P L A N T   B R E E D I N G   A N D   S E E D   S C I E N C E
Volume 48 (no. 2/2) 2003

O.V. Solodukhina, V.D. Kobylyanskij

N.I. Vavilov All–Russian Research Institute of Plant Industry 44, Bolshaya Morskaya Str., 190000, St. Petersburg, Russia

PROBLEMS OF WINTER RYE BREEDING FOR RESISTANCE TO LEAF AND STEM RUSTS

ABSTRACT

Since 1967, over *2,500* rye (*Secale cereale* L. and *S. montanum* Guss.) populations have been studied at the N.I.Vavilov Research Institute of Plant Industry in order to determine genetic diversity of the crop with respect to leaf rust (*Puccinia recondita* Rob.) resistance. Plants possessing race–specific resistance to leaf rust were found in 51 accessions (cultivars, landraces and wild species). In 2000, a study of 420 rye accessions revealed stem rust (*Puccinia graminis* Pers. f. sp. *secalis* Erikss. et Henn.) resistant genotypes in 69 of them. Control of leaf rust resistance was found to be dominant monogenic in 44 accessions, and digenic in cultivar Chulpan 2. In some accessions, e.g. Avangard 2, Novozybkovskaya 4–2 and Derzhavinskaya 2, leaf rust resistance of individual plants was determined by one dominant gene, while in other plants of the same accessions it was determined by two dominant genes. In most resistance sources (Sanim, Chernigovskaya 3, Kharkovskaya 55) genetic control of the character is determined by the *Lr4* gene, in Jmmunnaya 1 by *Lr5,* in Chulpan 3 and Immunnaya 4 by *Lr6,* in Novozybkovskaya 4–2 by *Lr7,* and in Lovaszpatonai by *Lr8,* in Yaroslavna 3 by *LriO.* Stem rust resistance is controlled by the dominant gene *Sri.* By pyramiding effective resistance genes two new winter rye cultivars have been bred.

These are Estafeta Tatarstana (1999) and Era (2001) characterized by a high–level resistance to leaf and stem rust, to powdery mildew.

Key words: breeding, genetic resources, rust, *Puccinia graminis*, *Puccinia recondita*, resistance, rye, *Secale*

INTRODUCTION

The problem of rye resistance to rust pathogens has been of interest for breeders, phytopathologists and botanists for the last 150 years (Körnicke, 1865; Körnicke, Werner, 1885; Eriksson, Henning, 1896; Novikov, 1907; Yachevsky, 1909; Vavilov, 1913).

As is known from literature sources, the development of stem and leaf rust in long–stem rye leads to the loss of up to 60% and to 30% of grain yield, respectively (Chumakov, Sidorenko, 1973; Trushko, 1974; Koroleva, 1976).

Communicated by Hartwig H. Geiger

The major problems of rye breeding for rust resistance are the search for and broadening of genetic range of sources and donors of resistance, determination of genetic bases of resistance, development of strategy and methods of breeding cultivars that would possess long–term resistance.

Leaf rust of rye, caused by the fungus *Puccinia recondita* Rob (sin. *Puccinia dispersa* Erikss. et Henn.), is one of the widely spread rye diseases. The problem of resistance to this disease has become more vital due to the production of short–stem rye cultivars. In photosynthesis of short–stem rye, then long–stem rye one the role of leaves are more, then the role of stem, so the cultivation short–stem rye cultivars is associated with the increased harmfulness of all leaf diseases (Kobylyanskii, 1982). Our research showed short–stem rye to have changed its response to the affection by rust pathogens. The grain yield losses from the rust affection increased up to 39% and even up to 60–80% in the case of an early strong epidemic, while yield losses caused by the stem rust development reduced to 35.8% (Kobylyanskii, 1982; Solodukhina, 1985; Solodukhina, Kobylyanskii, 2000).

Growing resistant varieties would be most effective, ecologically safe and economic in protection the crop from the disease.

Kornicke and Werner (1885) for the first time reported the discovery of resistant plants in rye cultivars. Later, many authors noted a higher degree of resistance in cultivars such as Zeelander, Probsteier, Champagner and Johannis–Roggen (Novikov, 1907; Yachevsky, 1909; Vavilov, 1913; Mains, Leighty, 1923). Meanwhile, genotypes resistant to brown rust have been revealed in many populations of wild perennial rye (S. *montanum* subsp. *Kuprjjanovii* (Grossh.) Tzvel.) and in cultivars bred in Russia, Ukraine, Belarus, Poland, Germany, Austria, Hungary and Canada (Kobylyanskii, 1975; Kobylyanskii, Solodukhina, 1996).

Very little is known of genetic control of leaf rust resistance. First reports on dominance of resistance over susceptibility were published by E.B. Mains (1926) and Th. Roemer (1939). Only in 1975–1978 and later similar information was published by other researchers (Kobylyanskii, 1975; Torop, Torop, Tymchenko, Anfinogenov, 1978).

Stem rust of rye caused by *Puccinia graminis* Pers. *f secalis* Erikss. et Henn., occurs in all regions of winter rye cultivation. All species of wheatgrass *(Agropyrum* sp.) and other grasses with a wide distribution in Russia serve as an additional source of infection (Trushko, 1973). According to Eriksson (1902), *P. graminis* populations include numerous host–specific forms capable of affecting rye, barley, wheat and oats.

Strong stem rust attacks may lead to a loss of 50 to 60% of grain yield in long–stem rye (Chumakov, Sidorenko, 1973; Trushko, 1974; Koroleva, 1976).

Körnicke (1865) reported, "all of rye cultivars tested in 1863 were affected by *P. graminis*". The first successful attempt to find rye genotypes possessing resistance to a pathogen population was undertaken by

Mains in 1926. Later, resistant plants were identified in populations of S. *montanum* (Kobylyanskii, 1975).

Plant genotypes with resistance to the Moscow and St.Petersburg populations of stem rust occur at varying frequency in modern cultivars like Jlmen, Orlovsky gibrid, Kharkovskaya 55, Kharkovskaya 60, Kustovka, Kombayninyai, Kazanskaya, Krupnozernaya, Novozybkovskaya 4, Derzhavinskaya 29, Chulpan, Rossul, Alfa, etc. (Solodukhina, Kobylyanskii, 2000).

MATERIALS AND METHODS

The search for rust resistant plants was carried out in 2,920 accessions from the Vavilov Institute of Plant Industry rye collection in 1967–2000. Screening was done under both artificial and natural infection.

Rust resistance in the accessions was evaluated according to the supplemented scale of Mains and Jackson (1926):

Scale	Description
0	– Uredopustules do not form.
0;	– Very small necrotic spots without pustules occur
1	– Very small uredopustules are confined to large necrotic spots. There are necrotic spots without pustules.
2	– Medium–sized uredopustules form on necrotic spots.
3	– Medium–sized uredopustules, no necrosis, chlorosis may occur.
4	– Large uredopustules, no necrosis, chlorosis occurs under unfavorable conditions.
X	– Heterogeneous type. Uredopustules vary in size, chlorosis, necrosis and normal rust pustules without necrosis occur.

To study damage from the disease, F_2 plants from crosses between resistant and susceptible short–stem plants were used (Solodukhina, 1985). Experiment was conducted on artificially infected plants at field conditions. Plants resistant and infected in different degree were compared.

Genetic control of resistance was studied applying the classical principles of Mendelian genetics. Segregation of BC_1 hybrids of backcrosses of resistant and susceptible plants and F_2 crosses obtained by free pollination of plants heterozygous for the resistance gene was analyzed. Dominant genes controlling the resistance were identified with the use of the method formerly proposed by us (Solodukhina, 1994). It involves the following stages:

Stages	Description
1.	Obtaining heterozygotes for the gene studied and a test gene;
2.	Obtaining a diheterozygote by pair wise crossing heterozygotes for the gene studied and the test gene;
3.	Test crosses of the progenies obtained at the second stage.

Whether genes under study were allelic or not was judged from segregation of the hybrid plants obtained at the third stage of the test crosses.

Donors of *Lr* and Sr genes were produced through multiple backcrosses between resistant plants gene sources and susceptible plants highly productive winter rye forms. New population cultivars were bred carrying all the identified *Lr* and, *Sr* genes, as well as other genes controlling disease resistance (mildew, root rots) (Kobylyansky, Solodukhina, 1996).

RESULTS AND DISCUSSION

Leaf rust

A study of over 2500 rye populations showed few cultivar populations to contain resistant plants. In all the cases, resistance was of the heterogeneous type (X). Resistant plants were discovered in 51 accessions (cultivars, local varieties and wild species of rye) (Table 1). In some cases, resistance is observed only at the tillering stage, while in other cases it is maintained throughout the vegetation period and decreases slightly towards the flowering phase.

In all cases resistance strongly limits the development of the leaf rust pathogen.

The identified sources of resistance represent a combination of homozygous and heterozygous genotypes. This makes it difficult to apply classical methods of genetic analysis.

Inheritance of leaf rust resistance was studied at the population level by observing segregating progenies of single–plant crosses (test crosses). Genetic control of the character was studied in 45 sources of resistance. The donor Sanim produced on the basis of cv. Sangaste was the first one in which genetic control of race–specific leaf rust resistance was identified. In all cases, segregation in backcrosses yielded resistant (R) and susceptible (5) plants in a ratio of 1R: 15, indicating monogenic dominant inheritance of the character (Solodukhina, 1994). In the donor Sanim, the Lr4 gene governs resistance to most races of the pathogen leaf rust.

In the resistance sources Wojcieszyckie 2 and Landrace (K– 101 26)–2, an additional dominant gene was observed. It occurred in a small number of resistant genotypes as shown by inheritance studies (Solodukhina, 1994).

Table 1

Frequency of genotypes with qualityv resistance to leaf rust in diploid rye accessions (St.Petersburg, 1967–2000)

Accession	Frequency [%]	Accession	Frequency [%]
	S. rnontan um		
subsp. *kuprijanovii* (K–9584)	18.2	Edelhofer	0.7
Grunschnittroggen	56.4	Lovaszpatonai	0.6
Zarechanskaya zelenoukosnaya	42.5	Ludowe	0.6
Kustovka Landrace	21.6	Abruzzi	0.6
Derzhavinskaya 29	14.4	Wrens Abruzzi	0.6
Chulpan	7.2	Kierschesstahler	0.6
Gotor	4.5	Getera	0.6
Alfa	3.7	Schlagler	0.6
Yantarnaya	2.7	Slavyanskaya	0.5
Talovskaya 12	2.4	Avangard	0.5
Landrace K–10 126	1.9	Chernigovskaya	0.4
Novozybkovskaya 150	1.7	Volzhanka	0.4
Shpanskaya	1.7	Geant de Flandre	0.4
Sangaste	1.6	Braunrostresistenter	0.4
Vetvistaya	1.5	Forrageroklein	0.3
Tevrizskaya	1.5	Dlinnokolosaya	0.3
Baltiiskaya	1.4	Volkhova	0.3
Wojcieszyckie	1.3	Orlovskaya 9	0.2
Yaroslavna	1.2	Kazanskaya 5+6	0.2
Pierre	1.2	LandraceK–11178	0.2
Novozybkovskaya 4	1.2	Orlovsky gibrid 3	0.2
Krupnozernaya	1.0	Kharkovskaya 60	0.2
Krona	1.0	Debrett	0.2
Musketcer	0.9	Benyakonskaya	0.2
Shchorsovka	0.8	Mississipi Abruzzi	0.2
Elbon	0.8		

Resistances found in accessions Avangard 2, Novozybkovskaya 4–2 and Derzhavinskaya 29–2 produced two types results. In some cases, resistance was under dominant monogenic control, while in other cases it was of the dominant digenic. Thus, in different plants resistance may be governed by one, two or even more genes (Kobylyanskii, Solodukhina, 1996).

When identifying genes, in the first place the donor Sanim was tested as the source of the *Lr4* gene. Genetic analyses showed that in most offer sources of resistance (Sanim, Chernigovskaya 3, Kharkovskaya *55)* the character is controlled by the *Lr4* gene. But new genes being non–allelic to *Lr4,* have been found in the following accessions: *Lr5* in Immunnaya 1, *Lr6* in Chulpan and Immunnaya 4, *Lr7* in Novozybkovskaya 4–2, *Lr8* in Lovaszpatonai and *Lr] 0* in Yaroslavna 3.

When studying the effectiveness of the resistance genes, it was found in some cases that plants carrying different *Lr* genes differed in their response to the leaf rust pathogen in the field. Cases were registered when heterozygous and homozygous plants showed similar response to the pathogen in the field. In other cases, the response depended on the allelic status homozygous or heterozygous of the resistance genes (Table 2). Plants of the resistance source Immunnaya 4 (gene *Lr6)* had no difference in their response to the pathogen irrespective of the allelic status. Both heterozygous (Rr) and homozygous (RR) plants were characterized by the response type 0;, 1 throughout the seedling, tillering and stem growth phases. In the grain filling phase, heterogeneous response was observed, i.e. response types 0; 1, 2 and 3 occurred on one and the same plant with the normal fungal pustules (type 3) occupying 10% of the leaf area. It may be supposed that towards the end of the vegetation period the pathogen population accumulates virulent clones against which the *Lr6* gene is of low effectiveness in maturing plants.

Table 2

Effectiveness of genes (Mains and Jackson Scale) for resistance to leaf rust in the homo– and heterozygous state and in different phases of plant development (St. Petersburg, 2000)

Cultivar and *Lr* gene	Allelic status	Plant development phase		
		Seedling	Tillering – stem growth	Grain filling
Immunnaya 4 (*Lr6*)	Rr	0;1	0;1	0;1,2,3(10%)*
Immunnaya 4	RR	0;l	0;1	1,2,3(10%)
Lovaszpatonai 2 (*Lr8*)	Rr	0;3	0;3	0;1,2,3 (20%)
Lovaszpatonai 2	RR	0	0;	0;

* Leaf area, in %, occupied by normally developed fungal pustules with type 3 responses

Plants of another source of resistance, Lovaszpatonai 2 carrying the *Lr8* gene, also in their response to the pathogen depending on their allelic status. Heterozygous (Rr) plants displayed resistance (type X) during all stages of plant development – from

seedling stage to grain filling. At first (seedling from to stem growth) along with the response of high resistance (type 0;), individual normally developed pustules of the pathogen (type 3) were observed. Towards maturity the response types 0;, 1, 2, 3, were observed in plants, and the normally pustules occupied 20% of the leaf area. Plants of accession Lovaszpatonai 2 being, homozygous for any of the resistance genes, dis–

played a very high degree of resistance from germination (type 0) all the way to plant maturity (type 0;).

Different expression of genes which depends on their homo– or heterozygous status in the plant is of importance for selecting affective genes to be used in rye breeding, and for controlling the degree of plants' homozygosity and heterozygosity in a rye population.

Stem rust.

The response short–stem plants under stem rust and leaf infection are different. To determine the loss from the development of stem rust in short–stem rye we estimated weight of 1000 grains (TGW), as a main metric index of damage from rust diseases. (Table 3).

Table 3

Reduction of Thousand–grain weight (TGW) in plants of short–stem rye infected by stem rust (St.Petersburg, 1997)

Disease severity [%]	TGW	
	Weight [g]	Percentage of control [%]
0–10	36.3	100
20–40	30.7	84
50–60	26.3	72
70–100	23.3	64
LSD_{05}	0.8	

Our research has demonstrated a strict dependence of TGW decrease on the degree of infection by stem rust.

At maximum disease development (70–100%) thousand–grain weight (TGW) decreased to 36% on average. At the same time, individual rye genotypes were highly tolerant and never showed a TGW decrease over 20% with disease severity reaching 70–100%, while there were also cases of low tolerance with an up to 80% decrease of TKW at a similar infection level.

In order to determine the genetic diversity for stem rust resistance, 420 accessions from the rye collection of the Vavilov Institute were studied. The accessions originated from European countries, America and Eastern Asia. Against the natural high infection of stem rust, resis–tant or immune plants were identified in 69 accessions (landraces, cultivars, weedy and perennial wild rye). The frequency of resistant plants has no relation to the geographic origin of the accessions.

As to the type of resistance, all plants were clearly divided into two groups. The greater part of rye populations (54) included immune plant forms with the response types 0 to 0; (qualitiv resistance). Frequencies of such plants in rye populations varied from 0.1 to 100%. All plants (i.e. 100%) in the *S. rnontanurn* population from Italy were immune to stem rust. In fodder rye cultivars resistant plants amounted to 10 – 85%, while in grain rye their frequency ranged from 0.1 to 10%. (Table 4).

Table 4

Frequency of plants immune (0,0;) to stem rust in 54 diploid rye accessions at the end of milk ripeness.

Accession	Origin	Frequency	Accession	Origin	Frequency
S. rnontanum	Italy	100	Polko	SAR	2
Pulawskie Zielonkove	Poland	71	Inka	Ukraine	2
Derzhavinskaya 29	Russia	85	Zubrovka	Belarus	2
Derzhavinskaya 50	Russia	70	Maly Gat.R 198	Italy	2
Pulawskie Wczesne	Poland	63	Landrace	Bulgaria	2
Yan An	China	30	2OS9p x 505	Sweden	2
Weidmannsdank	Sweden	30	Cerasi 630	Italy	1.7
Chrysanth Hauserroggen	Germany	30	Villa Pouca de Aguiar	Portugal	1.4
Pico Urugwaj	Uruguay	20	K–i 1308	Portugal	1.4
Pastewne Zielone	Poland	15	Taezhnaya	Russia	1.3
Trenelense	Argentina	10	K–949 1	Yugoslavia	1.3
Landrace K–9549	Russia	10	Kisvardai Legelo	Hungary	1
Field weedy rye K– 10107	Russia	10	Belleyei 179 sarga	Hungary	1
Uraiskaya 2 Hi, Er	Russia	8.6	St 1762	Germany	1
Frederick	USA	8	Usyuzhna	Russia	0.8
Krajove Kribice	Czech Rep.	6.7	Hja 7009	Finland	0.8
Ceranja de Morerueiia	Spain	6	L–Sari~	Czech Rep.	0.7
Field weedy rye K9684	Azerbaijan	5	Conrah	GB	0.7
SCW 4	Germany	5	Landrace K–9501	Yugoslavia	0.7
RS 782/71	Czech Rep.	4.5	Kamalinskaya 4	Russia	0.7
Tennessee	USA	3.3	Grunschnittroggen	Germany	0.7
Kaltenberger	Austria	3.2	Sentinel	GB	0.5
Wrens	USA	3	Radstadter Bergland	Czech Rep.	0.4
Landrace K–9522	Yugoslavia	3	Stooling	SAR	0.4
Beka	Hungary	3	Bedecin	Romania	0.3
Persiyanka Hl	Russia	2.8	D.Troubsko	Poland	0.3
Duoniai	Lithuania	2.5	Ilmen	Russia	0.1

Fifteen rye populations contained plants slightly injured by stem rust (quantitative resistance). Individual or sparsely dispersed small pus–tules covering less than 10% of the stem surface were observed. The fre–quencies of such genotypes varied from 1 to 100%. The largest number of resistant plants (80–100%) was recorded for the weedy rye from Turkey and Daghestan (Table 5).

Table 5

Frequency of genotypes with quantitative resistance to stem rust in diploid rye accessions in the end of milky ripeness phase

Accession	Origin	Frequency [%]
Field weedy rye K–4285	Turkey	100
Landrace K–i 1144	Portugal	100
Rothenbrunner	Switzerland	100
Field weedy rye K– 10020	Armenia	80
Landrace K–9541	Yugoslavia	80
Field weedy rye K–7744	Daghestan	70
Field weedy rye K–10520	Azerbaijan	50
Dakold	USA	50
Kabardinka	Russia	50
Landrace K–9201	Karelia	50
Field weedy rye K–9728	Azerbaijan	10
Saratovskaya 7	Russia	5
Yaselda	Belarus	5
Vetvistaya Hi	Kazakhstan	1.3
Landrace K–9533	Yugoslavia	1

The frequent occurrence of rye forms resistant to the widely specialized fungus *P. grarninis* is quite new. It confirms our knowledge that frequency of stem rust resistant plants not depends on the pathogen specialization. As to N. J. Vavilov, he wrote, "... the rate of pathogen specialization determines a higher or lesser probability of existence, of resistant cereal plants and hence the possibility of breeding varieties resistant to the fungus" (Vavilov, 1986).

The first attempts to study genetic control of stem rust resistance were undertaken by Mains in 1926. The author found dominant inheritance of this trait (Mains, 1926). Later, similar information appeared in other literature sources (Kobylyanskii, 1975; Tan, Luig, Watson, 1976; Sharakhov, 1996).

In our experiment to determine the number of genes controlling resistance to the stem rust, BC_4 progenies from crosses between resistant plants (0 type response) derived out from cvs. Kharkovskaya 55 and Rossul, and susceptible rye forms Getera 2 and Hja69 10, as well as F_2 of plants the last backcross were studied. Over 300 BC_4 plants and more than 400 BC_4 F_2 plants were analyzed. The segregation observed in BC_4 corresponded very accurately to the 1:1 ratio ($x^2 = 0.01... 0.03$), and to the 3:1 ratio in F_2 progenies ($x^2 = 0.06$). This proves the dominant monogenic control of resistance to the St.Petersburg and Moscow stem rust populations. The resistance gene was designated *Sri.* This gene is sufficiently effective for producing resistant rye cultivars.

For breeding stem rust–resistant cultivars, we are proposing s strat–egy (Solodukhina, 1994; Kobylyanskii, Solodukhina, 1996). The pro–posed strategy is of developing rye populations with complex resistance to several pathogens. The most reliable way of ensuring long–term re–sistance to diseases is to unite in one population a maximum number of genes governing resistance to several pathogens. The strategy includes the following steps:

— Parallel backcrossing of the best genotypes from a highly produc–tive population with donors (sources) of different genes for resis–tance to one or different pathogen species;
— Stabilization of the backcross progenies by increasing the fre–quency of resistant genotypes up to 90%;
— Composing races specific resistant progenies to one or different pathogens into common population.

Various sources of resistance to both pathogens, as well as informa–tion on the inheritance of resistance are available and breeding strate–gies have been proposed.

Practical application of the proposed strategy yielded positive results. To a certain degree, the problem of winter rye breeding for resistance to leaf and stem rusts has been solved. By now, with the author's partici–pation, two new winter rye cultivars — Estafeta Tatarstana (1999) and Era (2001) have been bred. Complex resistance to leaf and stem rusts, and mildew characterize these. Estafeta Tatarstana is a complex popu–lation composed of 17 dominant short–stem high–productive donors of resistance to leaf rust *(Lr4, Lr6, Lr7),* stem rust *(Sri),* and mildew *(Er, Rrn2).* Twenty Russian and introduced cultivars and wild species were used to produce the donors of resistance which make up the population of cv. Estafeta Tatarstana.

The cultivar Era was created by means of the individual family selec–tion from a complex population which contained *5* donors of complex re–sistance to rusts and mildew. The population of cv. Era includes genotypes carrying resistance to brown rust *(Lr4, Lr5, Lr6),* stem rust *(Sri)* and mildew *(Er, Rm2).*

These new cultivars are grown on over 280000 ha without application of fungicides and produce high yields of ecologically pure grain.

REFERENCES

Chumakov A. E., Sidorenko E. L. 1973. Rust in Cereals. In: Distribution of Crop Diseases in the Soviet Union from 1968 to 1972. Leningrad. pp. 4 1–48.
Eriksson J. 1902. Uber die Spezialisierung des Getreideschwarzrostes in Schweden und anderen Ländern. Centralbl. J. Bacteriol. u Parasiten. A.2. Bd.9. S.590–607. ss.654–658.
Eriksson J., Henning F. 1896. Die Getreideroste und Maaszegelen gegen dieselben. Stock–holm (Ref. N.J. Vavilov).
Kobylyanskii V.D. 1975. Rye (genetics, taxonomy and breeding problems): Abstr. Senior Doc–torate (Biol.) Thesis. Leningrad, VIR. 57 pp.
Kobylyanskii V.D. 1982. Rye: Genetic Bases of Breeding. Moscow, Kolos Publishers, 272 pp.
Kobylyanskii V.D., Solodukhina O.V. 1996. Genetic bases and breeding utilization of hetero–geneous resistance of rye to brown rust. International symposium on rye breeding and

genetics. EUCARPIA. Vortrage fuer Pflanzenzuchtung. Stuttgart. Germany. H.35. pp.155–163.

Koernicke F. 1865 Der gegenwärtige Stand der Rostrage. Naturhistorische Mitteilungen Königsberg (Ref. N. I. Vavilov).

Koernicke F., Werner H. 1885 Handbuch der Getraidebaues. Berlin. Bd. 1.2. (Ref. N. I. Vavilov)

Keroleva L. A. 1976. Immunological analysis of rye cultivar populations for identifying forms resistant to stem rust. In Rust in cereals, Moscow, p.193.

Mains E. B. 1926. Rye resistance to leaf rust, stem rust and powdery mildew. J. Agric. Res. Vol. 32, No 3, pp. 201–221

Mains E. B., Leighty C. E. 1923. Resistance in rye to leaf rust, *Puccinia disperse* Erikss. J. Agric. Res. Vol. 25 No 5 pp. 243–252

Mains E. B., Jackson H. S. 1926. Physiological specialisation in leaf rust of wheat, *Puccinia triticina* Ericss. Phytopathology. Vol. 16 pp. 89–120

Novikov M. A. 1907. Rust pathogens in our cereal plants. Agriculture and Forestry. No 3, p. 309–339,. No 4, p. 42–62,. No 5, p. 208–250

Roemer T. 1939. Handbuch der Pflanzenzüchtung, 2. Roggen (*Secale cereale* L.) parey, Berlin

Sharakov A. A. 1996. Study of winter rye resistance to stem rust (*Puccinia graminis* Pers. F. sp. *Secalis*) International symposium on rye breeding and genetics. EUCARPIA. Vortrage für Pflanzenzüchtung. Stuttart, Germany, H. 35, pp. 198–199

Soloduchina O. V. 1994. Rye resistance to brown rust and powdery mildew: The potential of hereditary variability. Rus. J. Genet. Vol. 30 No 10 pp. 1171–1180

Soloduchina O. V., Kobylyanskii V. D. 2000. Genetic determination of stem rust resistance in rye. Rus. J. Genet. Vol. 36 No 5 pp. 550–552

Soloduchina O. V. 1985. Detrimental effects of brown rust in short–stem diploid rye crops. Coll. Papers on Appl. Bot. Genet. Breed. Vol. 92, pp. 47–51

Tan B. H., Luig N. H., Watson J. A. Genetic analysis of stem rust resistance in *Secale cereale. I* Genes for resistance to *Puccinia grarninis* f. sp. *Secalis.* // Zeitschrift für PflanzenzUchtung. Berlin West. 1976. Bd. 76. H. 2. ss. 121–132.

Torop A. S., Torop A. A., Tymchenko L. F., Anfinogenov G.V. 1978. Sources of Rye Immunity to Diseases of Greatest Abundance. Coil. Papers of the Agric. Res. Inst. for the Centr. Black Soil Belt. Vol. 15. Issue 3. pp.33–40.

Trushko M. M. 1973. Sources of stem rust infection in Siberia. Siberian Agric. Newsletter. No.4. pp.46–50.

Trushko M. M. 1974. Specific Features of the Development of Brown Rust and Stem Rust in Western Siberia. Abstr. Ph.D. Thesis. Leningrad. pp. 24

Vavilov N. J. 1913. On resistance of cereals to parasitic fungi. Coll. Papers of the Breed. St. of the Moscow Agric. Inst. No.1, pp.1–100.

Vavilov N. J. 1986. Plant immunity to infectious diseases. Moscow, Nauka Publishers, pp. 520

Yachevsky A. A. 1909. Rust in cereals in Russia. St.Petersburg. p p. l87