Potential use of *Aegilops speltoides* Taush genes for durable defense of common wheat from leaf rust in Western Siberia

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Abstract. Common wheat is the main grain crop in Russia. Leaf rust caused by the fungus *Puccinia triticina* Erikss. regularly affects crops and leads to economic damage. To protect wheat, the use of genes of related cereals is promising. The effect of Lr-genes introduced from *Aegilops speltoides* Tausch was estimated in Western Siberia and the Southern Urals in 2013-2018. Plant damage was assessed in the field, and the frequency of virulent clones in *P. triticina* population was detected. The *Lr28* and *LrSp* genes provided plant immunity, and virulent clones were absent in the population. An outbreak of reproduction of a clone virulent to *Lr47* was first recorded in the steppe zone of the Omsk region, bordering with Northern Kazakhstan in 2013, with subsequent migration to the East, North and West. Virulence to *Lr47* disappeared in the Southern Urals in 2018, but is annually detected in Western Siberia with a low frequency. The tendency to overcome the adult *Lr35* gene and the low efficiency of *Lr36* in Western Siberia and the Southern Urals was noted. The breeding of wheat varieties with *Ae. speltoides* genes and their cultivation should take into account the pathogen variability and migration.

1. Introduction

Wheat is one of the most common crops, providing about a quarter of the world's food needs. An important factor limiting the grain production is the disease damage. However, according to the FAO, diseases cause annual losses of more than 20 % of wheat grain worldwide [1]. Integrated pest management, based on the cultivation of resistant varieties, reduces losses and allows to get products that meet high environmental requirements.

Common wheat *Triticum aestivum* L. is affected by leaf, stem and yellow rust diseases, caused by pathogenic fungi. Rust fungi are characterized by gigantic prolificacy and ability to migrate far distances by air [2]. As a result, in the main regions of wheat cultivation (North America, Australia, Russia, China, etc.), huge populations of pathogens are formed on crops [2–4]. In recent decades, there has been an increase in the harmfulness of all wheat rusts [2, 5]. Causative agent of leaf rust *Puccinia triticina* Erikss. is the most plastic among other fungi. Consequently, leaf rust regularly damages crops worldwide, which leads to annual global losses of 5–10 % of wheat grain [3]. In this regard, there is an increased interest in the monitoring of the processes in the populations of rust fungi and breeding varieties with durable resistance to diseases.
To defend the common wheat, the genes of relative cereals are traditionally used. However, alien loci, as a rule, reduce the useful features of the breeding material both due to the close coupling with undesirable genes, and insufficient compensation for the missing fragment of recipient chromosome. Thus, a small set of introgressed genes were included in commercial cultivars. Using DNA markers, it was found that Russian varieties were mostly protected by the alien \textit{Lr9}, \textit{Lr19}, and \textit{Lr26} genes, less often by the \textit{Lr24}, \textit{Lr37} genes, \textit{1AL/1RS} translocation, replaced chromosomes \textit{Lr6Ag1}, \textit{Lr6Ag2} [6].

The diploid species \textit{Aegilops speltoides} Tausch (2n = 14, SS) is considered a promising source of wheat disease resistance genes. This species was one of the parent forms in the evolution of polyploid wheats. Due to the relatedness of the S and B genomes, small translocations can be transferred to the wheat by the recombination, which makes it possible to obtain breeding material with improved traits. A set of identified genes \textit{Lr28, Lr35} (adult plant resistance), \textit{Lr36}, \textit{Lr47}, \textit{Lr51}, \textit{Lr66} [http://www.shigen.nig.ac.jp/wheat/komugi/] and the prospective \textit{LrSp} were transferred from the \textit{Ae. speltoides} to the wheat genome [7].

To determine the strategy for using alien genes in wheat varieties, it is important to have information about their effectiveness in different regions. In the territory of the Southern Urals, Western Siberia and Northern Kazakhstan, wheat crops cover millions ha, forming the “wheat belt”. The populations of leaf pathogens in this zone differ from those existing in other regions [8, 9]. The Asian population of \textit{P. triticina} differs from the European one in virulence and DNA markers [9], but its subpopulations existing in Western Siberia, the Southern Urals and Northern Kazakhstan have significant similarities. Western Siberian population is aggressive, and its clones may have 13–15 virulence genes [10]. In this regard, Western Siberia and the surrounding regions may be considered as a good natural testing ground for estimation of the effect of \textit{Lr}-genes against leaf rust.

The aim of the research was to evaluate the effectiveness of the \textit{Lr28, Lr35, Lr36, Lr47}, and \textit{LrSp} genes introgressed from \textit{Ae. speltoides} in Western Siberia, in connection with the changes in the \textit{P. triticina} population, to determine the prospects for their use in wheat defense.

2. Materials and methods
The materials used for the research were the cultivars and lines of spring common wheat: cv. Thatcher (TS-PI-297016), its near-isogenic lines Tc\textit{Lr28} (RL-6079, translocation T4AS.4AL-7S#2S), Tc\textit{Lr35} (RL-5711, \textit{T2BS-2SS.2SL}), Tc\textit{Lr36} (ER84018, 6BS); cv. Pavon (\textit{Lr47}) (k-44748, 7AS-7S#1S-7AS.7AL); Od35/1 line with gametocide \textit{Gc}-and \textit{LrSp} genes [11]. Adult plant resistance (APR) was investigated using cv. Thatcher (\textit{Lr22b}) and Tc\textit{Lr35} lines. The susceptible cv. Pamyaty Azieva was used as a control in the field and laboratory experiments.

The investigations were carried out in the Omsk region, located in the center of Western Siberia and bordered in the South. with the Republic of Kazakhstan. The Omsk region has the area of 139700 square km, and includes four climate zones: steppe, forest-steppe (south and north), subtaiga and taiga. The climate of the Omsk region is sharply continental, characterized by severe winters, large differences in seasonal and daily temperatures, as well as irregular rainfall. Due to the climate grain crops are concentrated mainly in the steppe and southern forest-steppe (1.171 and 0.653 million ha, respectively), a small part is located in the northern forest-steppe (0.293 million ha). Usually fungal propagules do not overwinter, so the development of the disease starts after the new spores transfer to wheat in the second half of the growing season.

Field experiments were implemented in the southern forest-steppe of Western Siberia (Omsk) in 2013-2018. The samples of wheat were estimated on the natural infectious background in dynamics, starting with the appearance of leaf rust on crops (in the III decade of July – I decade of August). The crop damage was estimated as a percentage [12]. Based on the results of the evaluation, the curves of disease progress on the susceptible cv. Pamyaty Azieva (control) and the cv. Thatcher (\textit{Lr22b}) and Tc\textit{Lr35} with APR were plotted, and the Areas Under Progress Curve of rust (AUPC) were calculated. Then the Resistance Index (RI) was determined as the ratio of the AUPC of the analyzed sample and the control. According to RI the samples were distributed into the classes: 0.10–0.35 – highly resistant; 0.36–0.65 – medium-resistant; 0.66–0.80 – low-resistant, and more than 0.8 – susceptible [13].
An annual monitoring of the *P. triticina* population for virulence to the *Lr28, Lr36, Lr47,* and *LrSp*-genes was implemented with a phytopathological test. Spore samples were collected in 2013-2018 on the commercial wheat crops in eight district centers of the Omsk region. The article presents the data from six districts located in the zones: steppe (Pavlogradka, Sherbakul, Cherlak), southern forest-steppe (Omsk, Moskalenki), northern forest-steppe (Gorkovskoe) (Fig. 1). To support the reliability, a big amount of isolates were analyzed: in 2013 – 412, 2014 – 362, 2015 – 358, 2016 – 392, 2017 – 380, 2018 – 226 no. Additionally, spore samples were collected near Chelyabinsk (Southern Urals) and Novosibirsk. Spore samples were propagated on the 10-day-old seedlings of the cv. Pamyaty Azieva, and monopustule isolates were obtained from them. The presence of avirulence / virulence genes in the isolates was determined by the reaction of plants with the corresponding resistance genes. According to the "gene-for-gene" theory, a resistant plant reaction indicates the presence of dominant avirulent *P* genes in isolates, and a susceptible one – virulent *p* alleles [14].

3. Results

Estimations of leaf rust development on cultivars and lines were performed in Omsk in 2013-2018 (except for 2015) on intensive background of the disease, when susceptible cv. Pamyaty Azieva was damaged up to 70–100 %. In 2015, due to late starting of infection, the samples "avoided" the disease (the damage was lower by 40 %) (table 1). During the research period, the lines Tc*Lr28* and Od 35/1 (*LrSp*) line were immune. The cv. Pavon (*Lr47*) was slightly damaged (5–10 %) in 2013, 2014 and 2017, with single pustules in the remaining years. Damage of the Tc*Lr36* line ranged from low to moderate (10–30 %).

It is known that the genes of adult plant resistance (APR) may reduce the rate of rust development ("slow rusting"). Appearance of APR was studied on the cv. Thatcher (*Lr22b*) and its isogenic line Tc*Lr35*. Previously, it was found that adult *Lr35* is weakly acts at the tillering stage, but increases by the ear stage [15]. In 2013–2018 the final damage to cv. Thatcher was strong, and that to Tc*Lr35* – weak or medium (table 1). To comprise the action of the *Lr22b* and *Lr35* genes, indicators AUCD and Resistance Indexes were analyzed (except for 2018, when the earlier stem rust development partially suppressed the leaf one) (table 2). In all years except for 2015, the AUCD was high due to intense plant damage. The indicators of the cv. Thatcher in all years were close to susceptible control. It shows that the fungus completely negotiated *Lr22b* gene in Western Siberia. On the line Tc*Lr35* leaf rust developed slower, according to the "slow rusting" type. In 2013-2015, Tc*Lr35* was considered highly resistant according to RI (0.14–0.28), but in 2016-2017 it moved to the medium-resistant group (RI = 0.42–0.45).

Table 1. Field estimation of leaf rust damage of common wheat cultivars and lines with resistance genes from *Ae. speltoides* (in percentage) in Western Siberia, 2013–2018

| Samples         | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 |
|-----------------|------|------|------|------|------|------|
| Pamyaty Azieva – control | 100  | 90   | 40   | 90   | 100  | 70   |
| Thatcher (*Lr22b*) | 90   | 80   | 40   | 80   | 90   | 60   |
| Tc*Lr28*        | 0    | 0    | 0    | 0    | 0    | 0    |
| Tc*Lr35*       | 10   | 30   | 10   | 40   | 50   | 30   |
| Tc*Lr36*       | 30   | 10   | 5    | 20   | 20   | 20   |
| Pavon (*Lr47*) | 10   | 5    | 1    | 1    | 5    | 1    |
| Od 35/1 (*LrSp*) | 0    | 0    | 0    | 0    | 0    | 0    |

In addition to field estimations, the fungal population was analyzed for virulence to *Lr*-genes introgressed from *Ae. speltoides*. During the research period virulent isolates to *Lr28* and *LrSp* were not detected. But the dynamic changes in the frequency of virulent isolates to *Lr36* and *Lr47* were observed in spore samples from the districts of the Omsk region. Virulent to *Lr36* clones were
constantly present in the samples from different zones (Fig. 1 a). Big fluctuations in the frequency of *pp36* isolates (from 11 to 47 %) were mentioned in the West of forest-steppe zone (Moskalenki). Since local weather conditions (rainfall, temperature, etc.) can significantly affect the pathogen development the average data for regional population of *P. triticina* is important. The average frequency of isolates virulent to *Lr36* in the Omsk region did not change to 2018 (Fig. 2).

| Samples               | 2013 AUPC | 2014 AUPC | 2015 AUPC | 2016 AUPC | 2017 AUPC |
|-----------------------|-----------|-----------|-----------|-----------|-----------|
| Pamyaty Azieva –      | 1893      | 1588      | 1065      | 1425      |
| control               | 1         | 1         | 1         | 1         |
| Thatcher (Lr22b)      | 1779      | 1340      | 925       | 1283      |
| TcLr35                | 284       | 438       | 506       | 684       |
|                       | 0.15      | 0.28      | 0.14      | 0.45      |

The frequency of the clones virulent to *Lr47* changed significantly during the observed period. In 2013, sharp increase of virulent isolates (68 %) was recorded in the spore samples from the steppe zone (Pavlogradka), bordering the Northern Kazakhstan (Fig. 1 b). In 10-14 days virulent isolates were also identified in the southern and northern forest-steppe (Omsk, Moskalenki, Gorkovskoe), but with a lower frequency (25–32 %), lower frequency was determined in the samples from the East (Cherlak, 5 %). Probably, such distribution was associated with the spore transfer by air flows to the North and North-West, and to a lesser extent to the East. In 2014, the frequencies of clones virulent to *Lr47* near Pavlogradka and Omsk decreased, but they were detected with the same or greater frequency in the West and East. In 2016 and 2017, virulent clones were more frequent in the steppe, and in 2018 – in the southern forest-steppe (Omsk, Moskalenki – 10%). Then there was reduction in the frequency of virulent to isolates to 4.5 –9 % in 2017– 2018 in the Omsk region (Fig. 2).

The frequency of clones virulent to *Lr36* and *Lr47* in *P. triticina* populations in neighboring regions was also analyzed. In the spore samples from the South Urals the frequency of isolates with *pp36* alleles was high in 2013-2017 (41–85 %), and decreased to 17 % in 2018. The maximum frequency of *pp47* isolates was noted in 2013 (32 %), later in 2014-2018 it gradually decreased to complete disappearance (18, 15, 7, 9, 0 % respectively). To assess the possibility of the pathogen to migrate from the Omsk region to the West and East, the frequency of isolates with *pp47* alleles was determined in spore samples collected in 2014 near Chelyabinsk and Novosibirsk (the distance between cities in a straight line is 760 and 610 km, respectively). The frequencies of isolates in the samples from Chelyabinsk and the Omsk region were close, and in those from Novosibirsk they were 2 times higher (table 3). This correlates with an increased frequency of isolates virulent to *Lr47* in the Eastern districts of the Omsk region, bordering the Novosibirsk region (Fig. 1 b). Analysis of the results taking into account cultivars showed that there were no virulent clones on the cv. Duet (*Lr9*). But the frequency of the *pp47* clones on susceptible cultivars from the three regions was significant, especially on the cv. Pamyaty Azieva in the Novosibirsk region (60 %). This confirms the previously revealed selective effect of the varieties on the accumulation of *P. triticina* clones [7, 11].

Thus, the obtained results showed that *P. triticina* populations existing in the territory of Western Siberia and the Southern Urals undergo dynamic changes in virulence to the genes of *Ae. speltoides*. The introgressed genes showed different effect against the leaf rust.

4. Discussion

The increasing harmfulness of wheat rust diseases is considered now as a threat to global food security. International organizations (CIMMYT and Global Rust Research Center – GRRC) and Russian scientific institutions are involved in solving the problem [2, 5, 8]. In this regard, the interest to breed varieties with new genes and support their durable resistance has increased.
The accumulated experience of wheat cultivation in the world has shown that cultivars with single genes, especially of wheat origin, often lose their resistance. Some alien genes may be ineffective before being introduced into cultivars [10]. At the same time, some genes (single or in combinations) maintained durable resistance against leaf (\(Lr34\)) and stem rust of wheat (\(Sr31\)) [4].

**Figure 1.** Frequency of the isolates virulent to \(Lr36\) (a) and \(Lr47\) (b) in spore samples from steppe(I), II southern forest-steppe (II) and northern forest-steppe (III) zones. Districts of the Omsk region: 1 – Pavlogradka, 2 – Cherlak, 3 – Sherbakul, 4 – Moskalenki, 5 – Gorkovskoe.
Figure 2. Frequency of isolates virulent to \( Lr36 \) (1) and \( Lr47 \) (2) in \( P. triticina \) population in the Omsk region.

Table 3. Frequency of isolates virulent to \( Lr47 \) in spore samples from Western Siberia and Southern Urals, 2014

| Collection point | Isolates analyzed | Distribution of isolates on cultivars |
|------------------|-------------------|--------------------------------------|
|                  | in total, no virulent, % | Pamyat Azieva | Omskaya 35 | Duet | in total, no virulent, % | in total, no virulent, % | in total, no virulent, % |
| Omsk             | 258 9.7 56 3.6 60 8.3 22 0 | 120 7.5 100 9.0 28 0 |
| Omsk region      | 362 12.7 120 7.5 100 9.0 28 0 |
| Novosibirsk      | 35 25.7 15 60.0 - - - - |
| Chelyabinsk      | 56 14.3 16 25.0 20 20.0 - - |

However, with large-scale cultivation, even very effective alien genes can be overcome, as happened with the \( Lr9 \) and \( Lr24 \) genes in North America, \( Lr9 \) in Western Siberia, and \( Lr19 \) in the Volga region [3, 11]. But in combination with others, \( Lr19 \), \( Lr24 \), and \( Lr34 \) genes effectively defense cultivars from leaf rust in many regions of the world [4, 5].

Although the species \( Ae. speltoides \) is considered a promising issue of genes, its potential was poor used in breeding, mainly in the USA and Canada [16]. In Russia, the genes \( LrSp \) and \( Lr28 \) from \( Ae. speltoides \) are still included in single spring varieties and lines [5, 7]. The global review of \( P. triticina \) populations showed that virulent to \( Lr28 \) and \( Lr35 \) clones appeared with low frequency only in North American and European \( P. triticina \) populations, but virulence to \( Lr36 \) and \( Lr47 \) was not detected in 2000-2010 [3]. In this regard, it is of interest to evaluate the effectiveness of \( Ae. speltoides \) genes against the vast Asian population of \( P. triticina \). The presented results show that in 2013-2018 a stable high resistance to leaf rust in the field was determined by the \( Lr28 \) and \( LrSp \) genes, but the efficiency of \( Lr47 \) was changed. First time an outbreak of clones virulent to \( Lr47 \) was detected on the border with Northern Kazakhstan in 2013. Judging by the frequency of isolates, there was a gradual spread of spores to the West Siberia and the Southern Urals. Later in the Urals population virulent to \( Lr47 \) clones disappeared, but in the Omsk population they were detected annually with a low frequency, although \( Lr47 \) was not used in regional cultivars [6].

The durable absence of virulent to \( Lr28 \) clones worldwide indicates that \( p28 \) allele sharply reduces the viability of pathogen. It is possible, \( LrSp \) gene will have the same effect. The gradual decrease in the frequency of virulent to \( Lr47 \) clones in Western Siberia shows that \( p47 \) allele significantly reduces the fungal fitness, but not to a lethal level. Probably, virulent clones overwinter in mild conditions in the Kazakhstan, and then enter the Omsk region annually. This process is important to consider, since under favorable conditions the pathogen can damage varieties with the \( Lr47 \) gene. In contrast, high frequency of virulent to \( Lr36 \) clones in populations of Western Siberia and the Southern Urals shows that \( p36 \) allele does not reduce fungal fitness.

For stable protection of cultivars from leaf rust, it is considered promising to use adult resistance genes, which is confirmed by the results of the CIMMYT. However, with time, some APR-genes
(Lr12, Lr13 and Lr37) were overcome, but Lr34 and Lr35 stay effective worldwide [3, 4]. Previously, the high efficiency of the Lr35 was showed in Siberia in 2005-2008 [15]. However, in 2016-2017, the trend to overcome Lr35 gene was shown. Further observations are needed to make a definitive conclusion about its effectiveness.

Thus, among the five studied genes introgressed from Ae. speltoides, only two (Lr28, LrSp) showed stable action, the effectiveness of Lr47 and Lr35 varied, and Lr36 was low effective in the region. Previously, it was also shown that in Western Siberia P. triticina overcame unidentified genes from Ae. speltoides in the L-500, Od, and ANK lines [11]. These results show that the coevolution of P. triticina with cereals occurs ahead of the wheat breeding. On the example of the North Caucasus region, it was shown that stable phytopathological environment is possible to support due to mosaic placement of varieties with different genes. Even poorly effective resistance genes can be used to create heterogeneity [16]. Based on this experience, the known and unidentified Ae. speltoides genes may be used in various combinations in breeding programs for Russia. However, planting of wheat varieties in regions should take into account the variability of P. triticina and its migrations.

5. Conclusion
In general, in the Asian population of P. triticina the changes in virulence to Ae. speltoides genes were determined. The genes introgressed from Ae. speltoides showed different effectiveness against leaf rust in Western Siberia and the Southern Urals. Three genes are promising for breeding: Lr28, LrSp and Lr47. It was noted the tendency to decrease the effectiveness of the adult resistance gene Lr35. The Lr47 and Lr35 genes preferably should be used in gene combinations. This information is important when breeding wheat for leaf rust resistance in Russia. Due to the possibility of long-distance migration of P. triticina, it is necessary to coordinate programs implemented in Russian and Kazakh breeding centers, and to create effective cultivar mosaics based on Ae. speltoides genes in neighboring regions.

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