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GENETIC ANALYSIS OF A CROSS-POLLINATED SPECIES, *SECALE CEREALE* L., FOR THE CHARACTER WITH POLYMORPHIC GENETIC BASIS

Theoretical basis and an algorithm of calculations for frequencies of genes and genotypes in the population of species with obligate cross-pollination under assessment for the character of polymorphic genetic basis are proposed. Use of four rye populations and the F_1 and F_2 from their crossings allows to determine genetic control of β-amylase spectrum through identification of two genes, establishment of the allele number in each gene, and showing the linkage between β-Amy-1 and the gene for self-incompatibility S2.

Introduction. The interest to genetics of cultivated rye (*Secale cereale* L.) is caused by its importance as the pivotal cereal crop in the regions with poor sour soils and inclement winters, where cultivation of winter common wheat (*Triticum aestivum* L.) is ineffective. In addition, rye is an important source of resistance genes to pathogens, pests, and abiotic factors of environment for common wheat. By now, several genes, *Lr, Sr, Pm*, the resistance genes to Hessian fly and to the high content of aluminium in the soil were transferred from rye into wheat [1].

Investigations on rye genetics are hampered in mainly by its biological peculiarity, namely, by obligate cross-pollination caused by genetic system of self-incompatibility [2]. To overcome this difficulty, special genetic plant material (usually inbred rye lines) is developed and used. Such plant material is developed by selection of the most productive plants out of self-pollinated generations of spontaneously forming self-fertile rye mutants [3]. However, the inbred lines are characterised by low cytogenetical stability as well as by inbred depression that restricts their use in genetic analysis [3]. This approach is long and laborious, it has also some other defects. The self-incompatibility genes are located in three chromosomes out of seven chromosome pairs in rye genome [4], and the self-fertile lines are produced as a result of artificial selection. This can influence results on localisation of genes located in the same chromosomes, where the self-incompatibility genes are situated, by distortion of Mendelian segregations. Differencies in chromosome localisation of a number of genes for morphological and biochemical characters revealed in quite different plant material (the wheat-rye addition and substitution lines, on the one hand, and self-fertile rye lines, on the other hand) can be considered as an indirect evidence of the possibility of such contradictions [1, 5, 6].

Rye populations which we have investigated were developed by Dr. V. Skorik from the same initial population by directed selection for the plant height trait with continual cross-pollination inside the populations during 20 years. Concerning the other genes, which are not involved in control of the plant height, the rye populations kept their peculiar level of heterozygosity securing the preservations of fertility inside the population of this obligate cross-pollinator [7] that allows us to consider them as populations with free pollination.

Genetic analysis of the rye population as for the trait of electrophoretical spectrum of β-amylase

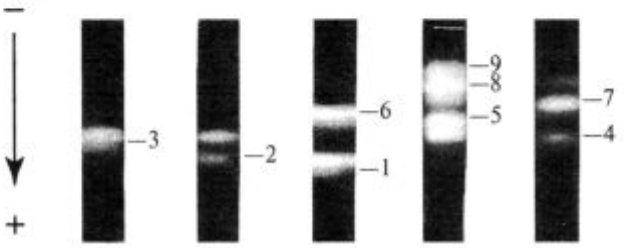


Fig. 1. Patterns of β-amylase spectrum in the rye populations

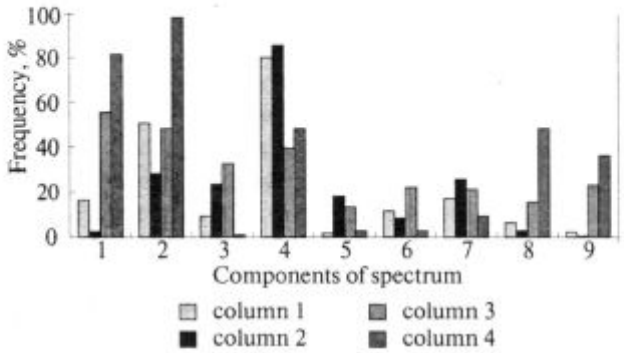


Fig. 2. Frequencies of components in electrophoretical spectrum of β-amylase in the populations BK (column 1), G 1 (column 2), G 2 (column 3), and G 3 (column 4)

was performed when realising the program on the search for marker genes, linkage of which with the genes for short stem allows to optimise genetic analysis and breeding of rye for this most important trait [8].

Material and methods. Four populations of rye (*Secale cereale* L.), Gnom 1 (G1), Gnom 2 (G2), Gnom 3 (G3), and Bolgarskaya Korotkostebelnaya (BK) were used as the object of genetic analysis. We have described their origination in detail earlier [7]. Hybrid populations F_1 and F_2 were obtained and analysed from the following crosses:

	Gnom 1 × Gnom 3
Gnom 3 × Gnom 2	Gnom 2 × Gnom 3
Gnom 3 × Bolgarskaya Korotkost.	Bolgarskaya Korotkost. × Gnom 3

Hybrid seeds F_1 were obtained using the usual for rye technique: in female plants, the spikelets were cut with scissors in a top one third of the glume; in two days, after appearance of loose stigma out of flowers, the male spike with mature pollen was put under parchment bag to the prepared female spike.

Each enumerated population was grown in field conditions in four repetition under its own textile bag. In such manner, it was isolated from the outside pollen. The free cross-pollination was realised inside the population. To characterise the plants on their β-amylase spectra, four seeds from each plant were taken and used for obtaining four spectra of β-amylase according to the methods elaborated for wheat [9]. A four seed sample is minimum, which allows us to distinguish the homozygous and heterozygous plants for the critical gene ($p < 0{,}01$). The results were processed according to the algorithms generalized by Rokitskii [10].

Results and discussion. Several typical β-amylase spectra out of the obtained spectrum body are presented at Fig. 1. The frequency of every isozyme (the spectrum component) was calculated using the binomial $(p + r)^2$, where p is the frequency of allele a_1, producing the considered band of the electrophoretical spectrum, and $r = 1 - p$ is the frequency of its absence, allele a_0. The corresponding component appears in the spectrum, when the plant possesses a_1 allele in any dose. The index p_1, the frequency of this allele, is calculated as $p_2 + 2p(1 - p_1) = g_1$, where g_1 is the portion of dominant phenotypes in the studied population. Therefore,

$$p_1 = (2-\sqrt{4-4g_1})/2 \qquad (1)$$

When the gene is polymorphic (there are several alleles) and the second allele produces its own component in the spectrum, the frequencies of three alleles were calculated [11], and the results were the same (Fig. 2). According to the corresponding calculations [10], four rye populations differed from each other for the frequencies of the components in the β-amylase spectrum.

To test the genes for their capacity to be independently transmitted from parents to offspring the following steps should be realised (the work example in the paper is based on the data of cross G1 × G3): basing on the frequencies of two genes tested (Table 1), to calculate the frequencies of the gametes with different combinations of these genes in two parental populations (step 1, Table 1); to determine the frequencies of the genotypes for these genes in F_1 offspring from the cross of these parental populations (step 2, Table 1); to determine the frequencies of gametes produced by F_1 plants. The frequencies of the gametes in F_1 are obtained from Table 1, step 2, as it is demonstrated in step 3. Using the calculated frequencies of gametes (step 3), to determine the frequencies of the genotypes involving two genes tested (step 4, Table 1). Through the use of the value of the empirical sample

Table 1

Testing the pair of any components in the β-amylase spectrum as to independent transfer of the genes controlling them into offspring

Cross component characterisation on *β-Amy* allele frequencies

	Allele frequencies on 1st gene (a)		Allele frequencies on 2nd gene (b)	
Gnom 1	a_1	0.012	b_1	0.614
Gnom 1	$(1-a_1)$	0.988	$(1-b_1)$	0.386
Gnom 3	a_2	0.555	b_2	0.269
Gnom 3	$(1-a_2)$	0.445	$(1-b_2)$	0.731

Step 1

Gamete forming in the Gnom 1 population

	$0.614(b_1)$	$0.386(1-b_1)$
$0.012\ (a_1)$	0.0074	0.0046
$0.988\ (1-a_1)$	0.6066	0.3814

Sum of gamete frequencies = 1

Gamete forming in the Gnom 3 population

	$0.269(b_2)$	$0.731(1-b_2)$
$0.555\ (a_2)$	0.1493	0.40571
$0.445\ (1-a_2)$	0.1197	0.3253

Sum of gamete frequencies = 1

Step 2

Forming of the F_1 genotypes

Gnom 1 ⇓ / Gnom 3 ⇒			a_2b_2 K	$(1-a_2)b_2$ L	$a_2(1-b_2)$ M	$(1-a_2)(1-b_2)$ N
			0.1493	0.1197	0.4057	0.3253
a_1b_1	1	0.0074	0.0011	0.0009	0.003	0.0024
$(1-a_1)b_1$	2	0.6066	0.0906	0.0726	0.2461	0.1973
$a_1(1-b_1)$	3	0.0046	0.0007	0.0006	0.0019	0.0015
$(1-a_1)(1-b_1)$	4	0.3814	0.0569	0.0457	0.1547	0.1241

Sum of gamete frequencies = 1

Step 3

ab = K1+1/2K2+1/2K3+1/4K4+1/2L1+1/4L3+1/2M1+1/4M2+1/4N1 = 0.1252
(1−a)b = L2+1/2K2+1/4K4+1/2L1+1/4L3+1/2L4+1/4M2+1/2N2+1/4N1 = 0.3163
a(1−b) = M3+1/2K3+1/2M1+1/2M4+1/2N3+1/4K4+1/4L3+1/4M2+1/4M1= 0.1583
(1−a)(1-b)=N2+1/2L4+1/2M4+1/2N2+1/2N3+1/4K4+1/4L3+1/4M2+1/4N1 = 0.4002

Step 4

Calculation of frequencies of the genotypes on components of β-amylase spectrum in F_2

			ab K	(1−a)b L	a(1−b) M	(1−a)(1−b) N
			0.1252	0.3163	0.1583	0.4002
Ab	5	0.1252	0.0157	0.0396	0.0198	0.0501
(1−a)b	6	0.3163	0.0396	0.1001	0.0501	0.1266
a (1−b)	7	0.1583	0.0198	0.0501	0.0251	0.0634
(1−a)(1−b)	8	0.4002	0.0501	0.1266	0.0634	0.1601

Sum of genotype frequencies = 1

Step 5

ab = K5+K6+K7+K8+L5+L7+M5+M6+N5 = 0,3348 · 852 = 285 (62)
0b = L6+N6+L8 = 0,3532 · 852 = 301 (699)
a0 = M7+M8+N7 = 0,1518 · 852 = 129 (40)
00 = N8 = 0,1601 · 852 = 136 (51)

F_2 (852), to calculate theoretical values of the phenotypic classes and compare them with the empirical values (empirical values are represented parenthetically after the calculated ones) using χ^2 (step 5). If the χ^2 value exceeds appreciably the table values for df = 3, genes a and b cannot be considered as independent at transmission from parents to offspring.

Following the algorithm (1)–(5), the genes controlling all nine components of β-amylase spectrum were tested in pairs for independent transmission. The χ^2 values (Table 2) indicate that it is necessary to test the hypothesis of two allele groups representing two independent genes: the spectrum components 5, 6 and 7 (one gene) are transmitted independently of spectrum components 1, 2, 3, 4, 8, and 9 (another gene) in the majority of pair combinations of the components.

Comparison of the spectra obtained from different seeds in four parental populations and F_2 from all crosses shows both the spectra without any components and spectra containing 8 components out of 9. So, the spectrum can contain all six components controlled by the second gene, whereas only two components out of three ones controlled by the first gene were discovered in all spectra. Rye is diploid organism and any gene can be represented in its genome by two alleles only. So, the first gene has four alleles in the populations studied. Expression of three alleles of four ones results in the spectrum components 5, 6, and 7, while the fourth allele does not control synthesis of any isozyme (null-allele).

Comparing theoretical frequencies of phenotypic classes for the first gene *β-Amy* in F_2 (they are calculated according to the algorithm step 1–step 5, Table 1) with the empirical ones in the column BC, Table 3 shows their discrepancy in all cases (see the χ^2 value in the same column). The character of this

Table 2

Results of studying the paired associations of the β-amylase spectrum components as to independent inheritance of the genes controlling them (χ^2 values, df = 3)

Component pair	Cross			Component pair	Cross		
	BK × G3	G1 × G3	G2 × G3		BK × G3	G1 × G3	G2 × G3
1–2	88,375	354,042	24,495	3–7	40,037	25,689	22,884
1–3	91,902	300,22	9,150	3–8	40,854	45,508	61,117
1–4	68,949	388,062	55,788	3–9	46,470	124,460	39,331
1–5	**10,998***	311,549	**9,085**	4–5	**14,044**	154,036	34,693
1–6	**6,759**	276,117	**4,058**	4–6	**10,952**	113,916	34,764
1–7	**14,950**	272,782	25,093	4–7	**15,936**	109,537	45,264
1–8	22,904	294,495	56,344	4–8	23,063	152,141	84,436
1–9	21,675	359,747	34,819	4–9	25,992	202,87	67,104
2–3	118,379	183,822	15,647	5–6	**5,686**	54,959	**2,740**
2–4	45,664	177,716	38,541	5–7	**10,792**	52,000	25,546
2–5	19,823	111,763	**3,05**	5–8	**12,104**	74,788	55,55
2–6	18,043	71,906	**11,187**	5–9	**15,64**	148,731	34,167
2–7	21,813	66,316	35,906	6–7	**15,08**	**8,263**	33,641
2–8	24,939	92,148	54,559	6–8	**6,785**	32,761	54,732
2–9	32,114	159,879	33,085	6–9	**10,527**	109,11	33,302
3–4	58,443	126,926	41,930	7–8	36,109	28,144	65,513
3–5	38,900	68,932	**9,212**	7–9	19,176	104,514	45,028
3–6	34,77	26,120	**9,801**	8–9	18,883	144,941	46,071

* The values, which do not exceed the table values (α =0,001), are marked in thick print.

Table 3

The frequencies of gametes and phenotypes on the first gene of *β-Amy* in generations F_1 and F_2 from crossing four different rye populations

Phenotype classes	Empirical		Theo-retical	Compo-nent	Gamete frequencies			
					F_1		F_2	
	BC	AC*			BC	AC*	BC	AC*
				BK × Gnom 3				
77	47	64	64	7	0,1165	0,1745	0,1766	0,1206
66	4		31	6	0,058		0,0375	
55	9	9	11	5	0,02	0,02	0,0422	0,02884
00	238	238	207	0	0,8055	0,08055	0,7436	0,8509
76	13		5					
75	6	9	1					
65	3		1					
χ^2	33,92	17,72	320					
				Gnom 3 × BK				
77	29	66	63	7	0,1165	0,1745	0,1186	0,1156
66	21		30	6			0,0961	
55	11	11	10	5	0,02	0,02	0,0385	0,0210
00	233	233	202	0	0,8055	0,8055	0,7468	0,8633
76	16		4					
75	0	2	1					
65	2		1					
χ^2	24,94	8,15	312					
				Gnom 2 × Gnom 3				
77	46	70	42	7	0,126	0,2075	0,2875	0,1968
66	1		26	6	0,0815		0,065	
55	2	2	8	5	0,026	0,026	0,0125	0,0075
00	127	127	118	0	0,7665	0,7665	0,635	0,7957
76	23		4					
75	0	1	1					
65	1		1					
χ^2	41,63	4,29	200					
				Gnom 3 × Gnom 2				
77	7	11	54	7	0,126	0,2075	0,0327	0,0233
66	1		34	6	0,0815		0,0115	
55	10	10	11	5	0,026	0,026	0,0404	0,0214
00	238	238	153	0	0,7665	0,7665	0,9154	0,9554
76	3		5					
75	0	1	2					
65	1		1					
χ^2	88,35	84,66	260					
				Gnom 1 × Gnom 3				
77	132	158	211	7	0,1585	0,204	0,1561	0,0981
66	24		56	6	0,0455		0,0299	
55	18	18	121	5	0,0945	0,0945	0,0217	0,0112
00	675	675	419	0	0,7015	0,7015	0,7922	0,8906
76	2		12					
75	0	1	26					
65	1		7					
χ^2	204,87	199,85	852					

* BC — empirical frequencies before combining classes 77, 66, 76 in class 77, as well as the classes 75, 65 in class 75; AC — empirical frequencies after class combining.

discrepancy as well as our experience concerning assessment of spectra allow us to suggest that the components 6 and 7 are not always distinguished from each other. In addition, in all cases the empirical frequency of phenotypes 00 exceeds the theoretical one. To correct the frequencies, the phenotypic classes 77, 76, and 66, as well as 75 and 65 were combined (the column AC in Table 3). Now we have four phenotypic classes instead of seven ones and the fitting value of χ^2 (see values χ^2 in column AC) for three crosses out of five crosses studied. In two crosses, G3 × G2 and G1 × G3, the empirical distribution of phenotypic classes was not corrected by class combining. Just these two distributions are characterised by essential excess of the 00-penotypes in comparison with three other crosses and lack of spectrum components affects all three components, 5, 6, and 7. Our experience allows us to perceive any methodical discrepancy at developing the β-amylase spectrum, which can not be now fixed and corrected. Obviously, just owing to this circumstance, the above crosses did not show the independent transmission of alleles of the two hypothetical genes *β-Amy* (Table 3). According to the Hurdy-Weinberg law [11], the frequencies, formed in the population of gametes produced by the F_1 plants, will agree with the frequencies of gametes produced by plants F_2 under free interchange of gametes when there is no selective pressure against specific ones. Gamete frequencies with different alleles of the first gene *β-Amy* in these two generations are shown in Table 3. Frequency fluctuations of the same gametes in two consecutive generations were found to be casual by comparison of their confiding interval at the signification level 0,001. According to our data, they depend mainly on the experience error when developing and assessing the electrophoregrammes. So, transmission of the first gene of *β-Amy* from parents to offspring is suggested to be independent of any selection factor.

Since 2nd gene of *β-Amy* can be represented in the same genotype with six components of spectrum, the cluster nature of the alleles of this gene may be deducted. To observe in diploid organism the phenotypic dispersion from the absence of any isozyme (component) in the spectrum up to six isozymes including all possible combinations of different isozymes, which was actually in our case, minimum 12 alleles controlling synthesis of specific isozymes and 0-allele should be available in the parental populations (Table 4). The allele compositions are supposed by common determining of sufficient minimum of alleles taking into account

Table 4

Allele frequencies of cluster 439812 in populations of the cross components*

Alleles	Bolg.korotkost.		Gnom 1		Gnom 2		Gnom 3	
	BC	AC	BC	AC	BC	AC	BC	AC
439000	0	0	0.0059	**0.003**	0.0577	**0.0385**	0.0046	0.0046
000812	0	0	0	0	0.0144	0.0144	0.2315	**0.1944**
409000	0.0174	**0.0116**	0	0	0.0769	**0.0577**	0.1667	0.1667
400800	0.0145	**0.0087**	0	**0.006**	0.0288	**0.0144**	0.0231	0.0231
430000	0.0872	0.0872	0.1905	**0.1964**	0.101	**0.0577**	0	0
000012	0.1221	0.1221	0.0178	**0.0119**	0.4038	0.4038	0.4120	0.412
000802	0.0174	**0.0116**	0	0	0.0096	0.0096	0.0417	0.0417
009000	0	0	0	0	0	0	0.0092	0.0093
400000	0.5058	0.5058	0.5357	**0.5268**	0.1683	**0.1298**	0.0556	**0.0509**
000002	0.1889	0.1889	0.1488	**0.128**	0.0961	**0.0817**	0.0556	**0.0417**
000800	0.0232	**0.0116**	0.0149	0.0149	0.0240	0.024	0	0
030000	0	0	0.0327	**0.0179**	0	0	0	0
000000	0.0232	**0.0523**	0.0536	**0.0952**	0.0192	**0.1683**	0	**0.0556**

* Frequencies, in which the values in the BC and AC columns differ from each other, are in thick print.

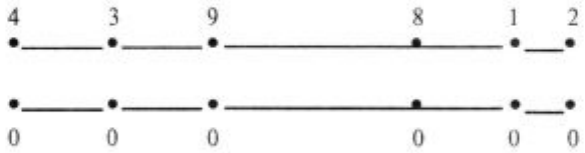
Table 5

Empirical and theoretical values of the phenotypical classes on the β-amylase spectrum in F_2 from crossing the four rye populations*

Phenotyp. classes	BK × G3			G1 × G3			G2 × G3		
	E	BC	AB	E	BC	AC	E	BC	AC
439000	9	3.34	3.31		20.27	18.99		6.47	4.44
439812	2	0.17	0.14		1.04	0.63		1.53	0.90
439800	7	0.04	0.03	11	0.17	0.14	1	0.47	0.26
439012		0.40	0.39		1.94	1.37		5.08	3.51
439802		0.04	0.04		0.19	0.13		0.32	0.22
439002		0.18	0.17		0.92	0.55		0.94	0.53
000812	3	43.64	36.06	3	92.53	78.36		35.05	31.85
409812	2	6.99	5.69	7	16.89	14.19	1	6.10	4.78
400812	6	25.83	22.71	11	67.47	61.76		11.26	9.96
430812		3.23	2.71		18.78	16.27		2.48	1.20
009812		0.34	0.29		0.91	0.77	1	0.23	0.19
030812		0	0		3.23	1.48		0	0
409000	5	21.04	22.59		54.69	60.58		9.32	11.97
409800		1.85	1.29	1	2.79	3.24		1.90	1.42
409012	3	15.73	15.24	1	30.52	30.10	2	19.87	18.30
409802	2	1.74	1.52	8	2.958	2.96	1	1.25	1.15
409002	4	7.20	6.58		14.51	12.04	4	3.69	2.77
400800	3	5.87	4.56	104	10.37	13.06		2.06	2.11
430800	16	0.69	0.52	68	4.13	4.03		0.65	0.29
400802	19	7.14	6.19	105	12.92	12.87	2	2.20	1.58
430000	60	8.77	9.88	87	70.95	75.07	2	2.96	2.50
430012	13	7.45	7.45		34.88	35.47	2	8.24	4.71
430802		0.82	0.74		3.38	3.49		0.52	0.29
430002		3.41	3.22	1	16.58	14.19		1.53	0.71
000012	66	45.71	51.75	37	86.60	96.15	102	47.23	61.61
009012		0.79	0.79		1.69	1.67	2	0.75	0.75
400012	44	47.97	47.58	43	108. 28	104.33	5	18.26	14.74
030012	1	0	0		5.99	3.22	1	0	0
000802		3.94	3.64	3	6.51	7.40		1.50	2.33
009802		0.09	0.08		0.16	0.16		0.047	0.05
030802		0	0		0.58	0.32		0	0
009000		0.04	0.17		0.23	0.61		0.02	0.21
009002	1	0.36	0.34		0.81	0.67		0.14	0.11
009800		0.03	0.02		0.06	0.06		0.02	0.02
039000		0	0		0.13	0.07		0	0
400000	3	27.30	34.41	95	87.96	108.21	10	2.93	5.68
400002	46	21.96	20.54	219	51.47	41.75	21	3.39	2.23
000002	1	5.69	8.23	33	13.56	17.03	33	1.44	3.52
030002	1	0	0	2	2.85	1.29		0	0
000800	2	0.13	0.21		0.39	1.00		0.07	0.57
030800		0	0	1	0.21	0.11		0	0

* BC — theoretical frequencies are calculated using gametes out of BC columns of Table 4, AC are calculated using the gametes out of the AC column of Table 4.

the composition of all zygotes. Appearance of any spectrum out of the totality of spectra which we have recorded in four parental populations and in F_2 from three crosses may be justified through the pair combination of these alleles. Sorting the spectra for the components 1, 2, 3, 4, 8, and 9 allows us to determine availability and frequency of the alleles listed in Table 4 in parental populations using formula (1). Such simple deliberation was initial: the genotype producing gametes contains two alleles, they may be either identical or distinguish. In overwhelming majority of cases, the observed spectra allow us to differ heterozygotes from homozygotes taking into account the listed minimal set of alleles (column BC, Table 4). The main exception is formed by those genotypes, which may be heterozygous over the gamete with 0-allele. In such cases, the frequency of 0-allele was compared with the frequency of that allele pairing with which the 0-allele forms the zygote of doubtful genotype. When the frequency of 0-allele is essentially lower than the frequency of expressing allele, the genotype is regarded as homozygote. Then, involvement of 0-allele is excluded, decreasing in that way its frequency in population. When the frequency of 0-allele is comparable with the frequency of expressing allele, the genotype is regarded as heterozygous (column AC, Table 4). In addition, there are other doubtful conclusions about composition of gametes giving rise to specific zygote, such cases are not numerous and the possible errors are disregarded. The frequencies of different alleles combining one or another components of spectrum vouch for such order of genes controlling the specific components in the cluster:



Recombination inside of cluster, which was realised during evolution of rye, resulted in the great number of alleles, which is detected in genetic analysis of the rye populations for β-amylase spectrum. The number of presumed alleles is restricted with that minimum, that can explain the appearance of actual genotypes. It is possible that the number of alleles is greater. However, using the material represented, it cannot be revealed.

According to the algorithm (1)–(5), the theoretical values of phenotypic classes in the F_2 populations of the studied crosses were calculated. The empirical frequencies never agreed with the theoretical ones (Table 5). However, there are two common peculiarities: 1) lack of genotypes including the alleles, which high frequencies are inherent in the cross components; 2) the reciprocal crosses show different results (data are not presented). These two peculiarities are typical in a situation, when the critical gene is linked with the self-incompatibility gene. One of the genes for self-incompatibility, *S2*, is indeed situated on chromosome 5R [5], where the identified β-amylase gene, *β-Amy-1*, is localised [5]. Possibly, the gene which we have identified is identical to *β-Amy-1* gene. Comparison of the frequencies of gametes in two consistent generations, F_1 and F_2, shows two manners of change in frequencies of gametes with different alleles for gene *β-Amy-1*: abrupt decrease in high frequencies and abrupt increase in low frequencies. At that, in contrast to the situation that was considered for the first gene, which can be presumed to be *β-Amy-2* gene earlier localised, on chromosome 1RL [5], confiding intervals for the frequencies of the same alleles in generations F_1 и F_2 never intersect. Such peculiarity is typical for inheritance of genes linked with gene for self-incompatibility [11]. So, the gene identified in our rye populations is suggested to be identical to gene *β-Amy-1*, situated on chromosome 5R and linked with self-incompatibility gene *S2*, situated on the same chromosome [5].

РЕЗЮМЕ. Дано теоретические обоснование и представлен алгоритм расчетов, связанных с определением частот генов и генотипов в популяции при работе с полиморфным признаком, когда генетическому анализу подвергается вид с облигатным перекрестным опылением. Ипользование четырех популяций ржи и гибридов F_1 и F_2 от их скрещивания друг с другом позволило установить генетический контроль спектра β-амилазы, идентифицировав два гена, установив количество аллелей для каждого из них и показав наличие сцепления между геном *β-Amy-1* и геном самонесовместимости *S2*.

РЕЗЮМЕ. Дано теоретичне обгрунтування і наведено алгоритм розрахунків, пов'язаних із встановленням частот генів і генотипів в популяції при роботі з поліморфною ознакою, коли генетичному аналізу піддано вид з облігатним перехресним запиленням. Використання чотирьох популяцій жита і гібридів F_1

та F_2 від їх схрещування одного з одним дало змогу встановити генетичний контроль спектра β-амілази, ідентифікувавши два гени, встановивши кількість алелів для кожного з них і показавши наявність счеплення між геном *β-Amy-1* та геном самонесумісності *S2*.

REFERENCES

1. *McIntosh R.A., Hart G.E., Devos K.M., Gale M.D., Rogers W.J.* Catalogue of gene symbols for wheat. // A.E.Slinkard (Ed.) Proc. 9-th Intern Wheat Genet. Symp. Saskatoon, Saskatchewan, Canada, 2–7 August, 1998. — Univ. Extension Press, 1998. — V. 5. — 235 p.
2. *Fehr W.R.* Principles of cultivar development. V. 1. Theory and technique. — New York; London, 1987. — 536 p.
3. *Smirnov V.G., Sosnikhina S.P.* Genetics of Rye [in Russian]. — Leningrad, 1984. — 264 p.
4. *Voylokov A.V., Korzun V., Berner A.* Mapping of three self-fertility mutations in rye (*Secale cereale* L.) using RFLP, isozyme and morphological markers // Theor. Appl. Genet. — 1997. — **97**. — P. 147–153.
5. *Melz G., SchlegelR., Thiele V.* Genetic linkage map of rye (*Secale cereale* L.) // Theor. Appl. Genet. — 1992. — **85**. — P. 33–45
6. *Malyshev S.V., Korzun V.Y., Zabenkova K.I., Voylokov A.V., Berner A., Kartel N.A.* Comparative molecular-genetic mapping of the rye genome (*Secale cereale* L.) and other cereals // Tsitologiya i Genetika [Cytology and Genetics]. — 2003. — **37**, № 5. — P. 9–20.
7. *Skorik V.V., Skorik N.V.* Genetical statistical characterisation of the new donors of short stem in rye // Tsitologiya i Genetika [Cytology and Genetics]. — 2002. — **36**, № 6. — P. 16–20.
8. *Martynenko V.S., Skorik V.V., Antonyuk M.Z.* Genetic analysis of the short stem populations of rye (*Secale cereale* L.) for the trait plant height // Tsitologiya i Genetika [Cytology and Genetics]. — 2003. — **37**, № 5. — P. 21–29.
9. *Antonyuk M.Z., Ternovskaya T.K.* Isozymes of beta- and alpha-amylase for identification of genetic material of three *Aegilops* species involved in the common wheat genome // Tsitologiya i Genetika [Cytology and Genetics]. — 1995. — **29**, № 2. — P. 3–8.
10. *Rokitskii P.F.* Biologic Statistics [in Russian]. — Minsk, 1973.
11. *Li Ch.* First Course in Population Genetics / Translation into Russian. — Moscow: MIR, 1978. — 554 p.

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