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GENETIC ANALYSIS OF THE *T. AESTIVUM/AE. SHARONENSIS* INTROGRESSIVE LINES OF COMMON WHEAT FOR RESISTANCE TO POWDERY MILDEW

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Results of investigation of peculiarities of common wheat hybridological analysis for a discrete character, resistance for powdery mildew, governed by the alien gene from Ae. sharonensis are present. Relation between genome structure of crossed introgressive lines and deviation of empirical ratios of segregation in F_2 from theoretical, based on the assumption about monogenic inheritance of considered character is established. The approach to the quantitative count of influence of such connection on distortion of actual segregation in comparison with theoretically expected ratio is developed.

Introduction. It is known, that use of the introgressive lines, there are chromosome-addition, chromosome-substitution, and translocation lines, in hybridological analysis results usually in appearance of such ratios of phenotypic classes in segregating generations that differ essentially from the theoretical ones expected from the certain assumptions about the genetic control of investigated characters [1]. When crossing the chromosome-addition or chromosome-substitution lines with wheat, the alien chromosome in F_1 is in monosomic state. Behavior of univalent chromosomes in meiosis of wheat plants was investigated in detail. Frequency of transfer of monosomic chromosomes through female and male gametes averages 25 % and 4 %, correspondingly [2]. It is shown besides that individual wheat chromosomes have their own features of behavior in the metaphase 1 of meiosis PMC (pollen mother cells) [3, 4], and in some cases it will be reflected, apparently, in ratios of phenotypic classes in segregating generations. Hybrid F_1 between a line with one pair of substituted chromosomes and the recurrent wheat variety can be considered as a plant with two univalents [5]. This allows us to correct correspondingly the expected ratios of phenotypic classes. If the obtained theoretical calculations ratio does not prove to be true to the experimental data, it is necessary to study a possibility of prevailing (positive selection) or insufficient (negative selection) transfer of an alien chromosome. Results of such studying can be used later in a genetic analysis of the lines with the given alien chromosome [6, 7].

In our research, alien chromosome substitution and chromosome-translocation lines of common wheat are used. Genome of these lines involves the whole chromosome $4S^l$, known as gametocidal chromosome [8], or its segment (translocation). Study of behavior of alien, including gametocidal, chromosomes both in homo- and in hemizygous state shows, that their specific action can result in deviations from standard segregation ratios in hybrid offspring received with use of introgressive lines [7]. In turn, this considerably complicates the genetic analysis for the characters controlled by alien genes. Our research is directed to definition of stages of the genetic analysis, on which it is possible to take into account cytogenetical features of cross components for understanding results of segregation in hybrid generations.

Material and methods. The following plant material was used: i) introgressive lines of common

Table 1

The averages of bivalents, univalents, and multivalents per cell in metaphase 1 of meiosis in PMC of hybrids F_1 from crossing the introgressive lines with the variety Aurora[1]

Crosses	Cell number	Closed bivalents	Open bivalents	Univalents	Multivalents		
					III	IV	Total
Aurora	77	16,97 ± 0,18	3,81 ± 0,18	0,34 ± 0,09	0	0,03 ± 0,02	0,03 ± 0,02
788×Avrora	95	16,08 ± 0,15***	2,4 ± 0,15***	4,34 ± 0,11***	0,2 ± 0,04***	0,01 ± 0,01	0,22 ± 0,04***
790×Avrora	78	15,86 ± 0,18***	2,95 ± 0,18***	4,19 ± 0,1***	0,06 ± 0,03*	0 ± 0	0,06 ± 0,03
791×Avrora	55	13,89 ± 0,27***	4,33 ± 0,26	4,42 ± 0,18***	0,38 ± 0,07***	0 ± 0	0,38 ± 0,07***
834×Avrora	50	16,92 ± 0,18	2,56 ± 0,2***	2,98 ± 0,19***	0,02 ± 0,02	0 ± 0	0,02 ± 0,02
835×Avrora	95	16,06 ± 0,17***	3,63 ± 0,15	2,53 ± 0,13***	0 ± 0	0,02 ± 0,01	0,02 ± 0,01
890×Avrora	69	16,36 ± 0,18	2,36 ± 0,18***	4,07 ± 0,1***	0,16 ± 0,04***	0 ± 0	0,16 ± 0,04**
891×Avrora	66	15,92 ± 0,2***	2,55 ± 0,22***	3,85 ± 0,14***	0,41 ± 0,06***	0 ± 0	0,41 ± 0,06***
933×Avrora	59	16,88 ± 0,19	2,81 ± 0,18***	2,49 ± 0,14***	0,02 ± 0,02	0,02 ± 0,02	0,03 ± 0,02
936×Avrora	6	16,00 ± 0,73	3,67 ± 0,76	2,67 ± 0,42***	0 ± 0	0 ± 0	0 ± 0
937×Avrora	47	16,36 ± 0,23*	2,43 ± 0,23***	4,09 ± 0,1***	0,09 ± 0,04*	0,02 ± 0,02	0,11 ± 0,05
1023×Avrora	37	15,22 ± 0,22***	3,38 ± 0,18	4,16 ± 0,18***	0,22 ± 0,07**	0 ± 0	0,22 ± 0,07**
1024×Avrora	55	15,67 ± 0,19***	2,89 ± 0,2***	4,47 ± 0,16***	0,11 ± 0,04*	0,02 ± 0,02	0,13 ± 0,05*
1025×Avrora	47	14,69 ± 0,28***	3,85 ± 0,25	4,28 ± 0,18***	0,13 ± 0,06*	0,06 ± 0,04	0,19 ± 0,07*
1026×Avrora	56	15,7 ± 0,18***	2,88 ± 0,18***	4,21 ± 0,15***	0,21 ± 0,06***	0 ± 0	0,21 ± 0,06**
1077×Avrora	83	16,43 ± 0,13*	3,31 ± 0,13*	2,28 ± 0,09***	0,01 ± 0,01	0,05 ± 0,02	0,06 ± 0,03
1096×Avrora	57	16,16 ± 0,24**	3,23 ± 0,21*	2,74 ± 0,17***	0 ± 0	0,12 ± 0,04*	0,12 ± 0,04*
1166×Avrora	44	15,2 ± 0,23***	2,7 ± 0,23***	6,18 ± 0,14***	0 ± 0	0 ± 0	0 ± 0

[1]Note (here and in table 2): according to t-criterium, the average differs from the same index for the variety Aurora at significance level:* — 0,05, ** — 0,01, *** — 0,001.

wheat with genetic material from *Aegilops sharonensis* [9]; ii) the genome substitution form, Aurosis, obtained as a result of substitution of subgenome D of the winter common wheat variety Aurora (*Triticum aestivum* L., AABBDD) with genome S^lS^l of diploid species *Aegilops sharonensis* Eig. [10]; iii) the winter common wheat variety Aurora; iv) hybrid generations F_1, F_2 and F_3 from crossing of introgressive lines with each other and with the variety Aurora.

Hybrid seeds were obtained by artificial manual pollination of ears emasculated up to a stage of maturation of pollen grains. Resistance to powdery mildew was assessed on the nine mark scale [11], according to which the mark 9 characterizes plants without attributes of the disease and the mark 1 indicates a defeat of whole plant. Three years successively, the plant material was assessed for resistance to powdery mildew. The plants with an assessment of marks 9—7 were classified as resistant ones, the plants with an assessment 6 and lower were recorded as susceptible.

Chromosome configurations in M1 of meiosis were studied in mother cells of pollen from anthers fixed in 2 % acetocarmine after removing from ears, situated in a tube between the second and the third leaves.

Results and discussion. To determine the quality of alien introgressions in group of the introgressive lines resistant to powdery mildew and characterized earlier [12] as for biochemical and morphological marker characters, chromosome configurations in M1 of meiosis in PMC in hybrids F_1 of these lines with the recurrent variety Aurora (table 1) were investigated. For some cross combinations, a higher number of closed bivalents in comparison with the variety Aurora has been established. It does not contradict to the opinion about recessiveness of desynapsis genes, which presence was shown for the variety Aurora [13]. Hybrids F_1 of the variety Aurora with lines 788, 791, 890, 891, 1023, 1026 essentially differ from the variety Aurora on formation of trivalents. Hybrid with line 1096 is characterized with a higher frequency of quadrivalents. Results of studying the chromosome configurations in M1 of meiosis in hybrids F_1 between introgressive lines (table 2) testify that appearance of multivalents at crossing with the

TSitol. Genet. - Vol.39(3)   www.cytgen.com

Table 2

The averages of bavalents, univalents, and multivaents per cell in M1 of meiosis in PMC of hybrids F_1 from crossing the introgressive lines with each other

Crosses.	Cell number	Closed bivalents	Open bivalents	Univalents	Multivalents		
					III	IV	Всього
788×790	41	17,17 ± 0,26	3,15 ± 0,19*	0,29 ± 0,13	0 ± 0	0,27 ± 0,07**	0,27 ± 0,07**
788×1025	48	15,02±0,3***	4,98±0,28***	1,21±0,22***	0,04±0,03	0,17±0,06*	0,21±0,07**
788×1096	27	15,26 ± 0,27***	2,89 ± 0,27**	4,26 ± 0,25***	0,48 ± 0,1***	0 ± 0	0,48 ± 0,1***
790×791	23	16,91 ± 0,33	3,65 ± 0,29	0,22 ± 0,11	0,22 ± 0,11*	0 ± 0	0,22 ± 0,11
790×936	54	16,98 ± 0,23	3,24 ± 0,19*	0,98 ± 0,21**	0,02 ± 0,02	0,13 ± 0,05*	0,15 ± 0,05*
834×835	39	17,74 ± 0,19**	2,95 ± 0,2**	0,62 ± 0,17	0 ± 0	0 ± 0	0 ± 0
834×891	40	15,88 ± 0,21***	2,28 ± 0,2***	4,18 ± 0,23***	0,48 ± 0,08***	0,03 ± 0,03	0,5 ± 0,08***
834×1096	43	18,74±0,23***	2,05±0,21***	0,33±0,11	0±0	0,02±0,02	0,02±0,02
835×1025	18	15,39 ± 0,34***	2,61 ± 0,27***	3,94 ± 0,32***	0,61 ± 0,12***	0,06 ± 0,06	0,67 ± 0,11***
835×1096	54	18,15±0,25***	2,28±0,21***	0,93±0,19**	0±0	0,06±0,03	0,06±0,03
890×790	47	17,68 ± 0,23*	2,96 ± 0,23**	0,64 ± 0,16	0 ± 0	0,02 ± 0,02	0,02 ± 0,02
890×933	13	14,23 ± 0,51***	4 ± 0,51	5,23 ± 0,28***	0 ± 0	0,08 ± 0,08	0,08 ± 0,08
891×1024	59	17,44 ± 0,2	2,86 ± 0,18***	0,46 ± 0,12	0,02 ± 0,02	0,22 ± 0,06**	0,24 ± 0,06***
933×790	38	15,82 ± 0,22***	2,29 ± 0,23***	4,03 ± 0,17***	0,55 ± 0,08***	0,03 ± 0,03	0,58 ± 0,09***
933×834	76	18,51 ± 0,22***	2,24 ± 0,19***	0,5 ± 0,13	0 ± 0	0 ± 0	0 ± 0
933×1077	30	17,83 ± 0,2**	3 ± 0,2**	0,2 ± 0,11	0 ± 0	0,03 ± 0,03	0,03 ± 0,03
936×890	29	17,31 ± 0,39	2,79 ± 0,34**	0,66 ± 0,21	0,1 ± 0,06	0,21 ± 0,08*	0,31 ± 0,09**
937×790	58	17,02 ± 0,24	3,31 ± 0,22	0,72 ± 0,15*	0,07 ± 0,03*	0,1 ± 0,04	0,17 ± 0,05**
937×891	41	15,76 ± 0,24***	4,76 ± 0,21***	0,41 ± 0,13	0,02 ± 0,02	0,12 ± 0,05	0,15 ± 0,06*
937×1025	44	15,86 ± 0,28**	4,25 ± 0,27	1,64 ± 0,27***	0,05 ± 0,05	0 ± 0	0,05 ± 0,05
1023×790	15	17,87±0,26**	2,4±0,19***	1,47±0,36**	0±0	0±0	0±0
1023×791	48	18,1 ± 0,22***	2,27 ± 0,22***	0,77 ± 0,16*	0,02 ± 0,02	0,1 ± 0,04	0,13 ± 0,05
1023×1024	59	18,66 ± 0,18***	2,19 ± 0,16***	0,25 ± 0,09	0,02 ± 0,02	0 ± 0	0,02 ± 0,02
1024×790	19	19,63 ± 0,23***	1,11 ± 0,17***	0,16 ± 0,12	0,05 ± 0,05	0,05 ± 0,05	0,11 ± 0,07
1025×891	27	17,96±0,35*	2,37±0,32***	0,89±0,19*	0±0	0,11±0,06	0,11±0,06
1025×1077	25	13,56±0,32***	4,8±0,33**	4,8±0,26***	0,16±0,07*	0±0	0,16±0,07
1026×1024	32	18,25 ± 0,25***	2,13 ± 0,18***	0,47 ± 0,16	0,09 ± 0,07	0,13 ± 0,06	0,22 ± 0,09*
1077×791	56	15,79 ± 0,18***	2,77 ± 0,17***	4,3 ± 0,14***	0,2 ± 0,05***	0 ± 0	0,2 ± 0,05**
1096×790	29	15,38 ± 0,19***	3,17 ± 0,18*	4,38 ± 0,21***	0,17 ± 0,09*	0 ± 0	0,17 ± 0,09
1096×891	33	14,52 ± 0,23***	3,61 ± 0,25	4,76 ± 0,3***	0,33 ± 0,08***	0 ± 0	0,33 ± 0,08***
1096×1023	28	15,89 ± 0,24***	2,46 ± 0,28***	3,79 ± 0,22***	0,36 ± 0,09***	0,11 ± 0,06	0,46 ± 0,11***
1096×1077	48	19,27 ± 0,18***	1,4 ± 0,16***	0,58 ± 0,15	0 ± 0	0,02 ± 0,02	0,02 ± 0,02
1166×1024	74	16,34±0,17**	2,96±0,16***	2,81±0,16***	0,05±0,03*	0,11±0,04*	0,16±0,04**

variety Aurora of lines 791, 890, 1023, 1026 was caused obviously by presence of some chromosome segments in their genomes, which are the same ones at least for two no-homologous chromosomes. Chromosomes of lines 788, 891, 1096 form multivalents with chromosomes of the variety Aurora probably on other cause. During development of these lines, reciprocal translocations could arise in their genomes. That is why the meiosis in the lines happens without special abnormalities, whereas their chromosomes are capable to form multivalents with the variety Aurora and with some other lines. Reciprocal translocations displayed by crossing with the variety Aurora, could appear only due to rearrangement of wheat chromosomes. Analyzing data about chromosome configurations in M1 of meiosis in the hybrids between the introgressive lines and the variety Aurora, it is possible to make the certain conclusions about genetic structure of these lines. Thus, the quantity of univalent chromosomes at the highest association of chromosomes in M1 of meiosis PMC shows the quantity of the substituted chromosomes in a line, and the quantity of open bivalents is somewhat evidence of presence of translocations concerning genome of the variety

Table 3

Characterization of introgressive lines of common wheat for their genome structure

Lines in groups	Group characterization concerning introgression presence
1st group: 834, 835,933,1077,1096	One pair of substitution chromosomes, one translocation of alien chromosome to wheat chromosome
2nd group:788, 790, 791, 890, 891, 936, 937, 1024, 1026	Two substitution chromosomes, there is no identical substitution chromosomes with the 1st group; Translocation, which is present in the lines of the 1st group, is homologous to one out of the substitution chromosomes of the 2nd group
3rd group: 1023, 1025	Two substitution chromosomes and two translocations; There is no identical substitution chromosome with the 1st group; The two chromosomes changed through introgression in 1st group are changed also in the lines of the 3rd group
4th group: 1166	Three substitution chromosomes, two out of these chromosomes are homologous to the substitution chromosomes in the lines of the 2nd group

Table 4

Segregation for the character «resistance to powdery mildew» in the F_2 populations from crossing the introgressive lines with the variety Aurora

Crosses	The number of plants		
	Total	Resistant	Susceptible
788 × Aurora	103	83	20
834 × Aurora	77	72	5
835 × Aurora	99	99	0
933 × Aurora	79	78	1
1096 × Aurora	74	74	0

Aurora in this line. These translocations can include alien genetic material, but can be extremely wheat-wheat (table 3). It is visible, that genome of the lines was considerably changed in comparison with genome of the variety Aurora. The large rearrangements, such as chromosome substitutions and large translocations, concern from 1 up to 4 chromosome pairs in each line. By results of studying M1 of meiosis in hybrids F_1 between the lines (table 2), it is possible to group the lines that are most related on genome structure. Related lines will form 21 closed bivalent in M1. In total, six such groups have been established. Members of the same group are similar to each other on genome structure and definitely differ from the variety Aurora genome (table 3).

All studied lines were resistant to powdery mildew at a level of 8—9 marks for all three years. Plants F_1 from crossing of the resistant lines with the susceptible variety Aurora (marks 3—4) were resistant that shows the dominant character of inheritance of resistance. In some crosses enough quantity of seeds F_2 was obtained to investigate segregation for resistance to powdery mildew (table 4). In the (788 × the Aurora) F_2 population, the ratio of resistant and susceptible plants was 3 : 1 (theoretical classes: 77 resistant and 26 susceptible, $\chi^2 = 1,71$). Lines 834, 835, 933 and 1096 are characterized by identical pattern of M1 of meiosis in PMC of hybrids F_1 (table 1) from crossing with the variety Aurora: one pair of obligatory univalents confirms that there are always two chromosomes, which do not pair in the cells. This means that the lines have one pair either completely alien, or considerably reconstructed concerning chromosomes of the variety Aurora. As viewed in table 2, four listed lines have no obligatory univalents in M1 of meiosis in hybrids F_1 with each other. Therefore we consider that the lines have more or less identical genome structure concerning alien inclusions and can be used in genetic analysis for characters controlled by genes of alien origination as a single whole. Unlike lines 834, 835, 933, and 1096, the line 788 has four obligatory univalents in M1 of meiosis in hybrids F_1 not only with the variety Aurora, but also with each of the listed lines. This emphasizes its significant divergence from these lines and from the variety Aurora on genome structure. Out of 329 plants F_2 from crossing lines 834, 835, 933, and 1096 with the variety Aurora (table 4) six plants were susceptible to powdery mildew that does not correspond to the ratio 3 : 1 (theoretical classes: 247 resistant : 82 susceptible, $\chi^2 = 94,25$).

The combination 788 × Aurora has been investigated in addition with the use of generation F_3 (table 5). These resistant F_2 plants, which segregated in F_3, again shows the ratio resistant to susceptible 3 : 1 (theoretical classes 243 and 81, χ^2 = 1,89). However, a ratio «populations, which derived from the resistant F_2 plants and did not segregate : populations, which derived from resistant F_2 plants and segregated : populations, which derived from susceptible F_2» (table 5) does not conform to the expected ratio 1 : 2 : 1 (theoretical frequencies of the corresponding classes 18,5 : 32 : 18,5, χ^2 = 18,5). Character of distortion of the actual ratio in comparison with theoretically expected one shows failure of zygotes lacking the gene for resistance involved in alien chromosome and excess of zygotes which do not segregate in the following generation owing to their homozygosity for resistance gene. The quantity of F_2 plants, which according to assessment F_3, can be considered heterozygous for resistance gene, does not differ from the theoretically expected one. In our opinion, the segregation distortion is caused by location of the resistance gene in alien chromosome, so certain deviations from normal pattern of meiosis in hybrid plants and changes in frequencies of different gametes against those expected under the regular meiosis can take place.

Table 5

Study of population (788 × Аврора) F_3 for resistance to powdery mildew

Assessment of F_2 plants	Number of F_3 families assessed	Number of F_3 plants	
		Resistant	Susceptible
Resistant, the F_3 populations do not segregate	27	201	0
Resistant, the F_3 population segregate	32	233	92
Susceptible	15	0	118

It was assumed that the resistance gene is located in an alien chromosome, which does not pair with any wheat chromosome in hybrid plants. In this case we cannot apply the ratio 3 : 1 as theoretical, and should take into account features of behaviour of univalent chromosomes in M1 of meiosis in hybrids and use these features at calculation of theoretically expected segregation [7]. Let us suppose that only 21-chromosome pollen grains are functional and all female gametes can function. However, in M1 of the (788 × Aurora) F_1 hybrid, four univalents instead of two ones are present. According to that, we shall calculate a ratio of phenotypic classes. Two univalents of four are of wheat (w_1 and w_2), but they do not pair

Table 6

Calculation of the frequencies of gametes forming F_1 hybrids from crossing introgressive lines possessing alien chromosome with the variety Aurora

Gametes and their frequencies		$19+w_1+w_2$	$19+w_1+a$	$19+w_2+a$	$19+w_1+a_c$	$19+w_2+a_c$	$19+a+a_c$
		0,0352	0,0352	0,0352	0,0352	0,0352	0,0352
$19+w_1+w_2+a+a_c$	0,0039	0,0007	0,0007	0,0007	0,0007	0,0007	0,0007
$19+w_1+w_2+a$	0,0117	0,002	0,002	0,002	0,002	0,002	0,002
$19+w_1+w_2+a_c$	0,0117	0,002	0,002	0,002	0,002	0,002	0,002
$19+w_1+a+a_c$	0,0117	0,002	0,002	0,002	0,002	0,002	0,002
$19+w_2+a+a_c$	0,0117	0,002	0,002	0,002	0,002	0,002	0,002
$19+w_1+w_2$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+w_1+a$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+w_2+a$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+w_1+a_c$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+w_2+a_c$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+a+a_c$	0,0352	0,0059	0,0059	0,0059	0,0059	0,0059	0,0059
$19+w_1$	0,1055	0,0176	0,0176	0,0176	0,0176	0,0176	0,0176
$19+w_2$	0,1055	0,0176	0,0176	0,0176	0,0176	0,0176	0,0176
$19+a$	0,1055	0,0176	0,0176	0,0176	0,0176	0,0176	0,0176
$19+a_c$	0,1055	0,0176	0,0176	0,0176	0,0176	0,0176	0,0176
19	0,3164	0,0527	0,0527	0,0527	0,0527	0,0527	0,0527

because they are not homologous. Two alien chromosomes (a) do not pair for the same reason. But only one alien chromosome (a_c), in which the gene of resistance to powdery mildew is located, is critical for our research. Results of calculations with taking into account of four univalents are resulted in table 6. Calculation of frequencies of zygotes forming resistant (0,625) and susceptible (0,375) plants shows that the empirical ratio differs from the theoretical one (64 resistant and 39 susceptible, $\chi^2 = 22{,}41$) through excess of resistant plants. Similarly, the after-effects of the reduced viability of aneuploid female gametes containing only wheat chromosomes, and the zygotes generated from them take place. The following theoretical segregation was calculated according to such assumptions: 19- and 20-chromosomal female gametes without alien chromosomes do not function (these cells in table 6 are blacked out); viability of zygotes without alien chromosomes (in table 6 this cell is in a framework) makes up V = 0,1 as we had experimentally established earlier [14]. After the corresponding correction of zygote frequencies, theoretically expected ratios of classes F_2 (0,773 resistant and 0,227 susceptible) were obtained that agreed with empirical data ($\chi^2 = 0{,}56$).

To determine theoretical segregation ratio in F_2 from crossing of the lines, which differ from the variety Aurora with one pair of substitution chromosomes and show in M I of meiosis 2 univalents, the same reasons were used. A theoretical ratio of resistant and susceptible gametes was calculated under assumption that viability of a zygote without alien chromosome makes up V = 0,1 as well as in the previous case. And in this case, practically there is no distinction, whether we consider 20-chromosomal gametes to be viable (in recalculation on volume of sample of 329 plants, 320 resistant ones and 9 susceptible ones, $\chi^2 = 1{,}54$ in comparison with empirical classes 323 and 6), or we accept, that 20-chromosomal gametes without alien chromosome do not function (324 and 5, $\chi^2 = 0{,}18$).

If our considerations about dependence of inheritance of an alien gene on meiosis features in hybrids are true, cytological instability of hybrids should affect at crossing introgressive resistant lines with each other too: in F_2 from crossings the resistant lines with the same genetic control of a character there will appear susceptible plants. Indeed, in F_2, obtained from resistant F_1 hybrids , appearance of susceptible plants was observed very seldom, 16 susceptible plants among 4802 F_2 hybrids (0,33 ± 0,077 %) if the parental lines belong to the same group as to genome structure (table 3) or to any other, except for group 1. Such hybrids were named as hybrids of the first type. If one of the parents of a hybrid was from group 1 (in table 7 these combinations are underlined, these hybrids were named as hybrids of the second type), susceptible plants in F_2 appear more often: 35 of 2083 (1,68 ± 0,281 %). We believe, that this disparity is caused by basic difference in genome structure of lines of the 1-st group (table 3) from all others. These lines have translocation chromosome whereas lines of all other groups have the same whole alien chromosome. For this reason in M I of meiosis in hybrids of these lines with all others, the probability of appearance of two univalents instead of a bivalent between alien chromosome and chromosome with alien translocation is high. Actually, at crossing the line of the 1-st cytological

Table 7

Assessment of F_2 plants from crossing the introgressive lines with each other

Crosses	Resistant	Susceptible	Crosses	Resistant	Susceptible
788 × 790	355	0	890 × 933	29	2
788 × 834	79	3	891 × 1023	218	2
788 × 933	46	13	891 × 1096	21	1
788 × 936	74	0	933 × 790	203	1
788 × 1024	41	0	933 × 1077	70	0
788 × 1025	227	0	933 × 834	143	0
788 × 1096	157	1	933 × 835	368	0
790 × 891	351	0	933 × 1077	282	0
790 × 936	128	1	936 × 790	284	3
790 × 937	90	0	937 × 891	56	0
791 × 788	44	1	937 × 936	75	0
791 × 891	116	0	1023 × 790	369	0
791 × 1096	38	0	1023 × 791	54	1
834 × 790	226	2	1024 × 790	66	0
834 × 890	7	0	1024 × 791	87	2
834 × 891	100	1	1025 × 790	77	1
834 × 936	10	0	1025 × 890	42	0
834 × 1077	344	0	1025 × 891	200	1
834 × 1096	38	0	1077 × 791	59	1
835 × 936	48	1	1077 × 834	93	0
835 × 1025	156	0	1077 × 1025	315	4
835 × 1096	155	1	1077 × 1026	14	1
890 × 790	80	0	1096 × 790	228	4
890 × 791	72	0	1096 × 891	153	1
890 × 891	59	0	1096 × 1077	287	2

group with lines of any other groups, four univalents were observed in M1 of meiosis (table 2). As the resistance to powdery mildew was a single character of an alien origin, which was peculiar to all investigated lines, the gene for resistance was supposed to be located on this chromosome, which is present as a translocation in lines of the 1-st group and as a substitution chromosome in all other groups. Lines of group 1 differ from lines of other groups by presence of any alien chromosome, which is not present at other lines. This causes appearance of obligatory pair univalents in M1 of meiosis in hybrid. Therefore we have calculated frequencies of different gametes, meaning 4 possible univalents. As usually we consider, that only euploid gametes function among male gametes, whereas among female gametes, all gametes with the chromosome number not less than 21 are functional. According to this condition, all gametes with only wheat chromosomes are not involved in fertilization. Parameter of viability V is not taken into account in this case. Whether the portion of gametes does not take part in fertilization, or the death of zygotes with unbalanced chromosome sets takes place, the result will be the same: in population F_2 from crossing two resistant lines with the same resistant gene of the alien origin susceptible plants will appear . And this is not concerned with segregation for a critical gene, and caused by presence of univalent chromosomes instead of bivalents in M1 of meiosis. For hybrids of the second type, theoretically expected ratio 0,978 resistant : 0,022 susceptible plants was obtained. It agreed with empirical segregation (χ^2 = 2,34). Appearance of susceptible plants among the F_2 hybrids of the first type shows that in this case also euploid gametes lacking the critical chromosome with the gene for resistance can combine forming viable zygotes, though such events are infrequent.

Our reasons were confirmed at assessing the F_3 families obtained from the resistant F_2 plants out of different crosses. As we also expected, families segregating the susceptible plants were found only among hybrids of the second type. Moreover, combinations of the first type differ from combinations of the second type i) by the numerous samples of seed, ii) by the best seed germination, iii) by the best conservation of plants in passing the winter. In our opinion, all this points to different viability of zygotes. That zygotes at hybrids of the first type appear more viable, than zygotes of hybrids of the second type, shows indirectly that not only selection against gametes through their elimination out of fertilization takes place, but also the different viability of zygotes in dependence on their chromosome set can be considered when analysing data. That is, as we also expect, consequences of cytological instability at hybrids of the second type are more appreciable in comparison with hybrids of the first type.

The obtained experimental data prove that at genetic analysis of lines of common wheat with introgressions from *Ae. sharonensis*, two factors distort empirical segregation concerning the theoretical one calculated under assumption that one dominant gene takes part in segregation. The localization of a gene in an alien chromosome is the first factor because in M1 of meiosis in a hybrid with the recurrent wheat variety, the pair of obligatory univalents instead a bivalent is present and this influences frequency of different gametes. The reduced viability of gametes and zygotes lacking an alien chromosome was shown to be the second factor.

Conclusion. Cytological instability of hybrids between lines with introgressions from *Ae. sharonensis* is connected with structure of their genome concerning quantity and homologous belonging of alien inclusions. The abnormalities occurring during of meiosis in F_1 hybrids are the principal cause of appearance of aneuploids in F_2. Just they can influence the results of genetic analysis. Therefore, both alien, and wheat chromosomes in meiosis F_1 should be investigated in details concerning their behavior always when even one introgressive line is involved in crossing. Theoretically expected segregation can be determined only after cytological studying of lines concerning their cytological stability, features of chromosome pairing in meiosis of hybrids F_1 and fertility of plants F_2 with different partners on a crossing. Genetic analysis of lines for the character controlled by genes of an alien origin should be carried out on the more numerous samples, than at the analysis of genes, which segregate at normal behaviour of chromosomes in a meiosis. All investigated by us resistant to powdery mildew lines did not differ from each other for a gene governed the character: it is a dominant gene, which enters into wheat genome as an alien chromosome 3Sl or as its translocation on a wheat chromosome.

РЕЗЮМЕ. Приведены результаты изучения особенностей гибридологического анализа мягкой пшеницы по качественному признаку устойчивость к поражению мучнистой росой, когда он контролируется геном чужеродного происхождения (от *Ae. sharonensis*). Установлена связь между структурой генома скрещиваемых интрогрессивных линий и отклонением эмпирических соотношений расщепления в F_2 от теоретических, основанных на предположении о моногенном наследовании признака. Разработан подход к количественному учету влияния такой связи на искажение фактического расщепления по сравнению с теоретически ожидаемым.

РЕЗЮМЕ. Наведено результати вивчення особливостей гібридологічного аналізу м'якої пшениці за якісною ознакою стійкість до ураження борошнистою росою, коли вона контролюється геном чужинного походження (від *Ae. sharonensis*). Встановлено зв'язок між цитогенетичною структурою геному інтрогресивних ліній, що схрещуються, та відхиленням емпіричних співвідношень розщеплення у F_2 від теоретичних, основаних на припущенні про моногенне успадкування ознаки. Розроблено підхід до кількісного урахування впливу такого зв'язку на спотворення фактичного розщеплення відносно теоретично очікуваного.

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Received 17.02.05