resistance gene designated as *LrTt1* was found to be located 10 cM away from microsatellite marker *Xgwm312* (Figure 2). The mapping of the major resistance gene

Table 4. Localization of the loci determining the leaf rust resistance of the *T. aestivum* – *T. timopheevii* introgression lines

	Chromosome		
	1A	2A	5B
	flanking markers		
	Xgwm1097-Xgwm633	*Xgwm71b-Xgwm312*	*Xgwm408-Xgwm1257*
R^2	8.0	11.5	64.0
LOD	2.5*	3.5**	17.0**

R^2 – percentage of the variance of the trait associated with quantitative trait loci; LOD – log likelihood ratio; *$P < 0.01$; **$P < 0.001$

LrTt2 on 5B chromosome showed that the gene was localized between markers *Xgwm814* (6.8 cM) and *Xgwm1257* (4.9 cM) (Figure 2). Comparative analysis of PCR fragment sizes for three microsatellite markers (gwm1246, gwm1257, and gwm814) demonstrated that DNA of resistant plants amplified fragments typical for *T. timopheevii* indicating that resistant gene was derived from chromosome 5G.

According to literature, five leaf rust resistance genes *Lr11*, *Lr17*, *Lr37*, *Lr38*, and *Lr45* were located on chromosome 2A. All these genes did not originate from *T. timopheevii* (McIntosh *et al*. 2008). So far, only two leaf rust resistance genes transferred from *T. timopheevii* genome are known. One of them, *Lr18,* was localized on the long arm of chromosome 5B and is associated with a *T. timopheevii* derived telomeric band (Friebe *et al*. 1996). 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-Guedira *et al*. 2003). The QTL responsible for leaf rust resistance of *T. aestivum – T. timopheevii/Ae. tauschii* introgression line was found to be located in the same chromosome region as *Lr50* (Leonova *et al*. 2007). It should be noted that in our introgression lines translocated fragment in chromosome 2B did not possess loci associated with leaf rust resistance. Considering the origin and chromosomal location, it was possible to assume that *LrTt2* may be the same gene or a novel allele of *Lr18*. Molecular analysis of near-isogenic Thatcher line RL6009 containing *Lr18* gene with a set of *Xgwm* markers mapped to chromosome 5B indicated that Thatcher line differed from IL-2 and IL-3 lines both in translocation breakpoint and in the length of the PCR fragments amplifying with microsatellite markers (Leonova *et al*. 2010). In field examination it was demonstrated that introgression lines with *LrTt2* gene exhibited immune or resistant type of reaction to the native population of leaf rust whereas Thatcher line with *Lr18* gene displayed susceptible reaction type. The results of microsatellite genotyping and pathogen resistance test supposed that *LrTt2* may represent a new locus that originates from the 5G chromosome of *T. timopheevii*.

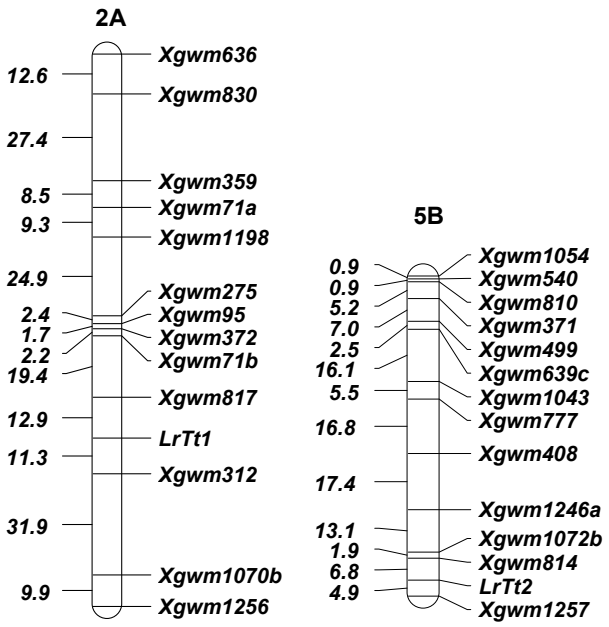

Figure 2. Genetic maps of the *LrTt1* and *LrTt2* regions on chromosomes 2A and 5B; the microsatellite marker names are indicated on the right side; genetic distances are given in centi Morgans on the left side

Thus, the obtained results have shown that selection of the *T. aestivum – T. timopheevii* introgression lines on pathogen resistance after single backcross leads to primary selection of genotypes containing, on average, from three to eight substitutions and translocations. Our results and literature data indicate that subspecies of *T. timopheevii* Zhuk. (ssp. *timopheevii*, ssp. *viticulosum*, ssp. *armeniacum*) may carry leaf rust resistance genes differing both in chromosomal localization in *T. timopheevii* genome and their efficiency against leaf rust flora (Tomar *et al*. 1988; Brown-Guedira *et al.* 2003; McIntosh *et al*. 2008; Leonova *et al*. 2010).

Microsatellite markers were shown to be an efficient tool for both evaluation of intervarietal polymorphism, genotyping of hybrid genomes and localization of gene/QTLs. The application of microsatellite markers allow for a more precise determination of the translocation regions in hybrids of common wheat containing alien chromosomal translocations as compared to cytogenetic methods. *T. aestivum – T. timopheevii* introgression lines can be used for investigation and mapping of genes for pathogen resistance and as a source of resistance genes in breeding programmes. The microsatellite markers closely linked with agronomic valuable loci may be used to transfer the loci from the introgression lines into other wheat cultivars.

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