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GENETIC STRUCTURE OF REGIONAL POPULATIONS OF *Mycosphaerella graminicola* (*Septoria tritici*), THE SEPTORIA LEAF BLOTCH AGENT OF WHEAT

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Abstract

Mycosphaerella graminicola (anamorph *Septoria tritici*), the causal agent of septoria tritici blotch (STB) of wheat, is dominating species in *Septoria/Stagonospora* complex on crops in the main grain-producing areas of Russia. Resistance to STB may be either quantitative (horizomtal) or isolate-specific (vertical). At present 17 genes for resistance have been identified (*Stb1-Stb17*). The gen-for-gen interaction in the «wheat—*M. graminicola*» pathosystem has been demonstrated by genetic analysis; therefore, the aviability of resistance genes in the host proposes the existence of specific virulence genes in the pathogen. The relative frequency of virulence genes within a geographic region may be calculated as a fraction of the isolates expressing this virulence genes from the overall number of isolates used in the study. The purpose of the present study was to estimate the virulence genes in populations of *M. graminicola* from different geographic regions of Russia on the basis of a gen-for-gen relationship, using the cultivars with known resistance genes, i.e. Bulgaria 88 (*Stb1*), Oasis (*Stb1*), Veranopolis (*Stb2*), Israel 493 (*Stb3*), Tadinia (*Stb4*), CS/Synthetic 7D (*Stb5*), Flame (*Stb6*), Estanzuela Federal (*Stb7*), W7984 (*Stb8*). A total of 47 isolates from the North-Caucasian region, 66 isolates from the Central-Chernozem region, 29 isolates from the Volga region, 64 isolates from the Central region, and 34 isolates from the North-West region were tested under greenhouse and grows chamber conditions**.** The virulence was estimated on seedlings at two-leaf stage, using two parameters, the infection degree of plants and sporulation of fungus in vivo. The effectiveness of *Stb*-genes to each regional population of *M. graminicola* was revealed on the basis of the frequency of virulence genes. The regional populations of *M. graminicola* differed in virulence genotype, spectrum and frequency of virulence genes. The populations from south zone (the North-Caucasian, the Central-Chernozem and the Volga regions) are more virulent in comparison with the central and the north-west populations. For example, 19.2 % of isolates from the north-caucasian population and 6.0 % of isolates from the central-chernozem population have no virulence genes, while in the central and north-west populations — 42.2 % and 44.1 %, respectively. Isolates from the Volga population of *M. graminicola* had most various combinations of virulence genes. High frequency of virulence to genes *Stb1*, *Stb5* and *Stb7* was revealed in all populations. The genes *Stb2*, *Stb3*, *Stb4* have considerable effectiveness to the central, the central-chernozem and the north-west populations of *M. graminicola*, however it distinctly reduced concerning isolates from the North-Caucasian and the Volga regions. The genes *Stb6* and *Stb8* were highly effective (*Stb8* — absolutely effective) to all investigated Russian populations of *M. graminicola* and may be recommended for using in selection as sources of resistance to STB.

Keywords: *Mycosphaerella graminicola,* population, isolate, virulence genes, frequency, effectiveness of *Stb*-genes

Septoria tritici blotch (STB) agent, *Mycosphaerella graminicola* (anamorph of *Septoria tritici*), is dominating species in *Septoria/Stagonospora* complex on crops in the main grain-producing areas of Russia (North Caucasian and Central Chernozem economic regions). Furthermore, the pathogen is common in central Russia and in southern Volga region, reaching 40-50 % of species composition.

The species also presents in North-West region, Kaliningrad region, as well as Western and Eastern Siberia.

Knowledge of genetic structure of pathogen populations, virulence gene frequency, spatial distribution and dynamics, as well as the efficiency of resistance genes are considered obligatory conditions of successful breeding for disease resistance. As compared to other diseases (rust, mildew, etc.), genetic basis of resistance against Septoria blight is less well understood. Furthermore, there are two types of interaction in wheat—*M. graminicola* system, i.e. resistance to STB may be either quantitative (horizontal) or isolate-specific (vertical). Both types are important for pathosystem.

Specificity of interaction between *M. graminicola* and wheat was firstly proved by Z. Eyal et al. [1, 2]. They analyzed many individual combinations «cultivar × isolate» and suggested that there are 28 complementary genes. Existence of interacting gene pairs was confirmed by the results of other studies using 80 isolates and 47 cultivars [3]. The gene-for-gene interaction was finally proved by molecular genetic studies of host and pathogen. This fact precluded all doubts against the interaction regarding to at least some known resistance genes [4-7].

In recent years, 17 main resistance genes against *M. graminicola* (*Stb1-Stb17*) were identified according to the interactions between wheat cultivars and fungus isolates. Experiments all over the world determined chromosomal localization and molecular markers of these genes which are proposed to be used in marker selection [8-14].

According to the gene-for-gene relationship, the existence of resistance genes in the host means the existence of specific virulence genes in the pathogen. Virulence gene frequency in the region can be calculated as a percentage of isolates expressing such genes against total number of the isolates found [2]. It also allows determining efficiency of *Stb* genes which is of great importance for breeding, as introduction of certain *Stb* gene will not cause effective resistance if the pathogen population is virulent to the cultivar with this gene. More specifically, French studies of 11 cultivars with known resistance genes and monopycnidial isolates from 5 regions of the country revealed that many *Stb* genes was ineffective against most French *M. graminicola* isolates [15]. Nevertheless, efficiency of some *Stb* genes is confirmed by the world practice. The gene *Stb1* introduced in winter wheat cultivars Oasis and Sullivan retained its effectiveness in Indiana and neighboring states for more than 25 years [8]. Spring wheat cultivar Tadinia has one dominant resistant gene *Stb4* used to control *S. tritici* in California for 30 years [9]. The gene *Stb6* is used as a source of resistance against STB worldwide [16]. However, there is lack of information about *Stb* gene effectiveness against Russian pathogen populations. There are only data obtained by Yu.V. Zeleneva [17] who studied isolated wheat leaves and found that the genes *Stb1*, *Stb4*, *Stb5* were most effective and the genes *Stb2*, *Stb3* were less effective against *M. graminicola* isolates from Central-Chernozem region.

Heretofore, there is no consistent methodology of assessment and differentiation between resistance and susceptibility. It is known that there is no immunity (complete resistance) against *M. graminicola* because necroses and/or pycnidia always present [18, 19]. Genetic base of STB resistance can manifest itself as a decreased lesion area and reduced fungus fertility. These parameters are controlled by different genes and they are both important for disease assessment [3]. Fungus fertility is usually evaluated by pycnidia number. Plant response is classified from almost immune (little necrosis without pycnidia) to very susceptible (large confluent spots and numerous pycnidia) [5, 20-22]. However, visual assessment of pycnidia size, especially using a point scale, is very subjective. And then, number of spores per pycnidium in susceptible cultivars was stated to be

2.0-2.5 times higher than in resistant ones [23]. Due to this fact, spore counting in Goryaev chamber is proposed to determine sporulation of fungus in vivo [24].

The purpose of our study was to estimate the virulence genes in populations of *Mycosphaerella graminicola* from different regions of Russia on the basis of a gene-for-gene relationship, using the cultivars with known resistance genes. This information will allow determining *Stb* gene efficiency, their functional activity in the territory of Russia and feasibility of their use in breeding programs as potential sources of STB resistance.

Technique. Infected plants were collected during crop examination in 2009-2015 vegetation period according to the standard method [25]. Pure culture of monosporous isolates of *Mycosphaerella graminicola* were obtained using streak technique [26]. Pieces of infected tissue with fungal pycnidia were rinsed under running water, then in several portions of sterile distilled water and then placed in sterile Petri plate onto specimen glass in drop of sterile water. Few minutes after, obtained suspension was transferred on potato glucose nutrient agar by inoculation loop. After 7-8 days of incubation at 20-25 °C, single colonies from the same conidium were separated to other plates. Isolate stability was monitored during three successive reinoculations of 10-day colonies on fresh nutrient medium. Cultural and morphologic characteristics of isolates were evaluated on day 30 after inoculation. Structural characteristics, diameter and color of the colonies were registered. Isolates from different morphologic groups with stable cultural and morphologic characteristics were chosen from a viewpoint of more complete covering of intraspecific variation in populations.

Monogenic cultivars with known resistance genes, the Bulgaria 88 (*Stb1*), Oasis (*Stb1*), Veranopolis (*Stb2*), Israel 493 (*Stb3*), Tadinia (*Stb4*), CS/Synthetic 7D (*Stb5*), Flame (*Stb6*), Estanzuela Federal (*Stb7*), and W7984 (*Stb8*), were used for tests. Studies were performed in greenhouse and growth chamber. The plants were grown in 400 cm^3 pots (10 plants per pot) up to fully unwrapped leaf 2. Fungal inoculum was cultivated on plates with potato glucose agar for 4-5 days at room temperature without additional lighting. Plants were infected with individual isolates by spraying spore suspension (1×10^7 spores/ml, 100 ml/m^2). A drop of Tween 20 detergent was added to suspension before application. After inoculation, the plants were placed into wet chamber for 48 hours at the temperature of 20-25 °C and then grown in growth chamber or box at 18-20 °C/22-24 °C (night/day), relative air humidity of 70-80 %, 16-hour photoperiod, and illumination of about 15000 lx.

Plant damage was evaluated 20 days after the inoculation by the method developed in All-Russian Research Institute of Phytopathology, using degree of plant infection and fungus in vivo sporulation as main parameters [24, 27]. Plant infection was determined visually by percentage of affected area of the leaves 1 and 2. In order to determine the sporulation, relevant leaves were cut off and placed for 3-4 hours in laboratory glasses with accurately measured amount of water. Then number of spores in suspension was counted using Goryaev chamber and the number of spores per relevant leaf (N) was calculated as $N = 2500 MV/n$, where M is the number of spores in 100 large squares of Goryaev chamber; V is amount of water in the glass, ml; n is the number of leaves in the sample; 2500 is the coefficient derived experimentally. The degree of plant infection was differentiated as low (up to 20 % of leaf area affected in average), medium (21-50 %), or high (more than 50 %). By sporulation intensity, isolates were differentiated as low-sporulating (up to 100 thousand spores/leaf), medium-sporulating (100-200 thousand spores/leaf) or high-sporulating (more than 200 thousand spores/leaf). By combination of these two parameters, isolates were differentiated into three groups: group I — low-virulent, group II — medium-virulent, group

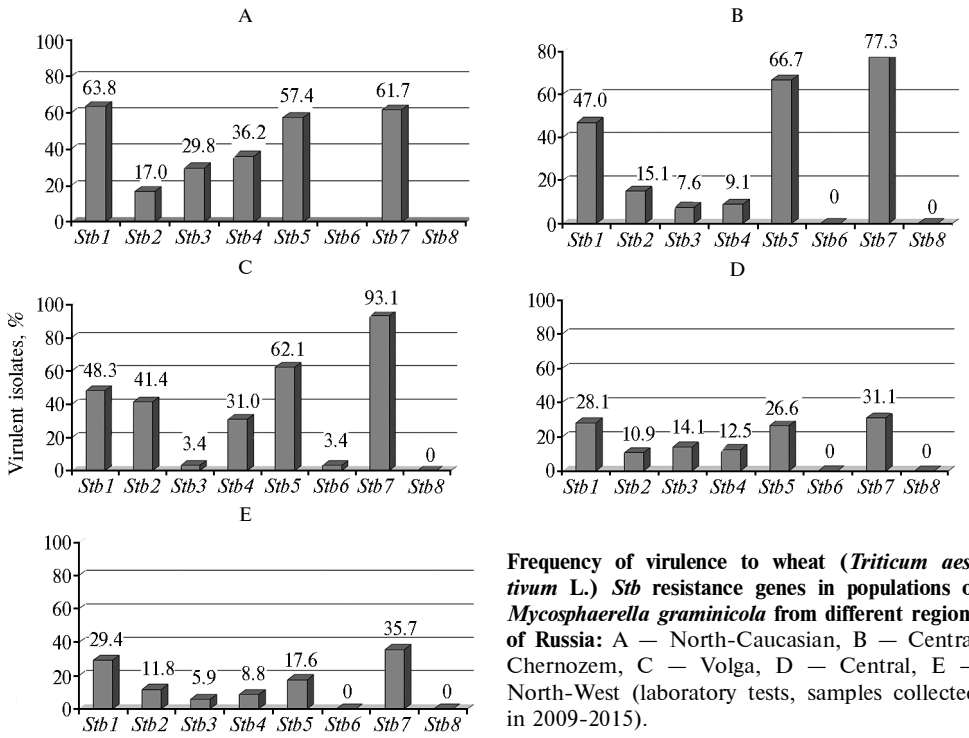
III — high-virulent.

The frequency and a set of virulence genes in the population, along with *Stb* gene effectiveness were assessed by percentage of virulent isolates among total tested ones. *Stb* genes were differentiated as effective if cultivars were susceptible to 0-20 % isolates, medium-effective when susceptible to 21-50 % isolates, and non-effective when susceptible to more than 50 % isolates.

Results. The following combinations of sporulation intensity and the degree of plant infection indicated virulence groups (Table 1). Isolates of group I was considered avirulent while isolates of groups II and III were considered to have the virulence gene.

1. Parameters to differentiate *Mycosphaerella graminicola* isolates into virulence groups with due regard to sporulation and infection development in the wheat plants (*Triticum aestivum* L.) in laboratory tests

Mean degree of plant infection, %	Sporulation intensity, thousand spores per leaf		
	low (up to 100)	medium (100-200)	high (more than 200)
Low (up to 20)	I	I	II
Medium (21-50)	I	II	III
High (51-100)	II	III	III



Frequency of virulence to wheat (*Triticum aestivum* L.) *Stb* resistance genes in populations of *Mycosphaerella graminicola* from different regions of Russia: A — North-Caucasian, B — Central Chernozem, C — Volga, D — Central, E — North-West (laboratory tests, samples collected in 2009-2015).

A total of 47 isolates from the North-Caucasian region (14 from North Ossetia, 19 from Stavropol Territory, 13 from Krasnodar Territory, 1 from Chechnya), 66 isolates from the Central-Chernozem region (26 grom Voronezh region, 10 from Tambov region, 10 from Lipetsk region, 12 from Kursk region, 8 from Belgorod region), 29 isolates from the Volga region (9 from Saratov region and 20 from Volgograd region), 64 isolates from the Central region (59 from Moscow region, 3 from Tula region, 1 from Bryansk region, 1 from Ryazan region), and 34 isolates from the North-West region (6 from Leningrad region, 9 from Pskov region, 19 from Novgorod region) were tested in order to determine genetic structure of *M. graminicola* populations. All isolates were tested on eight cultivars with monogenic resistance except those from north-cau-

casian population which were tested on six cultivars because we have not the cultivars with genes *Stb6* and *Stb8* at that time.

We have revealed the virulence to resistance genes *Stb1*, *Stb2*, *Stb3*, *Stb4*, *Stb5* and *Stb7* with the frequency which varied significantly in all the populations of *M. graminicola* (Fig.).

North-caucasian population demonstrated different virulence genotypes, i.e. isolates had different combinations of relevant genes. A total of 55.3 % of the isolates had wide virulence spectrum (3-6 monogenic cultivars affected), 25.5 % isolates had 1-2 virulence genes, and 19.2 % isolates had no virulence genes. The cultivars with resistance genes *Stb1*, *Stb5*, and *Stb7* were affected most commonly (by 57.4-63.8 % isolates). The cultivars with the genes *Stb2*, *Stb3*, and *Stb4* were affected more rarely, being susceptible to 17.0-36.2 % isolates.

A total of 50 % isolates from central-chernozem population had only 1-2 virulence genes, in 43.9 % isolates the virulence was wider, and 6.0 % isolates had no virulence genes. The cultivars with resistance genes *Stb1*, *Stb5*, and *Stb7* were affected most commonly (47.0-77.3 % of virulent isolates). The cultivars with the genes *Stb2*, *Stb3*, and *Stb4* were resistant against most isolates (virulence frequency was 7.6-15.1 %). There were no virulence to the resistance genes *Stb6* and *Stb8*.

Isolates from the Volga population of *M. graminicola* had most various combinations of virulence genes. Only one isolate was virulent to all the cultivars (3.4 %), 13.8 % of isolates had one virulence gene. Most isolates had 3-6 virulence genes (65.5 %), the vast majority (93.1 %) was virulent against the cultivar with the gene *Stb7*. The frequency of virulence to *Stb5* was 62.1 %, while that to *Stb1*, *Stb2* and *Stb4* was 31.0-48.3 %. There was low virulence (3.4 %) against *Stb3* and *Stb6*. The cultivar with the gene *Stb8* was resistant against all isolates from this population.

Among isolates from central population, 42.2 % had no virulence genes. Remaining one had mostly 1-2 genes (40.6 %), rarely 3-5 genes (17.2 %). In general, frequency of virulence against *Stb* genes was low, reaching 26.6-31.1 % against *Stb1*, *Stb5*, and *Stb7*, half as much (10.9-14.1 %) against *Stb2*, *Stb3* and *Stb4*. No virulence (0 %) was found against *Stb6* and *Stb8*.

North-west population of *M. graminicola* showed the poorest diversity on virulence genotypes. Most isolates had no virulence genes (44.1 %) or only one virulence genes (32.3 %). The portion of isolates with 3-6 genes was significantly less (14.7 %). Virulence to the resistance genes *Stb1* and *Stb7* was more common (29.4-35.7 %), while that to the genes *Stb2*, *Stb3*, *Stb4*, and *Stb5* was significantly less (5.9-17.6 %). There were no isolates virulent to the genes *Stb6* and *Stb8*.

Therefore, regional populations of *M. graminicola* differed on virulence genotypes, gene sets and frequency. The populations from south zone (the North-Caucasian, the Central-Chernozem and the Volga regions) are more virulent as compared to the central and the north-west populations with avirulent isolates. Furthermore, the populations from south zone demonstrated variety of virulence genotypes and higher number of isolates with wide virulence spectrum (3-6 genes). Such geographic distribution of virulence of *M. graminicola* in Russia indicates that south populations are more aggressive. It can be a reasons of domination of *M. graminicola* in *Septoria/Stagonospora* complex on crops in southern Russia.

In all *M. graminicola* populations, higher frequency of virulence to the cultivars with the resistance genes *Stb1*, *Stb5*, and *Stb7* was observed indicating these *Stb* genes to be worst effective (Table 2). Plant response was usually manifested as necrotic spots on leaves with large affected area and pycnidia with

medium and high sporulation. The genes *Stb2*, *Stb3*, *Stb4* demonstrated considerable effectiveness against central, central-chernozem and north-west *M. graminicola* populations, being, however, distinctly less effective against isolates from the North-Caucasian and the Volga regions. The gene *Stb6* was highly effective against all five populations of *M. graminicola*. Only Volga population demonstrated virulence to the cultivar with this gene (at a low frequency of 3.4 %). The gene *Stb8* was absolutely effective against all tested isolates. The plants rarely had seeable signs of infection, and sporulation was absent or much reduced.

2. Effectiveness of wheat (*Triticum aestivum* L.) *Stb* genes against regional Russian populations of *Mycosphaerella graminicola* (laboratory tests, samples collected in 2009-2015)

Region	Stb gene effectiveness (by percentage of virulent isolates)		
	effective (< 20 %)	medium-effective (20-50 %)	non-effective (> 50 %)
North-Caucasian	*Stb2*	*Stb3, Stb4*	*Stb1, Stb5, Stb7*
Central-Chernozem	*Stb2, Stb3, Stb4, Stb6, Stb8*	*Stb1*	*Stb5, Stb7*
Volga	*Stb3, Stb6, Stb8*	*Stb1, Stb2, Stb4*	*Stb5, Stb7*
Central	*Stb2, Stb3, Stb4, Stb6, Stb8*	*Stb1, Stb5, Stb7*	Absent
North-West	*Stb2, Stb3, Stb4, Stb5, Stb6, Stb8*	*Stb1, Stb7*	Absent

Thus, our study showed that 5 of 8 known wheat resistance genes (*Stb1-Stb5*) were functionally limited in natural populations of *Mycosphaerella graminicola* in Russia, and efficiency of the gene *Stb7* was not confirmed in all tested populations. Cultivars with the genes *Stb6* and *Stb8* were identified as potential sources of resistance to Septoria tritici blotch. They may be recommended for using in breeding and genetic programs focused on creation of wheat with resistance against *M. graminicola* in the Russian Federation.

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