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INHERITANCE OF RESISTANCE TO LEAF RUST BY COMBINING DIFFERENT GENETIC CONTROL SYSTEMS FOR THE TRAIT

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Resistance to leaf rust is one of the crucial factors in successful wheat production. The disease causes significant yield losses and reduces grain quality. Research related to resistance inheritance is helping to identify genetic factors that provide resistance to leaf rust. This allows breeders to create new wheat varieties with increased resistance to the disease. Using the material of F2 hybrid populations created by crossing parental components contrasting in leaf rust resistance, the patterns of inheritance of this trait were studied, depending on the combination of various genetic systems for resistance control in a single genotype. The genetic analysis identified the number of genes that control this trait and the types of their interaction. The possibility of obtaining positive transgressions for resistance to leaf rust, depending on the contrast of the parental pairs involved in crossing, was shown. It is assumed that the cytoplasm influences the effect of inheritance of resistance to leaf rust.

Key words: *winter bread wheat, leaf rust, resistance, segregation, hybrid population, second generation, genetic analysis.*

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ЗАКОНОМІРНОСТІ УСПАДКУВАННЯ ОЗНАКИ СТІЙКОСТІ ДО БУРОЇ ІРЖІ ПРИ КОМБІНУВАННІ РІЗНИХ ГЕНЕТИЧНИХ СИСТЕМ КОНТРОЛЮ ОЗНАКИ

Є. І. Кірчук, Є. В. Алєксєєнко, Є. А. Голуб, Н. О. Гончарук

Стійкість до бурої іржі є одним із ключових факторів в успішному вирощуванні пшениці. Хвороба спричиняє значні втрати врожаю та знижує якість зерна. Дослідження щодо успадкування стійкості дають змогу виявити генетичні фактори, які забезпечують опірність до бурої іржі. Це дає змогу селекціонерам розробляти нові сорти пшениці з підвищеною стійкістю до цієї хвороби. На матеріалі гібридних популяцій F2 створених у результаті гібридизації контрастних за ознакою стійкості до бурої іржі батьківських компонентів було проведено дослідження закономірностей успадкування зазначеної ознаки в залежності від комбінування в одному генотипі окремих генетичних систем контролю стійкості. У результаті генетичного аналізу було визначено кількість генів, які контролюють дану ознаку та типи їх взаємодії. Показана можливість отримання позитивних трансгресій за ознакою стійкості до бурої іржі в залежності від контрастності батьківських пар залучених до гібридизації. Висказано припущення, щодо впливу цитоплазми на характер успадкування стійкості до бурої іржі.

Ключові слова: *бура іржа, стійкість, розщеплення, гібридна популяція, друге покоління, генетичний аналіз, гібридизація.*

Introduction

Among the many means of protection, the most effective and environmentally friendly is the creation and implementation of varieties with genetically determined resistance to the main diseases in combination with other useful traits and properties (Бурденюк-Тарасевич і Лозінський, 2014; Моргун і Гаврилюк, 2014), which will allow to keep the development of the disease without the use of chemical protection means (Ковалишина та ін., 2017).

It is important for practical breeding for resistance to leaf rust to study the patterns of inheritance of this trait in crossing parents with different genetic systems of resistance to this disease. Such studies help to understand the mechanisms underlying the wheat immune system. This makes it possible to study the interaction between the plant and the pathogen in more depth and to develop new methods of plant protection against diseases. The results of studies on the inheritance of resistance to leaf rust can be used to develop more effective strategies for managing the disease. Based on this data, it is possible to make recommendations for selecting wheat varieties with resistance to leaf rust for specific regions and growing conditions.

The analysis of recent studies regarding the nature of inheritance of leaf rust resistance by hybrid material showed a high level of influence of the cytoplasm for inheritance of this trait. It was established that the fragmentation in F2 populations when used in crosses as a maternal component of varieties resistant to leaf rust was observed in the ratio of 9:7, 9:7, 3:1, 1:3, 13:3 and 3:13, which corresponds to the cumulative, epistatic and complementary interaction of oligogens with small resistance genes (Орлюк та ін., 2007; Karelov at all., 2011; Моргун і Топчий, 2016; Demydov at all., 2018; Хоменко і Сандецька, 2018; Базалій та ін., 2020).

Although scientists from different countries have been studying the inheritance of leaf rust resistance trait for decades, very little research has been conducted so far to determine the peculiarities of inheritance of leaf rust resistance in winter wheat by combining different genetic control systems for this trait, and such research is at the beginning stage in Ukraine. Therefore, the aim of the study was to investigate the patterns of inheritance of the resistance trait and to identify the peculiarities of fragmentation when combining different genetic systems that control this trait in F2 populations obtained by crossing parental components of different ecological and geographical origin.

Material and methods

The material for the study was F2 generation of winter bread wheat (Triticum aestivum L.) obtained by crossing parental components with different genetic systems (control) of resistance to leaf rust, different in terms of resistance. A study of 15 combinations of genetic resistance systems was conducted, which can be divided into 3 groups: 1) (Serbia-Odesa+Lr34)+Phito; (Serbia-Odesa+Lr34)+1AL/1RS; (Serbia-Odesa+Lr34)+1BL/1RS; (Serbia-Odesa+Lr34)+Western Europe; (Serbia-

Odesa+Lr34)+Wild relatives (Aeg. CL); 2) Wild relatives (Aeg. CL)+ Phito; Wild relatives (Aeg. CL)+1AL/1RS; Wild relatives (Aeg. CL)+1BL/1RS; Wild relatives (Aeg. CL)+Western Europe; Wild relatives (Aeg. CL)+(Serbia-Odesa+Lr34); Serbia-Odesa+Fito; 3) Serbia-Odesa+1AL/1RS; Serbia-Odesa+1BL/1RS; Serbia-Odesa+Western Europe; Serbia-Odesa+(Serbia-Odesa+Lr34). The experiment was carried out in the laboratory of the Department of Phytopathology and Entomology of the PBGI-NCSCI of the National Academy of Agrarian Sciences of Ukraine, during the juvenile period of development. Each combination was sown separately, 100 seeds per pot. stage, inoculation with leaf rust was carried out, after pre-drying the spores in a thermostat for 15 minutes at 45°C to bring them out of anabiosis and mixed with talcum powder to a homogeneous consistency. Before inoculation, drip moisture was created for pathogen development (Кірчук і Алєксєєнко, 2022). The Odesca polucarlicova variety served as a standard for susceptibility.

Calculations were performed using Excel software. The reliability of the segregation was checked using Pearson's x2 according to the formula:

$$\chi^2 = \sum \frac{(f - F)^2}{F}$$

F – theoretically expected.
f – obtained in the experiment.

To study the nature of inheritance of leaf rust resistance trait in F2 generation of winter wheat, the index of dominance (hp) was used. The value of hp was determined by the conventional method, according to the formula:

$$hp = (XF - Xmp) / (Xp - Xmp)$$

XF – the mean value of the hybrid.
Xmp – the mean value of the value of both parental forms.
Xp – the value of the parent form with the highest resistance rate.

The dominance index (hp) can vary from -∞ to + ∞ (Frey & Horner, 1957). We used the following gradation:

1) hp < -1 – negative superdominance, НД- (negative heterosis, or depression);
2) -1 ≤ hp < -0,5 – negative dominance, Д-;
3) -0,5 ≤ hp ≤ +0,5 – intermediate inheritance, ПУ;
4) +0,5 < hp ≤ +1 – positive dominance, Д+;
5) hp > +1 – positive superdominance, НД+ (positive heterosis).

Results and discussion

An important step in breeding is to study the inheritance of leaf rust resistance in F2 generation, which makes it possible to determine which genes are responsible for this trait and the nature of its inheritance. This increases the efficiency of breeders in choosing parental pairs with desirable genetic characteristics, including disease resistance, and allows for effective selection for this trait in early hybrid generations (Darwish at all., 2018; Ansari at all., 2018)

The main aim of these studies was to establish the pattern of inheritance of the leaf rust resistance trait in F2 populations obtained from crossing parental components with different genetic systems for this trait. In the studied hybrid combinations, the parental forms had contrast in this trait: medium-resistant (MR), medium-susceptible (MS) and susceptible (S). To determine the influence of the mother form on the trait of resistance to leaf rust, several crosses were carried out according to the following scheme: "susceptible x susceptible" (S x S), "susceptible x medium susceptible" (S x MS), "susceptible x medium resistant" (S x MR). It should also be noted that the maternal line was based on breeding material in whose genotype some genes were identified in previous studies and their combinations were obtained from sources of different ecological and geographical origin (L18716 (Serbia-Odesa + Lr34), L15914 (Aeg. SL), L22016 (Serbia-Odesa). Each of these lines was crossed with local varieties and lines carrying resistance genes from different genetic sources - Peremoha od. containing the 1AL/1RS translocation in its genotype, Shchedrist' od. with the 1BL/1RS translocation, Vidpovid' od., which carries effective leaf rust resistance genes - Lr26, Lr34, and lines obtained from the Phytopathology Department Ph.177 and Ph.142. A total of 15 combinations of crosses were made according to this scheme.

Data showing the pattern of inheritance of leaf rust resistance trait by bread winter wheat hybrids are presented in Table 1. The genetic analysis of F2 hybrid populations obtained from crossing parental components with different genetic systems for controlling resistance to leaf rust revealed that the presented crossing combinations showed polygenic inheritance of resistance to leaf rust, which corresponded to different types of gene interaction depending on their combination in a particular genetic system. In particular, in such combinations as: L18716 (S) × Peremoga od. (MS), L18716 (S) × Vidpovid' od (MR) and L22016 (S) × Shchedrist' od. (MR), a 3:1:3:9, 3:3:1:9, 3:3:1:9, 3:3:1:9 segregations from resistant to medium-resistant, medium-susceptible and susceptible was observed, which corresponds to complementary gene interaction. In the combinations of crossing L15914 (MR) × ph.142 (S), L15914 (MR) × 16918 (S) and L15914 (MR)×Peremoga od. (MS) showed a 3:1:12 and 13:3 segregation from resistant to susceptible, medium susceptible and susceptible, respectively, which corresponds to epistatic gene interaction.

The combinations L18716(S) × Ph.177(S), L15914(MR) × Vidpovid' od. (MR) and L22016(S) × Ph.177(S) with segregation 1:6:9; 9:1:6 from resistant to medium resistant and susceptible, which are complementary and polymeric. In the combinations L18716 (S) × Shchedrist' od. (MR), L15914 (MR) × Shchedrist' od. (MR) and L22016 (S) × Peremoha od.(MS) - and L22016 (S) × L16918 (S) with a segregation of 1:15 15:1, 1:15 from resistant to susceptible, the type of segregation corresponded to non-cumulative polymerisation (double dominant).

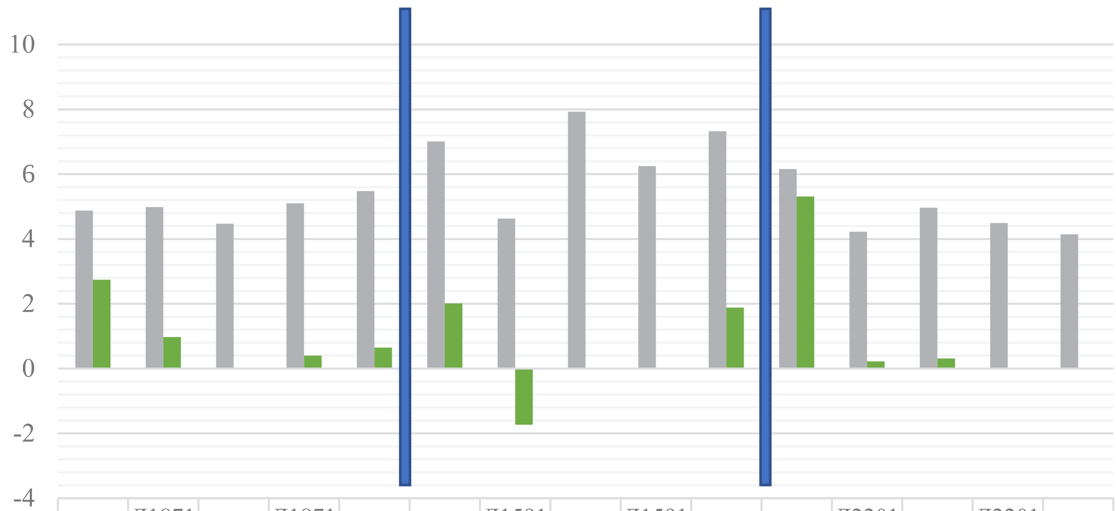
The degree of phenotypic dominance in F2 populations varied within a fairly wide range from negative dominance (Д-) to positive superdominance (НД+) (Fig. 1).

Analysing the F2 generation by the degree of phenotypic dominance, it was found that the highest efficiency of obtaining resistant lines was achieved by combining the following genetic systems: Serbia-Odessa+Lr34) + Phyto, (Aeg. CL) +Phyto, (Aeg. CL) + (Serbia-Odesa+Lr34) and (Serbia-Odesa+Phyto) in which inheritance was based on the pattern of positive heterosis (НД+), in two groups of combinations of genetic systems - (Serbia-Odesa+Lr34) +1AL/1RS and (Serbia-Odesa+Lr34) + (Aeg. CL) inheritance was observed according to the pattern of absolute dominance (Д+).

The combination of other genes and genetic systems was also quite effective and had an intermediate inheritance of resistance to leaf rust, except for the combination of crossing L15914 (Aeg. CL) with the variety Peremoha od. (1AL/1RS), in which the genes of susceptibility to leaf rust were dominant (Д-).

In order to completely understand the pattern of inheritance of the leaf rust resistance trait in F2 populations, the analysis of transgressive segregation of this trait was carried out (Table 2)

The data in Table 2. shows that the most effective donor of resistance to leaf rust, among the presented combinations, is the line L15914, which originates from Ae. Cylindrica. from Ae. Cylindrica. When used



	Л18716×Ф.177	Л18716×Перемога	Л18716×Щедрість	Л18716×Відповідь	Л18716×Л15914	Л15914×Ф.142	Л15914×Перемога	Л15914×Щедрість	Л15914×Відповідь	Л15914×16918	Л22016×Ф.177	Л22016×Перемога	Л22016×Щедрість	Л22016×Відповідь	Л22016×Л16918
F2	4,87	4,98	4,47	5,1	5,48	7,01	4,63	7,93	6,25	7,32	6,16	4,22	4,96	4,49	4,14
hp	2,74	0,97	-0,02	0,4	0,65	2,01	-1,73	0	0	1,88	5,31	0,22	0,31	-0,01	0

Fig. 1. The degree of phenotypic dominance in F2 populations depending on the combination of different leaf rust resistance control systems

Table 1

Pattern of inheritance of leaf rust resistance in F2 generation with different genetic control systems for this trait

№ of group	№ in/ord.	Crossing		P1	P2	F2	ratio		x^2	dominance class
		system	combination				received	expected		
1	1	(Serbia-Odesa+Lr34) +Phito	Λ18716(S)× Ph.177(S)	3	4	4,87	1,0:4,9: 10,0	1:6:9	1,82	**НД+**
	2	(Serbia-Odesa+Lr34) +1AL/1RS	Λ18716(S)×Peremoha(MS)	3	5	4,98	2,4:1,6:2,8:9,2	3:1:3:9	1,24	**Д+**
	3	(Serbia-Odesa+Lr34) +1BL/1RS	Λ18716(S)×Shchedrist'(MR)	3	6	4,47	1,8:14,1	1:15	3,88	**ПУ**
	4	(Serbia-Odesa+Lr34) +Western Europe	Λ18716(S)×Vidpovid'(MR)	3	6	5,1	2,2:3,9:0,9:8,9	3:3:1:9	2,56	**ПУ**
	5	(Serbia-Odesa+Lr34) +Wild relatives (Aeg. CL)	Λ18716(S)×Λ15914(MR)	3	6	5,48	5,9:10,1	7:9	1,61	**Д+**
2	6	Wild relatives (Aeg. SL) + Phyto	Λ15914(MR)× Ph.142(S)	6	4	7,01	12,1:3,9	13:3	1,77	**НД+**
	7	Wild relatives (Aeg. CL) +1AL/1RS	Λ15914(MR)×Peremoha(MS)	6	5	4,63	2,3:1,0:12,7	3:1:12	0,83	**НД-**
	8	Wild relatives (Aeg. CL) +1BL/1RS	Λ15914(MR)×Shchedrist'(MR)	6	6	7,93	15,7:0,3	15:1	1,78	**–**
	9	Wild relatives (Aeg. CL) +Western Europe	Λ15914(MR)×Vidpovid'(MR)	6	6	6,25	8,6:1,6:5,8	9:1:6	1,92	**–**
	10	Wild relatives (Aeg. SL) + (Serbia-Odesa+Lr34)	Λ15914(MR)×16918(S)	6	3	7,32	13,3:2,7	13:3	0,09	**НД+**
3	11	Serbia-Odesa+Phito	Λ22016(S)×Ph.177(S)	3	4	6,16	8,3:1,1:6,6	9:1:6	0,59	**НД+**
	12	Serbia-Odesa+1AL/1RS	Λ22016(S)×Peremoha(MS)	3	5	4,22	0,8:15,1	1:15	0,09	**ПУ**
	13	Serbia-Odesa+1BL/1RS	Λ22016(S)×Shchedrist'(MR)	3	6	4,96	2,1:2,7:1,5:9,7	3:3:1:9	2,69	**ПУ**
	14	Serbia-Odesa+Western Europe	Λ22016(S)×Vidpovid'(MR)	3	6	4,49	6,7:9,3	7:9	2,72	**ПУ**
	15	Serbia-Odesa+(Serbia-Odesa+Lr34)	Λ22016(S)×Λ16918(S)	3	3	4,14	0,5:15,5	1:15	1,16	–

Table 2

Transgressive segregation of brown rust resistance in F2 populations

№ of group	Crossbreeding combination	Number of plants studied	Intraspecific variability of F2 plants by the rate of resistance to leaf rust								
			Resistant (R)		Medium-resistant (MR)		Medium-susceptible (MS)		Susceptible (S)		Ts,%
			шт.	%	шт.	%	шт.	%	шт.	%	
	Λ18716×Ph.177	94	6	6,38	29	30,85	-	-	59	62,77	37,23
	Λ18716×Peremoha	40	6	15,00	4	10,00	7	17,5	23	57,50	25
1	Λ18716×Shchedrist'	77	9	11,69	-	-	-	-	68	88,31	11,69
	Λ18716×Vidpovid'	86	12	13,95	21	24,42	5	5,81	48	55,81	13,95
	Λ18716×Λ15914	89	33	37,08	-	-	-	-	56	62,92	37,08
	Λ15914× Ph.142	77	58	75,32	-	-	-	-	19	24,68	75,32
	Λ15914×Peremoha'	63	9	14,29	-	-	4	6,35	50	79,37	14,28
2	Λ15914×Shchedrist'	54	53	98,15	-	-	-	-	1	1,85	98,15
	Λ15914×Vidpovid'	80	43	53,75	-	-	8	10,0	29	36,25	53,75
	Λ15914×Λ16918	47	39	82,98	-	-	-	-	8	17,02	82,98
	Λ22016× Ph.177	90	47	52,22	-	-	6	6,67	37	41,11	58,89
	Λ22016×Peremoha	74	4	5,41	-	-	-	-	70	94,59	5,4
3	Λ22016×Shchedrist'	76	10	13,16	13	17,11	7	9,21	46	60,53	13,16
	Λ22016×Vidpovid'	98	12	12,24	-	-	-	-	86	87,76	12,24
	Λ22016×Λ16918	87	3	3,45	-	-	-	-	84	96,55	3,45

as a maternal component, the frequency of positive transgressions was the highest (from 53.7% when crossed with the variety Vidpovid' od., which has effective leaf rust resistance genes in its genotype, to 98.15% when crossed with the variety Shchedrist' od. with the 1BL/1RS translocation. The exception was the combination of crosses with Peremoha od.variety where the percentage of resistant forms was 14.29 and the frequency of transgression was 14.28. It is likely that the Peremoha od. variety has genes in its genotype that interact with each other to cause the dominance of susceptible forms over resistant ones. Another effective combination was L22016×Ph.177, in which the percentage of resistant forms was 52.22 and the frequency of transgression reached 58.89.

In the populations of second-generation hybrids, segregation for leaf rust resistance was observed. Most often (14.29-98.15 %) resistant forms were recorded in the second group of crossing combinations with the highest percentage of resistant forms in the crossing combination L15914×Shchedrist' od. (98.15 %). The exception was the combination of crosses L15914×Peremoha od. (14.29% of resistant forms) where the dominance of susceptible forms (79.37%) was observed. In the other two groups, susceptible forms of plants were most common (41.11-96.55%), except for one combination of crosses L22016×Ph.177 where resistant forms were 52.22% and susceptible forms 41.11%.

Conclusions. In order to increase the efficiency and accelerate the breeding work on creating genotypes resistant to leaf rust, it is important to know the patterns of inheritance of this trait by crossing parental components with different genetic resistance systems.

As a result of the study of the leaf rust resistance trait inheritance patterns in crossing parental components with different genetic resistance systems in F2 generation, it was found that in the presented crossing combinations, polygenic inheritance of leaf rust resistance was observed, with different types of gene interaction depending on their combination in a particular genetic system.

Thus, in such combinations of crosses as L18716 (S) × Peremoha od. (MS), L18716 (S) × Vidpovid' od. (MR) and L22016 (S) × Shchedrist' od. (MR), a split from resistant to medium-resistant, medium-susceptible and susceptible was observed with a ratio of 3:1:3:9, 3:3:1:9, 3:3:1:9, which corresponds to complementary gene interaction. Some of the combinations - L15914 (MR)×Ph.142 (S), L15914 (MR)×16918 (S) and L15914 (MR)×Peremoha od. (MS) - showed epistatic gene interaction with a segregation from resistant to susceptible, moderately susceptible and susceptible in the ratio of 13:3 and 12:3:1.

In combinations of Wild relatives + 1BL/1RS and Serbia-Odesa + Lr34 systems, a 1:15

segregatio was observed, which corresponds to a non-cumulative polymer.

The degree of phenotypic dominance in F2 populations varied within a quite wide range from negative dominance (Д-) to positive superdominance (НД+). It was found that the most effective for getting resistant genotypes are combinations of genetic systems - (Serbia-Odesa+Lr34) + Phyto, (Aeg. CL) +Phyto, (Aeg. SL) + (Serbia-Odessa+Lr34) and Serbia-Odessa+Fito in which inheritance was observed according to the scheme of positive superdominance (НД+) and (Serbia-Odesa+Lr34) +1AL/1RS and (Serbia-Odesa+Lr34) + (Aeg. SL) where inheritance was observed according to the scheme of positive dominance (Д+).

The combination of other genes and genetic systems was also quite effective and had an intermediate inheritance of leaf rust resistance.

The analysis of transgressive variability of leaf rust resistance trait in F2 populations showed that the effective donor of leaf rust resistance could be the line L15914, which originates from Ae. Cylindrica, when used as a maternal component, the frequency of positive transgressions was the highest (from 53.7% when crossed with the variety Vidpovid' od., which has effective leaf rust resistance genes in its genotype, to 98.15% when crossed with the variety Shchedrist' od. with 1BL/1RS translocation.

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