Principal approaches and achievements in studying race composition of wheat stem rust

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Wheat stem rust caused by the *biotrophic fungus Puccinia graminis* f. sp. *tritici* is a dangerous disease that seriously damages the economics in many countries of the world. The review contains information about epidemics of wheat stem rust and causes of their emergence worldwide. Recently wheat stem rust epidemics have been recorded in the northern regions of Kazakhstan and on the territories adjacent to Omsk Region of Russia. It has been shown that severe wheat stem rust epidemics occur mainly due to the emergence of new virulent races of the disease agent and to growing susceptible wheat cultivars. New methods of studying the race composition of the fungus are described as well as the use of the previous and current differential sets for race determination of *P. graminis* f. sp. *tritici*. The results of developing molecular markers and assessing their effectiveness in studying stem rust races are presented. Wheat stem rust races dominant in major grain-growing countries of the globe and their typical peculiarities are described. The paper contains information on identification of race Ug99 and of its variations including data on areas of their dissemination and on their virulence to *Sr*-resistance genes. The existence and emergence of other races of the agent potentially dangerous for commercially important genes for stem rust resistance is also described. Currently in nature strongly virulent races of *P. graminis* f. sp. *tritici* are circulating with wide geographical coverage and their virulence is absolutely different from the virulence of race Ug99. Historical and modern data on studying the race composition of the pathogen in Kazakhstan are summarized. It is stated that the use of the old standard differential set and an incomplete North American system of race nomenclature in experiments prevents measuring similarity between Kazakhstani races and the worldwide known races of the pathogen. It has been shown that there is a need to continue studies on the intraspecies structure of the disease agent's population in Kazakhstan with the use of the modern differential set, on determination of race composition and ways of emergence of new races potentially dangerous for commercial wheat varieties.

Key words: wheat; stem rust; resistance; race; *Sr* genes; virulence.

HOW TO CITE THIS ARTICLE:
Rsaliyev A.S., Rsaliyev Sh.S. Principal approaches and achievements in studying race composition of wheat stem rust. Vavilovskii Zhurnal Genetiki i Selektsii = Vavilov Journal of Genetics and Breeding. 2018;22(8):967-977. DOI 10.18699/VJ18.439

Received July 18, 2018
Revised October 9, 2018
Accepted October 10, 2018

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Основные подходы и достижения в изучении расового состава стеблевой ржавчины пшеницы

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Стеблевая ржавчина пшеницы, вызываемая биотрофным грибом *Puccinia graminis* f. sp. *tritici*, – опасное заболевание, наносящее серьезный экономический ущерб в большинстве стран мира. В обзоре приведены сведения об эпидемиях стеблевой ржавчины пшеницы и причинах их возникновения в мире. В последние годы отмечаются эпидемии стеблевой ржавчины пшеницы в северных регионах Казахстана и на территориях, сопредельных Омской области России. Установлено, что сильные эпидемии стеблевой ржавчины в основном происходят в связи с появлением новых вирулентных рас возбудителя болезни и возделыванием восприимчивых сортов пшеницы. Рассматриваются методы определения расового состава гриба, в том числе старые и современные наборы сортов-дифференциаторов для определения расовой принадлежности *P. graminis* f. sp. *tritici*. Представлены результаты разработки молекулярных маркеров и оценки эффективности их использования в изучении рас стеблевой ржавчины. Описаны доминирующие расы стеблевой ржавчины пшеницы и их характерные особенности в основных зерносеющих странах мира. Приведены данные по идентификации расы Ug99 и ее вариантов, включая их распространение и вирулентность к сортам с ранее эффективными генами устойчивости *Sr*, и информация о существовании и появлении других высоковирулентных рас *P. graminis* f. sp. *tritici*, отличающихся от расы Ug99 по признаку вирулентности и молекулярным маркерам. Обобщены исторические и современные данные по изучению расового состава патогена в Казахстане. Отмечается, что проведение экспериментов с использованием старого стандартного набора сортов-дифференциаторов и неполного набора североамериканской системы номенклатуры рас не позволяет оценить степень сходства казахстанских рас с известными расами гриба в мире. В Казахстане необходимо продолжить изучение внутривидовой структуры популяции возбудителя болезни с использованием современного набора сортов-дифференциаторов, а также определение расового состава и путей возникновения новых рас, потенциально опасных для коммерческих сортов пшеницы.

Ключевые слова: пшеница; стеблевая ржавчина; устойчивость; раса; гены *Sr*; вирулентность.

Stem (or black) rust caused by *Puccinia graminis* f. sp. *tritici*, an obligate biotrophic fungus, occurs wide where its hosts (wheat or other cereals) grow (Roelfs et al., 1992). Currently because of its scientific and economical significance the stem rust enters the top 10 of the fungal diseases of plants and the pathogen is able to cause the greatest damage in case of an epidemic/epiphytoty (Dean et al., 2012). All over the globe the stem rust occurs mainly in the regions with the continental climate where summer temperatures regularly exceed 25 °C (Singh et al., 2015). The disease caused wheat yield losses in different historical periods in Canada (Peturson, 1958), in South America (German et al., 2007), in the countries of the European continent and Indian subcontinent, in Australia (Park, 2007), South Africa (Pretorius et al., 2007), East Africa (Wanyera et al., 2006) and in China (Roelfs et al., 1992). Severe stem rust epidemics took place in the United States in years 1919, 1920, 1923, 1927, 1935, 1953, 1954 (Knott, 1971). Average losses of wheat yield because of these epidemics were 25.4 % in Minnesota, 28.4 % in North Dakota, and 19.3 % in South Dakota (Singh et al., 2015). It is specified that the epidemics of this disease in the United States have been associated with emergence and spread of stem rust races 56, 15 and 15B that are virulent to widely cultivated wheat varieties Ceres, Kanred (Sr5), Kubanka (Sr9g, c), Arnautka (Sr9d, a), Hope (Sr7b, Sr17) (Knott, 1971). Since 1954 only local epidemics occurred in the USA and in the whole North America (Singh et al., 2015).

Over the last 20 years reasonable worry is caused by spread of the aggressive race of *P. graminis* f. sp. *tritici*, that has been first detected in 1998 in Uganda and named Ug99 (abbreviation from "Uganda 1999") (Pretorius et al., 2000; Singh et al., 2008, 2011). Over the course of several years, it has rapidly captured wheat cultivation areas in the countries of Eastern and Southern Africa, in Zimbabwe, Sudan, Yemen, Iran, and Egypt. The studies have shown that 90 % of commercial varieties being a part of the global wheat gene fund are susceptible to different races of Ug99 lineage and this fact allows considering the pathogen as a major threat to the current world wheat production and to food security (Singh et al., 2011, 2015). Moreover, during last years severe epidemics of stem rust occur in European countries due to emergence of new virulent races of the pathogen different from race Ug99 (Mert et al., 2012; Bhattacharya, 2017; Olivera Firpo, 2017; Lewis et al., 2018).

In Kazakhstan, like in many grain-producing regions of the world, stem rust is a very dangerous disease of wheat that threats food security of the country. Mainly it is spread in the forest-steppe and steppe areas of the northern region. For instance, in 1964 mass epiphytoty of the disease on wheat resulted in the yield loss varying from 20–30 % through 50 % and over (Plakhotnik, 1969; Koishybayev, 2018). In 1967 the stem rust epiphytoty in the northern regions of Kazakhstan and in Western Siberia covered over 5 million hectars of area planted with wheat. The intensity of wheat affection was 70–90 %, and yield loss exceeded 50 % (Plakhotnik, 1969). The epiphytoty was caused by mass proliferation of races 17 and 21 of the pathogen and by high air humidity (Kulikova, Yurchikova, 1971).

Since 1990 till 2005 in Kazakhstan stem rust displayed itself on wheat rather late and spread on small area. Local evolvement of the disease was recorded only in years 2006–2008 (Rsaliyev, 2008; Kokhmetova et al., 2011; Koishybayev, 2018). Particularly, in Kostanai and North-Kazakhstan Regions in 2006–2007 foci with moderate and heavy progress of stem rust on spring wheat were reported. Spread of the disease varied within 20–40 %; on some fields this figure reached 80–100 % (Kokhmetova et al., 2011; Koishybayev, 2018). Races of the stem rust agent isolated in 2006–2007 in Kazakhstan were highly virulent to *Sr*-lines that were previously effective under conditions of the republic (Rsaliyev, 2008, 2011; Rsaliyev et al., 2010).

Recently in the northern regions of Kazakhstan and in the Western Siberia where spring wheat is mainly cultivated stem rust has turned to be one of the major diseases. In 2015 in Kostanai and North-Kazakhstan Regions as well as in adjacent Omsk Region of Russia stem rust epidemic affected over one million hectars of lands under wheat (Lapochkina et al., 2016; Shamanin et al., 2016; Koishybayev, 2018). The situation had repeated both in years 2016 and 2017; in 2016 the pathogen was detected on all the fields surveyed in North-Kazakhstan Region, especially on late-planted wheat crops, and it resulted not only in marked yield reduction but in lower grain quality (Koishybayev, 2018). It has been noted that such a severe epidemic in Western Siberia may evidence either of penetration of highly virulent races of the pathogen to the territory of the Russian Federation or of existence in the region of own aggressive races with wide range of virulence genes (Lapochkina et al., 2016).

So, mass evolvement of wheat stem rust worldwide is promoted both by social-economic changes as a whole and by the other evolution and selection-genetic factors. They include extension of lands under old susceptible wheat varieties, lost resistance of commercial wheat varieties, emergence of new virulent races, poor monitoring of rust populations and so on. Analyzing race composition and monitoring natural *P. graminis* f. sp. *tritici* populations on the basis of their virulence to differential wheat varieties and to the sources of resistance is the most topical task. Change in frequency only of a single virulence gene may cause dramatic consequences such as severe affection of the previously resistant variety by the disease.

Methods for analyzing race composition of wheat stem rust

Current research of race composition of the wheat stem rust includes several steps: (1) collecting rust samples, (2) isolating and reproducing single pustule isolates of the fungus, (3) differentiating races on the basis of virulence and molecular markers, (4) storing urediniospores of races.

Collecting rust samples. Method for sampling affected wheat organs depends on the assigned task. For comparative study of the stem rust populations samples are collected from production fields under commercial wheat varieties in different geographical areas and in the areas where the alternate host of rust grows as well as from wild cereals in nature.

Time of sampling the pathogen populations is very important because the race composition varies depending on vegetation period of plants. Size of sampling also depends on the assigned tasks. For instance, to determine genetic distance between populations at least 30–40 isolates of the fungus are

needed, and over 1000 isolates are necessary to detect races with rare virulence (Mironenko, 2004).

Collection of vegetative organs from plants with the disease symptoms along the diagonal of the field at the certain intervals depending on the size of the field is the most common method. At each point several samples are collected. It is considered, that in absence of original data on the population structure the hierarchical sampling scheme is the best to be used (McDonald, 1997). The essence of the hierarchical sampling of the population lies in marking-out the surveyed field into smaller uniformly distributed plots and in collecting the vegetative material in several uniformly distributed points on each plot (Mironenko, 2004). Examples of the hierarchical sampling of the population are described by McDonald (1997). Each of the collected samples is placed into a special packet with a form to indicate obligatory data: place (region, district, farm and geographical coordinates), wheat variety and sampling date. It should be noted that minimal humidity must be provided in the course of storing the herbarium specimen of the infected plant organ thus preventing loss of germination ability by the spores of the pathogen. The collected urediniospore material should be reproduced as far as possible for a week according to the adequate procedure (Konovalova et al., 1977).

Isolating and reproducing single pustule isolates of the fungus. One of the major steps in studying race composition of stem rust is isolating pure single pustule isolates of the fungus and their reproduction. Isolation of single pustule isolates of rust is associated with a number of issues: choice of substrate varieties, purification of the isolates of the pathogen from spores of other fungus species, choice of methods for inoculation of plants, etc. (Rsaliyev, 2008).

Substrate varieties are wheat varieties for reproduction of the pathogen population, purification from the other pathogens and for isolation of single pustule isolates. They must meet a number of requirements: high susceptibility to the pathogen under study, resistance or low susceptibility to the other rust species, immunity against powdery mildew, easy seed threshing, fast growth of seedlings, wide leaf lamina, weak sensitivity of plants to growing under conditions of low temperature, etc. (Rsaliyev, 2008). Earlier in Kazakhstan the studies were carried out to create and maintain the collection of rust fungi races on cereal crops. Wheat varieties good for biological purification of one rust species from the other one were detected as the result. For instance, wheat varieties K-RIBSP-66400 and 66454 are resistant to yellow rust and susceptible to stem rust, respectively they can be used for purification of stem rust from yellow rust. Universally susceptible varieties are used to reproduce stem rust spores. Maleic hydrazide (MH) in proportion 1 L of 0.1 % MH solution per 220–250 pots was used to slow down growth of plants, to improve their lodging resistance and to raise sporulating ability of the fungus (Rsaliyev, Savinkov, 1998; Rsaliyev, 2008).

Reproductive ability of *P. graminis* f. sp. *tritici* depends on resistance of the host plant. The higher is the resistance and respectively lower the type of infection the smaller is the number of spores produced by the pathogen. One urediniapustule of the stem rust agent produces from 10.000 to 24.000 spores per day at the infection type of 4 points. At the infection type of 2–3 points daily productivity of the pustule is 3.000–12.000 spores and only 100–1.000 spores at type 1 of infection. On one stem of the resistant variety the number of forming spores is 4–10.3 times less than on a stem of a moderately susceptible variety, and 5–12.4 times less than on a stem of a susceptible variety (Sanin et al., 1978).

Methods and techniques of isolating and reproducing single pustule isolates of the wheat stem rust, including care of experimental plants and optimal temperature-time regime during the experiments are described in details in different publications (Konovalova et al., 1977; Jin et al., 2008, 2009; Rsaliyev, 2008; Olivera et al., 2015). Most effective is isolation and reproduction of single pustule isolates of the fungus on a susceptible variety under greenhouse conditions for 2–3 months before their use.

The isolates with spores can be collected from the surface of the host plant onto a piece of smooth dry paper or aluminium foil. After that the spores are dried (20–30 % relative humidity) and stored in a container. There are different types of cyclone collectors for spore collection. With their help one can collect spores both in very small (from a separate uredinia) and in large amounts (Rsaliyev, 2008). Studying race composition of *P. graminis* f. sp. *tritici* is illustrated on Fig. 1.

Storing urediniospores of the fungus. There are different ways of storing spores depending on the requisite storage duration and amount of available spores:

- Stem rust urediniospores can be stored at room temperature for several weeks depending on humidity. Duration of spore storing can be increased via their drying and keeping at 20–30 % relative humidity (Roelfs et al., 1992).
- Freezing. After drying urediniospores can be stored at 5–8 °C for different periods (weeks or months) depending on basic conditions. They may be sealed in a hermetic airproof container and stored in an exiccator (a moist chamber). The spores on a dried stem or leaf may be stored in a fridge for a month, but in this case their relative humidity should not exceed 30 % (Konovalova et al., 1977; Zhapparova, Rsaliyev, 2012).
- Vacuum drying. Vacuum drying of urediniospores in ampoules allows their storing up to 10 years and even longer. The spores are dried under low air pressure (40–50 % vacuum) conditions for 2–2.5 h followed by sealing ampoules with spores in the burner flame. After sealing the ampoules are checked for vacuum, because its absence leads to loss of spore viability. In the course of long-term storage (over 1 year) the ampoules with spores are usually stored at +4…+8 °C (Roelfs et al., 1992). According to Roelfs et al. (1992) vacuum drying ensures spore storing up to 10 years. The major disadvantage of vacuum drying is the fact that at the moment of ampoule sealing micro cracks can be formed allowing humid air into ampoules and it can decrease germinating ability of spores.
- Liquid nitrogen. In many laboratories around the world spores are stored in liquid nitrogen. They are first dried till 20–30 % relative humidity and then sealed into glass ampoules or aluminium foil packets. Prior to usage the stem rust spores are processed with warm (40 °C) water for 5–7 min to interrupt hibernation caused by cold. While working with liquid nitrogen one should follow the standard precaution measures (Loegering et al., 1966).

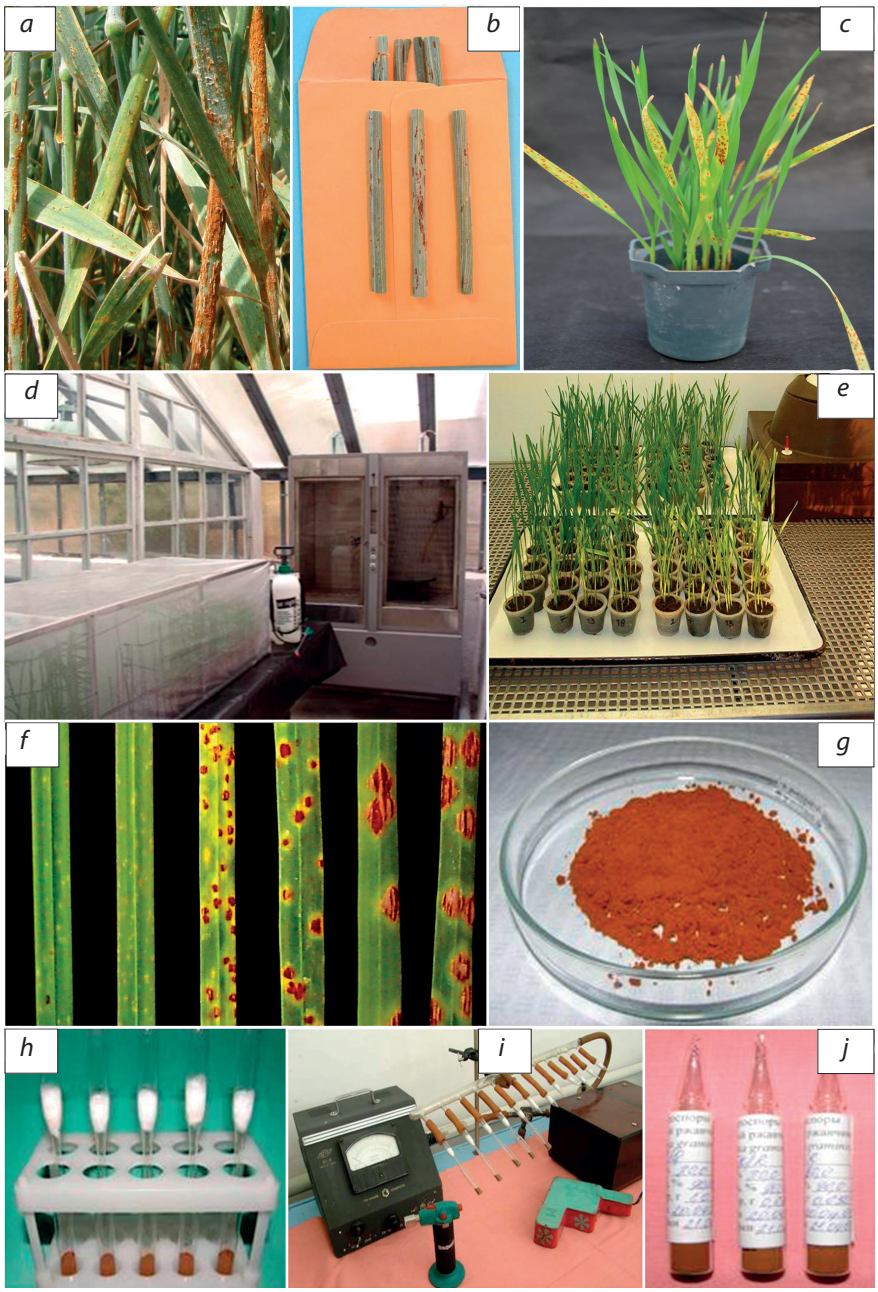

Fig. 1. Order of studying wheat stem rust race composition from collecting the fungal specimens till storing *P. graminis* f. sp. *tritici* spores:

a, the affected wheat variety in the field; *b*, the herbarium specimen of the infected plant organ; *c*, the isolated and purified pathogen on the susceptible wheat variety; *d*, inoculation of the differential varieties with the monopustule fungus isolates; *e*, the differential wheat varieties after inoculation; *f*, various infection types on the differential varieties; *g*, the collected urediniospores of the fungus; *h*, packing spores into ampules; *i*, vacuum drying (in ampules, vacuum unit, vacuummeter, gas burner, d'Arsonval apparatus, Tesla apparatus); *j*, the urediniospores of the stem rust races ready for use.

- Ultralow freezing. The spores neither change their virulent properties for 10 years and longer in the process of their storage at temperatures below –50 °C. They are dried up to 20–30 % relative humidity and then sealed into plastic bags, glass or plastic ampoules (Zhapparova, Rsaliyev, 2012).

Regeneration of spores after storage. After long-term storage urediniospores require additional processing for rehabilitation of their viability. There are two most simple methods of spore regeneration after storage (Konovalova et al., 1977):

a) gradual spore moisturing: the urediniospores are transferred from ampoules into test tubes and finely dispersed on their walls, then the tubes are placed into an exiccator with high relative humidity (100 %) above water, and in 24 h the material is ready for using;
b) thermal treatment of spores: the urediniospores are transferred from ampoules into test tubes and heated in an ultra thermostat at 50 °C for 30 min, then the tubes are transferred into a moist chamber with 100 % relative air humidity and held there during 2–3 hours.

Thus currently there are different ways of storing rust spores. At the same time, knowledge of the minimum and maximum storage periods of urediniospores provides additional information on the viability of rust and helps to organize the work on the differentiation of *P. graminis* f. sp. *tritici* races.

Race differentiation based on virulence and molecular markers. By present time various differential wheat varieties or ways of differentiating *P. graminis* f. sp. *tritici* races have been developed. Stakman and Piemeical were the first to describe in 1917 the races of wheat stem rust. Later the method of differentiation of the pathogen races proposed by Stakman et al. (1962) appeared to be a significant event in the field of population biology of rust fungi. In this method a type of reaction of the differential varieties was the major key of the pathogen race determination. The differential set includes the following wheat varieties: Little Club, Marquis (Sr5, 7b, 18, 19, 20), Reliance (Sr5, 16, 18, 20), Kota (Sr7b, 18, 19, 28), Arnautka (Sr9d, a), Mindum (Sr9d, a, b), Spelmar (Sr9d, a, b), Kubanka (Sr9g, c), Acme (Sr9g, d), Einkorn (Sr21), Vernal (Sr9e), Khapli (Sr7a, 13, 14). In many cases the reduced number of differential wheat varieties, the so called half set consisting of 6 varieties (Marquis, Reliance, Kota, Arnautka, Kubanka and Einkorn) showed identical results. Later the similar differentiation system was developed in Canada (Green, 1981), Australia (Watson, Luig, 1963) and modified in the USA (Roelfs, 1984).

In 1977 "Methodological recommendations on studying race composition of the cereal rust pathogens" assigned for differentiation of cereal rust populations

were adopted in the USSR (Konovalova et al., 1977). The race identification was based on determination of types of infection on differential varieties or tester cultivars. All isolates that similarly affect the wheat varieties of the differential set are identified as one race. Using the differentiation method the population of the species is split into subunits that differ in virulence, the ratio of these subunits in the population is determined and the regularity of its variability is traced (Konovalova et al., 1977). Kazakhstanean researchers Kulikova and Kurbatova (1977b) proposed to add test varieties Lee, Selkirk, Mironovskaya 808 and Bezostaya 1 to the basic set for identification of biotypes within the stem rust races.

Genetic differentiation that use isogenous *Sr* lines as differentiators has appeared to be an improved method of studying race composition of the fungus (Roelfs, Martens, 1988; Knott, 1990). It means that if a new race infects the line containing *Sr5* gene, it will infect all the varieties that possess only this resistance gene, and at high concentration of this race in the populations this gene should not be used in development of new varieties because they will be infected by rust. In 1988 US phytopathologists Roelfs and Martens have developed a unified international system for identification of *P. graminis* f. sp. *tritici* races. The authors have included three sets containing the isogenous lines with separate resistance genes into their system of differentiators. The first set contains *Sr5*, *Sr21*, *Sr9e*, *Sr7b*; the second one: *Sr11*, *Sr6*, *Sr8a*, *Sr9g*; and the third set contains *Sr36*, *Sr9b*, *Sr30*, *Sr17*. According to this system the responses of plants to infection with stem rust are divided into two types: resistant (R) and susceptible (S). On the basis of the plant responses (R and S) each group is assigned a letter code. As a result each race is characterized by an index consisting of three consonant letter of English alphabet (Roelfs, Martens, 1988).

Later Roelfs et al. (1993) included in this system the fourth extra set with the isogenous lines containing *Sr9a*, *Sr9d*, *Sr10* and *SrTmp* for detailed study of the stem rust population. However in 2008 Jin et al. (2008) have found that the differential set used in the North American system of the stem rust race nomenclature fails to identify the unique virulence of race Ug99 to *Sr31*, as well as variations inside race TTKS. Revision of the existing system for identification of *P. graminis* f. sp. *tritici* races resulted in adding four extra genes (*Sr24*, *Sr31*, *Sr38* and *SrMcN*) as a fifth set. The proposed differential set identifies virulence of the new race to *Sr31* and differentiates TTKS race as two separate races: TTKSK and TTKST. With a few exceptions the races virulent to *Sr24*, *Sr31* or *Sr38* rarely occur in the stem rust populations worldwide (Jin et al., 2008).

So, extension of the set by extra isogenous lines resulted in improvement of the process of identification of the stem rust races. The last system of race differentiation (Table 1) currently is the most complete and is used to determine race composition of the wheat stem rust population in many countries of the world.

During the last decade molecular markers are widely used in genetic study of *P. graminis* f. sp. *tritici* populations. Selective-neutral SSR-markers (simple sequence repeats) have been developed for genotyping the pathogen isolates (Visser et al., 2009; Zhong et al., 2009). Molecular polymorphism of the regional populations of *P. graminis* f. sp. *tritici* was studied with the help of selected SSR-markes in Etyhiopia (Admassu et al., 2010) and in South Africa (Visser et al., 2009). The markers of this type were used to assay race Ug99 and its variations (Jin et al., 2009; Visser et al., 2009). However these SSR-markers have not been very useful in differentiating different members of the Ug99 race group (Singh et al., 2015).

Complete genome sequencing of *P. graminis* f. sp. *tritici* isolate in the USA (Duplessis et al., 2011) and reuse of several additional isolates served a powerful tool for genetic study of the fungus and development of new molecular diagnostic methods. Use of data on genome sequence from ta PCR-based diagnostic method was developed for the Ug99 lineage (Szabo, 2012). The method is very specific for assessment of genetic variability in the stem rust populations and is able to discriminate between several of the members of the Ug99 race group (Singh et al., 2015).

For assay of *P. graminis* f. sp. *tritici* isolates the other methodological approach with use of SNP-markers has been developed. For instance, SNP assay for genotyping the fungus isolates in Germany was carried out (Olivera Firpo et al., 2017). However, currently it is possible to detect new aggressive races and to study effectiveness of *Sr* genes only on the basis of information on their virulence.

Ug99 race group

Ug99 lineage comprises several races that differ from each other in one or several virulence/avirulence genes. By present 13 races of Ug99 group have been detected in 13 countries (TTKSK, TTKSF, TTKST, TTTSK, TTKSP, PTKSK, PTKST, TTKSF+, TTKTT, TTKTK, TTHSK, PTKTK, TTHST). It shows that the pathogen continues progressing and expanding geographically (Singh et al., 2015, http://rusttracker.cimmyt.org/?page_id=22). A peculiar feature of the first race Ug99 (TTKSK) is its virulence to varieties and lines with *Sr31* gene inherited from rye (*Secale cereale* L.) as a chromosome translocation 1BL/1RS (Pretorius et al., 2000; Wanyera et al., 2006). *Sr31*, rust resistance gene, inherited from 'Petkus' rye is used worldwide in spring, facultative and winter wheat owing to spread of Aurora, Kavkaz and Lovrin varieties (Zeller, Hsam, 1983). However in many wheat-growing regions wheat resistance to leaf and yellow rust as well as to powdery mildew became ineffective soon after 1BL/1RS translocation realization. Only *Sr31* gene stayed a major component of wheat resistance to stem rust until a virulent race of *P. graminis* f. sp. *tritici* was isolated in Uganda in 1998 (Pretorius et al., 2000).

In 2006 and 2007 new variations of race Ug99 affecting wheat varieties with *Sr24* (TTKST) and *Sr36* (TTTSK) genes were found in Kenya (Jin et al., 2008, 2009). In 2009 race PTKST with combined virulence genes *Sr31* and *Sr24* was identified in South Africa (Pretorius et al., 2010). In each review, an update on the latest known status of the Ug race group and highlights of all major changes since 2010 are provided. Since 2010, specific races of Ug99 group have been identified in an expanded range. Particularly, race TTTSK was detected in three more countries, namely in Ethiopia, Uganda and Ruanda, as well as race PTKST identified in three more countries such as Eritrea, Mozambique and Zimbabwe (Singh et al., 2015). Race TTKSF is one of the most intriguing in Ug99 group as it is avirulent to *Sr31* gene. It has been first identified in South Africa in 2000 (Boshoff et al., 2002) and differs in virulence to genes *Sr8b* and *Sr38* versus the local races.

Table 1. International set of differential wheat varieties for races of *P. graminis* f. sp. *tritici*

Sets	Genes	Differential lines and varieties	Pedigree
1[a]	*Sr5*	ISr5-Ra CI 14159	Thatcher/Chinese Spring
	Sr21	T. monococcum/8*LMPG-6 DK13	Einkorn CI 2433
	Sr9e	Vernstein PI 442914	Little Club//3* Gabo/2* Charter/3/3* Steinwedel/CI 7778
	Sr7b	ISr7b-Ra CI 14165	Hope/Chinese Spring
2[a]	*Sr11*	Yalta PI 155433	Kenya C6402/Pusa4//Dundee
	Sr6	ISr6-Ra CI 14163	Red Egyptian/Chinese Spring
	Sr8a	Mentana W1124 PI 221154	Rieti/Wilhelmina//Akagomughi
	Sr9g	Acme CI 5284	Selection from Kubanka (CI 1516)
3[a]	*Sr36*	W2691SrTt-1 CI 17385	CI 12632 *T. timopheevii*
	Sr9b	Prelude*4/2/Marquis*6/Kenya 117A	Kenya 117A
	Sr30	Festiguay W2706 PI 330957	Festival/Uruguay C10837
	Sr17	Prelude/8*Marquis*2/2/Esp 518/9	Esp 518/9
4[б]	*Sr9a*	ISr9a-Ra CI 14169	Red Egyptian/Chinese Spring
	Sr9d	ISr9d-Ra CI 14177	Hope/Chinese Spring
	Sr10	W2691Sr10 CI 17388	Marquis*4/Egypt NA95/2/2*W2691
	SrTmp	CnsSrTmp	Triumph 64 (CI 13679)/Chinese Spring
5[в]	*Sr24*	LcSr24Ag	Little Club/Agent (CI 13523)
	Sr31	Kavkaz/Federation4	Kavkaz
	Sr38	Trident	Spear*4/VPM (PI 519303)
	SrMcN	McNair 701 (CI 15288)	Unknown

[a] Recommended by (Roelfs, Martens, 1988); [b] (Roelfs et al., 1993); [c] (Jin et al., 2008).

By present time race Ug99 and its variations have identified in Egypt, Ethiopia, Eritrea, Iran, Kenya, Mozambique, Ruanda, South Africa, Sudan, Tanzania, Uganda, Yemen, and Zimbabwe (Singh et al., 2015; http://rusttracker.cimmyt.org/?page_id=22). Among these countries Egypt is the most recent country where race Ug99 has been detected (Singh et al., 2015; Patpour et al., 2016).

In review articles at regular intervals Singh et al. (2008, 2011, 2015) showed the significance, emergence, evolution, and geographical distribution of the racial group Ug99. Each review presented update information on the last known statute of Ug99 group and major instants in alteration of the pathogen since 2010.

The rest widespread races of stem rust

Currently the phytopathologists are actively busy in detecting and monitoring other races dangerous for commercial wheat varieties and it has resulted in identification of various races within wide geographical range. In 2013–2014 a serious epidemic of stem rust occurred in the southern part of Ethiopia in the result of emergence of a new race (TKTTF) on a widely grown wheat variety Digalu (Olivera et al., 2015), and in connection with that the race is sometimes called 'Digalu'. The point is that race TKTTF absolutely differs from Ug99 in genetic structure and has the following virulence formula (avirulent/virulent): *Sr11*, *Sr24*, *Sr31/Sr5*, *Sr6*, *Sr7b*, *Sr8a*, *Sr9a*, *Sr9b*, *Sr9d*, *Sr9e*, *Sr9g*, *Sr10*, *Sr17*, *Sr21*, *Sr30*, *Sr36*, *Sr38*, *SrTmp* and *SrMcN*. Some wheat varieties and lines resistant to race Ug99 variations are susceptible to race TKTTF (Olivera et al., 2015). Race TKTTF and its closely related races have been detected in Turkey (Mert et al., 2012), Germany (Olivera Firpo, 2017), Iran, Lebanon, Ethiopia and Egypt (Singh et al., 2015). German TKTTF isolates phenotypically differ from TKTTF isolated in Ethiopia and Turkey (Olivera Firpo, 2017). This race was last recorded in United Kingdom, so it had been supposed that race TKTTF was disseminated all around Europe with air flows (Lewis et al., 2018).

In 2016 another virulent race TTTTF was identified in Italy (Sicily) on durum wheat (Bhattacharya, 2017). The researchers from the Global Rust Research Center shared a major concern in the warning report that TTTTF could infect not only durum wheat and bread wheat. Race TTTTF has complex virulence, but neither is it associated with race Ug99 and is avirulent to genes *Sr31*, *Sr24* and *Sr25*.

Currently the origin of races TKTTF and TTTTF is unknown and in this connection it is necessary to assay the fungal isolates in Africa, in the Middle East and in the Central Asia (Singh et al., 2015; Bhattacharya, 2017).

On the territory of the former Soviet Union the race composition of wheat stem rust was studied since 1937. Particularly, during two seasons Barmenkov (1939) detected 9 physiological races of the fungus in various regions of the USSR. After that the studies stopped for a long period of time and restarted only in 1959 (Konovalova et al., 1970).

In Kazakhstan during a long time the gene fund of virulence and race composition of stem, yellow and leaf rust is studied by the specialists of the Research Institute for Biological Safety Problems (RIBSP). From 1965 through 2005 at the institute

Table 2. Race composition of the *P. graminis* f. sp. *tritici* population in Kazakhstan during years 1985–2005

Origin of infection (crop, variety, wild cereal)	Reaction on the differential varieties, points												Race
	Little club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Eincorn	Vernal	Khapli	
Soft wheat, Tselinnaya 3S	4	4	0	3	1	1	1	3	3	3	0	1	1
Soft wheat, Saratovskaya 29	4	4	3+	3	4	4	4	3	3	3	1	1	11
Soft wheat, Kazakhstanskaya 4	4	4	4	3–	4	4	4	3–	3–	4	4	1	15
Soft wheat, Omskaya 19, Akmola 2	4	4	0	3	4	4	4	3–	4	3	0–1	0–1	17
Soft wheat, Tselinnaya yubileinaya, Akmola 2	4	4	0	3	4	4	4	4	3	1+	0	1	21
Durum wheat, Bezenchukskaya 139	4	4	0	2	4	4	4	3	3	3	1	0	24
Soft wheat, Akmola 2	4	4	4	4	4	4	4	4	3	1	0–1	0–1	34
Soft wheat, Kazakhstanskaya 17, Akmola 2	4	4	4	4	4	4	4	4	4	0	4	1–	40
Quack grass	4	2+	0	1	4	4	4	4	4	3+	3+	1	53
Soft wheat, Kazakhstanskaya 19	4	4	3–	3–	3–	3–	3–	4–	3+	1+	X	1	77
Russian wild rye	4	1+	3–	1–	3+	3+	3+	3+	3+	3+	3+	1	83
Quack grass	4	2	3+	1	4	4	4	4	3+	1	1	1	95
Slender wheat grass	4	4	3	3–	3+	3+	3+	3+	3+	3	X	1	110
Soft wheat, Tselinnaya 3S, Akmola 2	4	4	0	0;	4–	4–	4–	4–	4	3+	3+	1–	117
Soft wheat, Omskaya 19	4	2–	0	3–	4	4	4	4	4	1–	1–	1–	207
Soft wheat, Kazakhstanskaya 10	4	2	3	0	4	4	4	1	1	3	0	0	228

the old standard differential set was used to identify the stem rust races (Stakman et al., 1962; Konovalova et al., 1977). As the result in 1965 and 1966 the wheat stem rust population in the regions of Kazakhstan and West Siberia has been presented by a great number of races, though races 17, 21, 34, 40, 77 that are characterized by substantial aggressiveness to the zonal varieties of spring wheat have prevailed (Kulikova, Yurchikova, 1971). Studies on survival ability of the stem rust races in mixture on various wheat varieties have shown an ability of races 17 and 21 to force out the rest races in population, and that explains their permanent and everywhere prevalence (Kulikova, Kurbatova, 1977a).

Assay of the spores of the stem rust pathogen collected in 1985–2005 in the grain-growing regions of Kazakhstan has shown relative identity of the race composition of the fungal populations. Races 11, 17, 21, 34 were recorded in the aecidiopopulation. Uredopopulation of the fungus was diverse in its race composition: apart from 4 already mentioned races the following races were differentiated: 1, 15, 24, 40, 53, 77, 83, 95, 110, 117, 207 and 228. Thus on the territory of Kazakhstan during years 1985–2005 16 races of stem rust (Table 2) were differentiated following the old technique (Rsaliyev et al., 2005; Rsaliyev, 2008).

In 1985–2005 races 11, 17, 21 and 34 prevailed on wheat fields in Kazakhstan; sometimes shares of races 40 and 117 increased. In addition, the other races shown in Table 2 occurred in populations of years 1985–1990 and 1991–1995; frequency of their occurrence was within 5 % each (Fig. 2).

Since 2006 races of the wheat stem rust are differentiated in Kazakhstan following the method of Roelfs and Martens (1988) according to which race composition of the pathogen is determined with use of 12 isogenous lines with genes *Sr5*, *Sr21*, *Sr9e*, *Sr7b*, *Sr11*, *Sr6*, *Sr8a*, *Sr9g*, *Sr36*, *Sr9b*, *Sr30* and *Sr17*. In Kazakhstan an extra, the fourth, set of differential wheat varieties (*Sr24*, *Sr25*, *Sr27*, *Sr32*) was added for higher differentiating ability. The results of studies with use of the above method are shown in our previous publications (Rsaliyev, 2008, 2011; Rsaliyev et al., 2010). Particularly in 2006–2007 it has been found that Kazakhstanean population of stem rust contains strongly virulent races dangerous for the commercial wheat varieties in the republic. As it was stated before marked progress of the pathogen was observed in the northern regions of Kazakhstan during that period (Rsaliyev, 2008; Kokhmetova et al., 2011; Koishybayev, 2018). Some

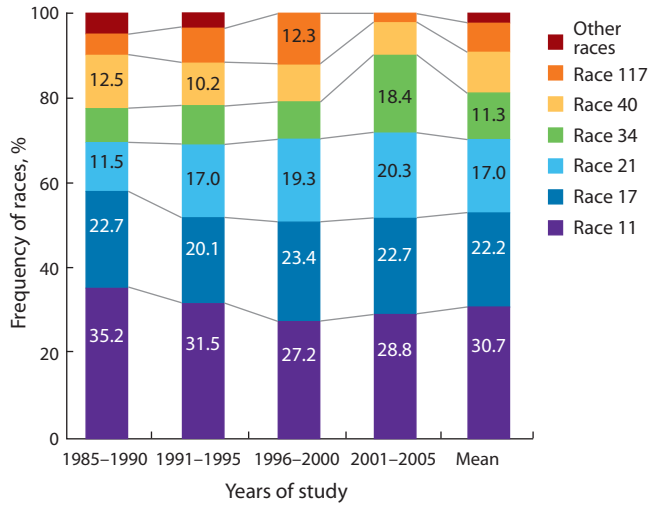

Fig. 2. Occurrence of *P. graminis* f. sp. *tritici* races on wheat in Kazakhstan.

races were virulent to all tested isogenous *Sr*-lines (Rsaliyev, 2008) available in North American nomenclature of *P. graminis* f. sp. *tritici* races (Roelfs, Martens, 1988). The analogous results were obtained by the other researchers; in particular, race TTTT with virulence to all 16 genes-differentiators (*Sr5*, *21*, *9e*, *7b*, *11*, *6*, *8a*, *9g*, *36*, *9b*, *30*, *17*, *9a*, *9d*, *10*, *Tmp*) of wheat stem rust was identified in 2003 in Texas, USA (Jin, 2005).

Skolotneva et al. (2013) have shown that in the central regions of Russia races of the pathogen virulent to lines *Sr – 5*, *21*, *9e*, *7b*, *6*, *8a*, *9g*, *36*, *30*, *9a*, *9d*, *10*, *Tmp*, *38*, *Wld* are frequent. It should be noted that in Kazakhstan till present time the basic isogenous lines (*Sr9a*, *Sr9d*, *Sr10*, *SrTmp*, *Sr31*, *Sr38* and *SrMcN*) that differentiate races Ug99, TKTTF and TTTTF according to Jin et al. (2008) were not used in studying race composition of the fungus (Rsaliyev, 2008, 2011; Rsaliyev et al., 2010). Due to that it is so far impossible to attribute to any group Kazakhstanean races of the fungus or to determine their similarity to the known races of the pathogen (Ug99, TKTTF, TTTTF or any other). To solve this problem and taking into account the deteriorating phytopathological situation associated with stem rust epidemics in major wheat-growing regions of Kazakhstan we initiated the study of the collection and modern isolates of the fungus with use of the latest differential set according to North American nomenclature of *P. graminis* f. sp. *tritici* races (Jin et al., 2008).

By present time the collection of rust fungi has been created in the RIBSP as the result of many years efforts. It contains historical and modern isolates of *P. graminis* f. sp. *tritici* that have been collected at different time from ten regions of Kazakhstan, seven regions of Russia and two regions of Kyrgyzstan. To determine similarity of Kazakhstanean races to new virulent races TKTTF and TTTTF the differential set has been supplemented with lines possessing *Sr13* gene that is absent in North American nomenclature of *P. graminis* f. sp. *tritici* races (Roelfs, Martens, 1988; Roelfs et al., 1993; Jin et al., 2008). *Sr13* gene was initially identified from durum wheat (*Triticum turgidum* ssp. *durum* (Desf.) Husn.), and then introgressed into genome of soft wheat (Knott, 1990). It is localized on chromosome 6AL, originates in Khapli variety (*T. durum*), and its testing line is Khapstein/9*LMPG (Knott, 1990). The gene demonstrates resistance to many races in Ug99 group (types of infection vary within 2–2+) (Jin et al., 2007).

Role of barberry in generation of new *P. graminis* f. sp. *tritici* races

In some countries composition of the fungal populations is studied on barberry species (*Berberis* spp.) that serve as the alternate hosts of the wheat stem rust for sexual recombination resulting in emergence of new virulent races of the pathogen (Jin, 2011; Skolotneva et al., 2013). Some North American races of stem rust, namely races 56, 15B and QCC, were initially found on barberry and afterwards were responsible for large-scale epidemics of the disease (Jin, 2011). However not all barberry species are susceptible to stem rust. As one knows among barberry species identified previously in Southern Africa only *B. holstii* and *B. vulgaris* are susceptible to stem rust (Glen, 2002). Recently in this country two foreign species of barberry (*B. julianae* and *B. aristata*) spreading in the natural ecosystems have been found, but their resistance to the pathogen is not studied yet (Keet et al., 2016).

In Kazakhstan rye and oat forms of the stem rust pathogen occur on the barberry species, and wheat form is utterly rare. Due to that barberry is immaterial here to spread of the infection on wheat fields (Dzhiyembayev et al., 1974). According to (Abiyev, Yesengulov, 1995) out of 10 barberry species growing in Kazakhstan only five demonstrated development of the fungus. At the same time according to observations of Koishybayev (2018) in 1996–2000 in arboretum near Shortandy (Akmola Region) spermogonia and aecia of stem rust developed on the barberry in the 2nd and 3rd decades of May. In spite of weak development of stem rust on the alternate host in 1999 Russian wild rye was severely affected by the disease (up to 50–75 %) (Koishybayev, 2018). Except wheat and barberry the major feeding plants for stem rust are *Hordeum vulgare* L., *Elytrigia repens* L., *E. geniculata* Nevski, *E. intermedia* Nevski, *Elymus sibiricus* L., *El. junceus* L., *Agropyron cristatum* L. (Koishybayev, 2018). So, high infectious potential of the fungus maintained in nature on wild cereals does not eliminate mass manifestation of stem rust under favorable conditions. Regular monitoring of the pathogen's progress on the alternate host (barberry species) is also necessary.

Thus, analysis of the published data evidences the topicality of studying populations of the agent causing stem rust of wheat, mechanisms of variability of the fungus for elaboration of the science-based genetic protection of wheat against the disease. Currently large-scale research is conducted in many countries of the world and the certain progress concerning identification of races of *P. graminis* f. sp. *tritici* has been achieved. New data will allow the researchers of wheat breeding and biotechnological centers to more effectively work towards obtaining forms of wheat resistant to the most virulent races of the pathogen and select the most promising donors of resistance in the wheat breeding process.

Acknowledgements

The work was carried out under financial support of the RK Ministry of Education and Science in the frames of the program of grant financing for years 2018–2020 (grant No. AP05132236) and of the RK Ministry of Agriculture in the frames of the program-target financing for years 2018–2020 (IRN BR06249329).

Conflict of interest

The authors declare no conflict of interest.

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