

Smut resistance in millet (*Panicum Miliaceum L.*) genotypes and control of this disease in Ukraine

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Abstract

In Ukraine, one of the most widely spread and dangerous fungal disease of millet (*Panicum miliaceum* L.) is smut (*Sorosporium destruens* (Schlecht) Yanki) belonging to the family Ustilaginaceae. The objective of this study was to study smut virulence, identified widely-spread smut races in Ukraine, inheritance of smut resistance. Ukrainian scientists of NSC «Institute of Agriculture» of NAAS have identified 13 spread smut races in Ukraine. In 2013, we identified a new race – Rs 13. Every smut race has its identification code. Seven varieties (Raduga, L. 832, L. 1245, ct. VIR 1456, Maslovskogo 3, Kyivske 87, ct. VIR 8751) are main genotypes-differentiators of smut races. Smut virulence significantly varied (35.1% - 96.2%): the highest virulence was observed in smut races Rs 2, Rs 3 and Rs 12 – 96.2, 93.0 and 93.7%, respectively; low virulence was seen in smut races Rs 1 (35.1%) and Rs 10 (35.9%). Seven smut races (Rs 2, Rs 3, Rs 7, Rs 8, Rs 9, Rs 12, Rs 13) had virulence of > 50%. We investigated the inheritance of resistance to 9 smut races in 7 millet varieties, which were clearly resistant or sensitive to these smut races: Gorlinka, ct. VIR 241, L. 811-06, Veselopodolianske 16, Pikulovichske, L. 829-04, and L. 1838-04. The results of this study revealed that in F₂ hybrid combinations inheritance of resistance to smut races Rs 1, Rs 2, Rs 3, Rs 4, Rs 5, Rs 6, Rs 7, Rs 9, Rs 12 was mono- or digenic and controlled by complementary or duplicate dominant genes, depending on parents. Using chemical mutagenesis, we developed new genotypes characterized by early ripening, high grain yield and quality and smut resistance. Thus, in Ukraine, based on the knowledge of inheritance of resistance genes and their interactions, widely-grown varieties resistance to races Rs 1 and Rs 10- Raduga, Kharkivske 71, Kharkivske 72; resistance to 8 races (RsRs 1, 4, 5, 6, 7, 9, 10, 11): Soniachne, Syaivo, Kyivske 87, Kyivske 96, Omriane, Veselka Kharkivske 31, Konstiantynivske, Vitrylo and Kharkivske 56 was resistance to RsRs 3, 6, 7 and 8 races.

Key words: millet, smut resistance, genotype, virulence, inheritance, chemical mutagenesis

Introduction

In Ukraine, the most widely cultivated millet species is millet (*Panicum miliaceum* L.). For last 10 years (2009-2019), the area under millet has grown from 51,000 to 156,400 hectares, and the average yield of grain has increased 1.5 to 3.5 t/ha. In our country, millet is a source of nutrients for humans and domestic animals. In

addition, this crop can be used for malt production at distilleries, for bioethanol production.

One of the most dangerous fungal disease of millet is smut (*Sorosporium destruens* (Schlecht) Yanki) belonging to the family Ustilaginaceae (Yashovskiy, 1987). This disease is widely spread in all over our country, and in different regions the infection can attack 15-20% of the total millet field area and 0.5-0.6% of

plants on this area are affected by smut. Ukrainian researches report that farmers can lose up to 20-30% of their yields (Volkodav, Barykov, 1990). Moreover, the millet grain quality worsens, and such grain cannot be used for human food or for livestock feed (Levchenko *et al.*, 2018).

Thereby, it is economically important not only to develop consistently high-yielding millet varieties with good grain quality, but also to breed for smut resistance.

Smut infection of seeds occurs in soil in spring until millet seeds begin to germinate. It was observed that the smut effect was various, depending on the germination stage. In smut-resistant varieties, smut hypha emergence and ramification were limited in plant tissues, and smut mycelium was the most actively destroyed at the stooling stage of millet. Smut mycelium was well-developed into tissues of susceptible varieties, as its growth was not hampered (Strahov, 1953, Sikora, Schonbeck, 1975). M. Koishibayev (1993) reported that smut did not reduce the grain germinability, on the contrary, slightly increased it. At the earlier stages of millet development, smut negatively affected the further growth of millet plants, however, the stooling was enhanced, and more stems were formed. Disease destroys the shoot tops and influences phytohormone excretion, increasing the stem number. A.Y. Trophimovich (1954), M.G. Enikeev (1963), K.Y. Kalashnikov (1971), A.F. Soldatov (1984), S.P. Starostin (1987), and K.V. Popkova (1989) observed that smut-resistant varieties had a lower average value of this character than susceptible ones. Smut decreased the plant height, which is a negative effect on plants. The 1000-seed weight and yield are important parameters in plant production, which help breeders select superior genotypes. Z.M. Bobkova, A.N. Hanigin (1981), M. Koyshibaev (1993) found that smut negatively affected the 1000-seed weight and grain yield and deteriorated the grain quality. Surprisingly, the 1000-seed weight in smut-resistant varieties was lower than in smut-susceptible ones. It can be attributed to a sudden increase in phytohormone levels in smut-susceptible varieties.

New smut races appear because of spontaneous mutations in pathogen populations (Yashovskiy, 1987). Therefore, it is necessary to develop new varieties carrying different genes of smut resistance. Breeders have to study and evaluate breeding material for different millet smut races.

Studying smut race composition is a complex and time-consuming process. In Ukraine this work was started by Yashovskiy I.V. at the Institute of Agriculture of NAAS and Konstantinov S.I. at Plant Production Institute named after V.Y. Yuriev of NAAS in 1970. The scientists investigated local smut races and smut races from different regions of Ukraine. They revealed that millet smut races had various parasitic activity. Geographically distant smut populations showed different virulence in the same varieties (Konstantinov and Shapina, 1979, Konstantinov, *et al.*, 1985, Yashovskiy, 1987). There are no Ukrainian varieties that would be resistant to all smut races (Yashovskiy, 1987). Thus, in millet breeding for smut resistance breeders had to use smut-resistant genotypes for certain territories or regions.

The objective of this study was to study smut virulence, identified widely-spread smut races in Ukraine, inheritance of smut resistance, development of smut-resistant varieties of millet by chemical mutagenesis seeds. Results of these investigations are presented in the article.

Materials and methods

For identification 12 spread smut races in Ukraine there were seven main genotypes-differentiators of smut races (Raduga, L. 832, L. 1245, ct. VIR 1456, Maslovskogo 3, Kyivske 87, ct. VIR 8751) (Table 1). Every smut race has its identification code. For example, race 1 (Rs 1) has the virulence code R-S-R-R-S-R-S, race Rs 4 – S-S-R-S-S-R-S, etc. Hence, unknown smut spores can be identified in accordance to these codes.

For example, in 2013, researchers of the Institute of Agriculture of NAAS observed a new unknown smut patotype, which received a new identification code: S-R-S-R-S-R. This smut race was named Rs 13.

Table 1: Identification of millet smut races

Smut sorus	Genotypes - differentiators of smut races							Race
	Raduga	L. 832	L. 1245	ct.VIR 1456	Maslovskogo 3	Kyivske 87	ct. VIR 8751	
1	R*	S**	R	R	S	R	S	Rs 1
2	S	S	R	S	S	R	S	Rs 4
3	S	R	R	S	S	R	R	Rs 5
4	S	R	R	S	R	R	R	Rs 6
5	S	R	S	R	S	S	R	Rs 2
6	S	S	S	S	R	S	S	Rs 3
7	S	S	R	S	R	R	S	Rs 7
8	S	R	S	S	R	S	R	Rs 8
9	S	S	R	R	S	R	S	Rs 9
10	R	R	R	S	S	R	R	Rs 10
11	S	R	R	R	S	R	R	Rs 11
12	S	R	R	S	S	S	R	Rs 12
13	S	R	S	R	R	S	R	Rs 13

* R - resistant, ** S – susceptible

The inheritance of smut resistance was studied on 7 varieties, which were clearly resistant or susceptible to 12 smut races: Gorlinka, ct. VIR 241, L. 811-06, Veselopodolianske 16, Pikulovychske, L. 829-04, and L. 1838-04. Genetic analysis of the smut resistance inheritance was conducted using Pearson's test for F_2 hybrids of millet (Volf, 1966). Analysis showed that all the mean χ^2 didn't exceed the χ^2_{st} ($P=0.05$), demonstrating statistical significance.

For development of smut-resistant varieties of millet by chemical mutagenesis seeds of varieties Kharkivske 34, Kharkivske 65, Myronivske 51, L. 70-6181, Orenburgskoye 82, Blagodatnoye were treated with chemical mutagens: 0.012 % and 0.025 % solutions of N-nitrosomethyl urea (NMU), N-nitrosoethyl acetate (NEA) in concentrations, 0.01%, 0.015%, 0.02% solutions of 1,4-bis-diazoacetylbutane (DAB), dimethyl sulfate (DMS), diethyl sulfate (DES), ethylenimine (EI). To reduce the

negative effects of mutagens, millet seeds were treated with modifiers (levomycetin, heteroauxin, nystatin).

Results and discussion

Millet smut races spread in Ukraine and their pathogenic properties

The pathogenic properties of smut races (Rs 1 - Rs 13) were studied by A.M. Prodanyk (2011, 2012, 2014, 2015) on 197 millet varieties in 2009 - 2015 (Fig. 1). The weather had no effect on the pathogenic properties of smut races. The smut virulence significantly varied (35.1% - 96.2%), with the average of 64.7%. Seven smut races (Rs 2, Rs 3, Rs 7, Rs 8, Rs 9, Rs 12, Rs 13) had virulence of > 50%. The highest virulence was observed for smut races Rs 2, Rs 3, Rs 12 – 96.2, 93.0, and 93.7%, respectively. In Ukraine, low virulence was shown for smut races Rs 1(35.1%) and Rs 10 (35.9%).

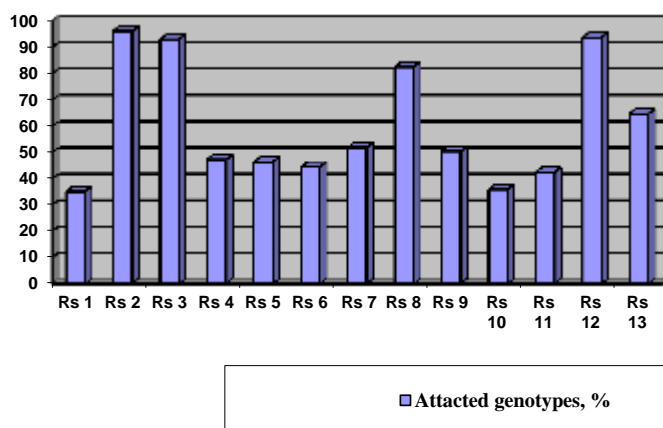


Fig. 1: Analysis virulence of 13 millet smut races in Ukraine

Studying the pathogenic properties of smut races in breeding for smut resistance can help to select genotypes with resistance to the most virulent smut races.

Inheritance of smut resistance in millet

Successful development of millet varieties is based on the knowledge of inheritance and interactions of genes controlling different agro-morphological characters. Establishment of inheritance patterns of resistance to this disease and development of new genotypes with resistance to different smut races are important objectives in millet breeding for smut resistance.

Inheritance of smut resistance in millet was investigated by S.I. Konstantinov (1967), I.P. Ungenfuht (1976), V.A. Ilin (1978), E.N. Zolotuhin (1981). In F_1 plants, dominance of smut resistance was observed, and, in F_2 generation, a segregation was seen, conforming to monofactorial inheritance. These data were also confirmed later by O.I. Shirokov and L.I. Maslenkova (1986). V.O. Tihonov (1995) established smut resistance gene symbols: *Sph 2* (to races 1, 9 and 2), *Sph 4* (races 5, 6 and 2), *Sph 5* (race 8) and proposed that all the genes of smut resistance were multiple allelomorphs or closely linked alleles of smut

resistance genes. However, V.N. Lisov (1973) and L.Y. Shapina (1982) reported polygenic inheritance of smut resistance in F_2 , especially when female germplasm was smut-resistant, and monofactorial inheritance was only observed in some cases. I.V. Yashovskiy (1987) studied the linkage between genes controlling smut resistance to race 4 and agro-morphological characters (anthocyan color of plants, panicle types, grain color, starch composition). He obtained independent inheritance of genes encoding these characters, and his results were similar to other scientists' reports (I.H. Maksimchuk (1956), M.M. Artemeva (1963), I.M. Elagin (1979)).

In 2000-2015, researchers of the Institute of Agriculture of NAAS studied the inheritance of resistance to 10 smut races in millet (Prodanyk, 2007, Prodanyk, 2010, Levchenko, *et al.*, 2018).

In combination Gorlinka x ct. VIR 241, variety Gorlinka had smut resistance to races Rs 4, Rs 5, Rs 6, Rs 7, Rs 10, and ct. VIR 241 showed smut sensitive to these races. The segregation in F_2 hybrids of millet showed a dihybrid ratio (15:1) for races Rs 4, Rs 5, Rs 6, Rs 7, but a monohybrid ratio (3:1) in race Rs 10 (Table 2). Our results revealed that the resistance to smut races Rs 4, Rs 5, Rs 6, Rs 7 was controlled by dominant alleles of 2 different independent genes with complementary interaction.

Table 2: Analysis of resistance to 5 smut races in F₂ millet hybrids (Gorlinka x kat. VIR 241)

Estimate	Plant phenotype parameters									
	Rs 4		Rs 5		Rs 6		Rs 7		Rs 10	
	R*	S**	R	S	R	S	R	S	R	S
Gorlinka	+		+		+		+		+	
ct. VIR 241		+		+		+		+		+
Real number of descendants in F ₂	49	5	57	6	69	2	84	5	37	8
Expected number of descendants in F ₂	50,6	3,4	59,1	3,9	66,6	4,4	83,4	5,6	33,8	11,2
Theoretical ratio	15:1		15:1		15:1		15:1		3:1	
Pearson's χ^2 - test significance	0,84		1,15		1,42		0,61		1,25	
χ^2_{st}	3,84		3,84		3,84		3,84		3,84	

*R- resistant, **S-susceptible

To explore the genetic inheritance of smut resistance to races Rs 1, Rs 4, Rs 5, Rs 6, Rs 7, and Rs 9, genotype L. 811-06 (carrying dominant genes of smut resistance to races Rs 1, Rs 4, Rs 5, Rs 6, Rs 7, and Rs 9) and variety Veselopodolianske 16 (carrying no dominant genes of smut resistance to races Rs 1, Rs 4, Rs 5, Rs 6, Rs 7,

and Rs 9) were hybridized (Table 4). In this combination, F₂ millet plants segregated with a ratio of 3:1 for smut races Rs 1, Rs 4, Rs 5, Rs 7, and Rs 9. It suggested monogenic inheritance of this trait. Smut resistance to race Rs 6 was controlled by duplicate dominant genes, with a dihybrid ratio of 15:1.

Table 3: Analysis of resistance to 6 smut races of millet in F₂ hybrids (L. 811-06 x Veselopodolianske 16)

Estimate	Plant phenotype parameters											
	Rs 1		Rs 4		Rs 5		Rs 6		Rs 7		Rs 9	
	R*	S**	R	S	R	S	R	S	R	S	R	S
L. 811-06	+		+		+		+		+		+	
Veselopodolianske 16		+		+		+		+		+		+
Real number of descendants in F ₂	55	21	56	20	32	7	42	4	44	12	36	9
Expected number of descendants in F ₂	57,0	19,0	57,0	19,0	29,2	9,8	43,1	2,9	42,0	14,0	33,7	11,3
Theoretical ratio	3:1		3:1		3:1		15:1		3:1		3:1	
Pearson's χ^2 - test significance	0,28		0,07		1,03		0,47		0,38		1,00	
χ^2_{st}	3,84		3,84		3,84		3,84		3,84		3,84	

*R- resistant, **S-susceptible

Thus, our results revealed that in F₂ hybrid combinations inheritance of resistance to smut races Rs 5 and Rs 9 was monogenic, resistance to race Rs 6 was controlled by duplicate dominant genes, and inheritance of resistance to races Rs 4 and Rs 7 could be monogenic or digenic (depending on parents).

Genetic inheritance of smut resistance to the most virulent in Ukraine races Rs 2, Rs 3 and Rs 12 was explored (Table 4). Variety Pikulovychske that is resistant to smut race Rs 3 was

crossed with genotypes L. 829-04 and L. 1838-04 (smut resistance to races Rs 2 and Rs 12).

In F₂ of combination Pikulovychske x L. 829-04, resistance to race Rs 2 segregated as follows: 35 smut-resistant plants to 96 smut-susceptible plants. It conformed to the ratio of 3:1. In another combination, Pikulovychske x L. 1838-04, the ratio of 3:1 was observed in F₂, showing monogenic control. The inheritance of smut resistance to race Rs 3 in combinations Pikulovychske x L. 829-04 and Pikulovychske x L. 1838-04 had a monohybrid ratio of 3:1, too.

Table 4: Analysis of resistance to smut races Rs 2, Rs 3 and Rs 12 in F₂ millet hybrids

Estimate	Plant phenotype parameters											
	Pikulovychske x L. 829-04						Pikulovychske x L. 1838-04					
	Rs 2		Rs 3		Rs 12		Rs 2		Rs 3		Rs 12	
	R*	S*	R	S	R	S	R	S	R	S	R	S
Real number of descendants in F ₂	96	35	76	21	92	33	84	31	77	24	81	7
Expected number of descendants in F ₂	98,2	32,8	72,8	24,2	93,8	31,2	86,2	28,8	75,8	25,2	82,5	5,5
Theoretical ratio	3:1		3:1		3:1		3:1		3:1		15:1	
Pearson's χ^2 -test significance	0,21		0,58		0,13		0,24		0,21		1,44	
χ^2 st	3,84		3,84		3,84		3,84		3,84		3,84	

*R- resistant, **S-susceptible

The segregation of resistance to smut race Rs 12 in F₂ plants of Pikulovychske x L. 829-04 had the ratio of 3:1 (33 plants were smut-resistant, and 92 plants were smut-susceptible). However, in combination Pikulovychske x L. 1838-04 smut resistance to race Rs 12 was controlled by duplicate dominant genes 15:1.

Based on the knowledge of inheritance and interactions of smut resistance genes, widely-grown in Ukraine varieties Raduga (Rs 1 and Rs 10); resistance to 8 races (RsRs 1, 4, 5, 6, 7, 9, 10, 11): Soniachne, Syaivo, Kyivske 87, Kyivske 96, Omriiane, Veselka were developed at the Institute of Agriculture of NAAS.

Development of smut-resistant varieties of millet by chemical mutagenesis

To obtain new smut-resistant varieties in millet breeding, one should use new methods of developing genotypes. Chemical mutagenesis is a modern method in millet breeding. Scientists of the Plant Production Institute named after V.Y. Yuriev in collaboration with scientists of the Institute of Chemical Physics studied effects of various concentrations of chemical mutagen solutions on millet plants, treating seeds of different varieties.

Seeds of varieties Kharkivske 34, Kharkivske 65, Myronivske 51, L. 70-6181, Orenburgskoye 82, Blagodatnoye were treated with chemical mutagens: 0.012 % and 0.025 % solutions of N-nitrosomethyl urea (NMU), N-nitrosoethyl acetate (NEA) in concentrations, 0.01%, 0.015%, 0.02% solutions of 1,4-bis-diazoacetylbutane (DAB), dimethyl sulfate (DMS), diethyl sulfate (DES), ethylenimine (EI). To reduce the negative effects of mutagens, millet seeds were treated with modifiers (levomycetin, heteroauxin, nystatin) (Rapoport, 1971, Rapoport, 1978, Konstantinov, et al., 1987).

In M₂, we observed different effects of chemical mutagens on millet plants: chlorophyll mutations (striata and albino), genotypes with a high grain yield per plant, genotypes with high protein content in grain (18-20%) and others (Konstantinov et al., 1987). Especial attention in this experiment was paid to new germplasms that were characterized earlier ripening, high grain yield, high grain

quality and good smut resistance (Konstantinov et al., 1993).

Individual selections among in mutant accessions resulted in smut-resistant varieties, which became widely-spread in Ukraine Kharkivske 31, Kharkivske 56, Kharkivske 71, Kharkivske 72, Konstantynivske, Vitrylo.

Conclusion

The weather had no effect on the pathogenic properties of smut races. The smut virulence significantly varied (35.1% - 96.2%), with the average of 64.7%. Seven smut races (Rs 2, Rs 3, Rs 7, Rs 8, Rs 9, Rs 12, Rs 13) had virulence of \square 50%. The highest virulence was observed for smut races Rs 2, Rs 3, Rs 12 – 96.2, 93.0 and 93.7%, respectively. In Ukraine, low virulence was reported for smut races Rs 1 (35.1%) and Rs 10 (35.9%).

Establishment of patterns of inheritance of resistance to this disease and development of new genotypes with resistance to different races of smut are important objectives in millet breeding for smut resistance. At the Institute of Agriculture of NAAS inheritance of resistance to 10 smut races (Rs 1, Rs 2, Rs 3, Rs 4, Rs 5, Rs 6, Rs 7, Rs 9, Rs 10, and Rs 12) was investigated on 7 millet varieties, which were clearly resistant or susceptible to these races: Gorlinka, ct. VIR 241, L. 811-06, Veselopodolianske 16, Pikulovychske, L. 829-04, and L.1838-04. The results revealed that in F₂ hybrid combinations inheritance of resistance to smut races Rs 2, Rs 3, Rs 5 and Rs 9 was monogenic, resistance to race Rs 6 was controlled by duplicate dominant genes, and inheritance of resistance to races Rs 4, Rs 7, and Rs 12 could be monogenic or digenic, depending on parents.

Thus, in Ukraine, based on the knowledge of inheritance of resistance genes and their interactions, methods of chemical mutagenesis, we developed widely-grown varieties characterized by early ripening, high grain yield and quality and smut resistance to races Rs 1 and Rs 10- Raduga, Kharkivske 71, Kharkivske 72; resistance to 8 races (RsRs 1, 4, 5, 6, 7, 9, 10, 11): Soniachne, Syaivo, Kyivske 87, Kyivske 96, Omriiane, Veselka Kharkivske 31, Konstantynivske, Vitrylo and

Kharkivske 56 was resistance to RsRs 3, 6, 7 and 8 races.

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