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Meiosis, chromosomal loss, yield components, and phenotypes were studied in the euploid ($2n = 56$) and aneuploid ($2n = 55$ to 49) Triticale plants and their offspring (about 450). The objective was to investigate the nature of the octoploid population and determine the effect of aneuploidy on yield with a view to choose plants for hybridization. It has been established that mostly a pair of chromosomes is lost in the aneuploids. The plants having lost 1-2 pairs of homologous chromosomes can maintain their chromosome number over several generations and behave as euploids. The forms with high number of univalents lose chromosomes over 1-3 generations to reach the hexaploid level. The phenotype of an aneuploid plant (octoploid or hexaploid) is determined not by the corresponding number of chromosomes, but by the presence of chromosomes belonging to genome D whose genes control the phenotype of the octoploid. No direct relationship has been established between the reduction in plant fertility and the number of chromosomes lost. The plants that have lost 8-14 chromosomes may be more productive than those that have lost 1-2 chromosomes, and sterility of individual plants is often not related to either meiotic disturbance or chromosome number. Highly fertile aneuploid plants may successfully compete with the euploids and may even exceed them in productivity; therefore, rejection of plants only on the basis of chromosome number is unnecessary. Selection of plants, mainly for crossing purposes, should be done on the basis of phenotypic uniformity and their productivity, and not on the basis of chromosome number.

Breeding of octoploid Triticales as an agricultural crop is complicated by large meiotic disturbances in the plants and a high proportion of aneuploids in the population. However, use of the octoploids to obtain most promising secondary hexaploid Triticales is the only way to utilize the valuable germplasm of the modern varieties of wheat and rye. Therefore, it is essential to study cytogenetically the octoploid Triticales, mainly as a component in the crosses.

Already a large number of explanations for meiotic disturbances in the Triticales have been offered, and they all lead to incomplete bivalent formation and appearance of univalents. It was believed that the latter is caused by premature "sliding" of chiasmata at MI of meiosis; however, the studies of Kaltsikes et al. (cited in [1]) have demonstrated that chiasmata in Triticales are less because they do not form. Besides, the number of univalents is determined by the hereditary mechanisms, and occurrence of univalents in Triticales is a stable expression of incompatibility in the hybrid nuclei.

A high correlation between the mean univalent frequency at meiosis and the aneuploid frequency in the progeny has been demonstrated convincingly [2, 3]. Sachs [4] believes that the aneuploid microsporocytes appear as a result of disturbance in the genetically controlled spindle function as well as mosaic pattern for chromosome number in the sporogenic tissue of Triticales appearing as a result of abnormality during archesporial mitotic divisions [5].

In 1962, Krolov [6] proposed a relationship between the somatic chromosome number of Triticales and their grain formation, i.e., the greater the deviation from $2n$, the lower is the grain development. This opinion has been fully confirmed during subsequent studies, and now the percentage of aneuploid plants is often used as a criterion for assessment of the Triticale lines or populations.

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In the present study, we have investigated meiosis and loss of chromosomes in the offspring of euploid and identified aneuploid plants, and compare their phenotypes to determine the nature of establishment of a Triticale population as well as to estimate the effect of aneuploid plants on the population yield.

MATERIALS AND METHODS

The study was carried out with 10 euploid and 10 aneuploid plants randomly selected from each of four Triticales obtained by colchicine treatment of the following amphihaploids AD 590 (*Triticum aestivum* var. Mironovskaya 808 × *Secale cereale* G-144), AD 595 (wheat Mironovskaya 808 × rye Voskhod 1), AD 737 (wheat Mironovskaya 808 × rye G-396), and AD 873 (wheat SV 60292 × rye G-396).

It is known that the octoploid Triticales have very low phenotypic variability. In this case, the female parent of three Triticales was the wheat variety Mironovskaya 808; therefore, all the Triticale derivatives were similar to one another and had spindle-shaped white awnless spike and mild pubescence under the spike, but differ in height and straw thickness. The plants were studied cytologically, their seeds were sown in separate rows in the next generation, and spikes from 20-25 plants in each row were fixed for cytological studies. The cytological study was done on acetocarmine squash preparations at MI and AI of meiosis in PMC. The objective of this study was not to identify the genotypes of the aneuploid plants, and random loss of chromosomes of all the three genomes was assumed [7-11].

Phenotypic description and laboratory analysis for the yield components were done on 448 plants raised in a glasshouse without bagging, since cross-pollination is practically absent under glasshouse conditions.

In each Triticale, the groups of aneuploid and euploid plants were compared on the basis of the major parameters. Since the mean values obtained in the aneuploid group are quite tentative, we did not determine the significance of difference among them.

EXPERIMENTAL AND DISCUSSION

The mean values for chromosome pairing in the 10 initial euploid plants and their offspring are given in Table 1. The mean number of bivalents, variation in the number of univalents, and fraction of aneuploids in the progenies (40.7%) fall within the usual range for an octoploid population. Chromosomal loss over one generation varied from 1 to 14 chromosomes. Our results are in agreement with the findings of Weimarck [12], who observed extremely high and low chromosome numbers in the euploid as well as aneuploid plants.

Although the bivalents in the initial aneuploid plants decreased with a reduction in chromosome number, it is very clear from the comparison of the plants with equal chromosome number that the chromosomal constitution of these plants is different, since chromosomal pairing is individual in each plant, which is also responsible for different nature of chromosomal loss in their offspring. According to theoretical expectations, one-third of the plants in the progeny of the plant with $2n = 55$ returned to euploid condition, another one-third lost the univalent chromosome and had $2n = 54$, and the last one-third group showed a tendency for further loss of chromosomes.

The 54-chromosome forms were the most stable, with 81.2% offspring maintaining the initial number, and one plant restored to 56 chromosomes. Most probably, loss of a single homologous pair does not cause a significant change in the course of meiosis. It must be noted that 84.8% of all the aneuploid offspring had an even chromosome number, i.e., there is a clear tendency for simultaneous elimination of a chromosomal pair, and not individual chromosomes, as was expected. This phenomenon was also observed by Weimarck [13].

The offspring of the 53-chromosome plants lost the single chromosome, and all of them had $2n = 52$, i.e., most probably 26 pairs of homologous chromosomes.

That the chromosomal constitution of a plant and not their number is the deciding factor is confirmed by the different behavior of the offspring of the initial plants with equal chromosomal numbers. While maintaining the general trend for chromosomal loss, they lose the chromosomes in a different manner. A part of the offspring of initial plants No. 5 and 9 reached hexaploid level within one generation and some others close to it ($2n = 46$ and $2n = 44$); the other part with an even number of homologous chromosomes either maintained $2n = 52$, or lost 1-2 pairs of homologous chromosomes each. Possibly, the aneuploids with balanced complex of homologous pairs of chromosomes can maintain the initial number of chromosomes or a similar chromosomal constitution over several generations.

TABLE 1. Cytological Characteristics of the Initial Euploid and Aneuploid Plants and Their Offspring

Line	Characteristics of the initial plants			No. of offspring of the euploid and aneuploid plants number of plants with different chromosome numbers														
	2n	chromosomal configurations	No. of univalent	56	55	54	53	52	51	50	49	48	47	46	44	43	42	41
Average of ten plants	56	26,29II+3,42I	2-8	32	1	7	1	3	1		1	2	2	2	3		1	
3AD 874-13	55	27,01I+1,01*	0	3	3			2			1		1					
3AD 874-10	54	26,37II+1,21I	0-2	1		13				1					1			
1AD 595-5/1	53	25,68II+2,08I	1-3					8										
2AD 874-15	52	23,81II+4,37II+0,03III	2-8												4	3	4	
1AD 737-6	52	23,96II+3,98I+0,03III	0-12							4		5	2	2				
1AD 595-4/13	52	24,61I+2,81	2-6					1										
1AD 590-4/11	51	21,66II+7,68I	5-11					3		1				1				
2AD 874-4	51	22,71I+5,6I	3-13					2									4	2
3AD 874-13	49	19,91II+7,18I+0,08III	7-11											1			4	2
5AD 737-4	49	22,47II+4,06I	1-7			1		1					1	3			3	1

*Diakinesis

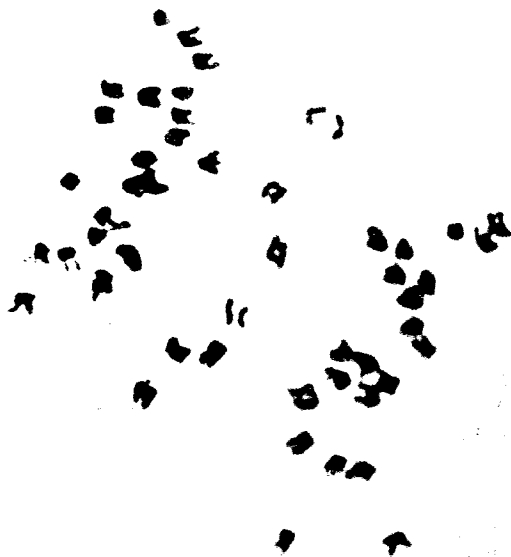


Fig. 1. AI of meiosis in the plants with $2n = 49$. Toward each pole 21 chromosomes separated and the 7 univalent chromosomes remaining at the equator split into chromatids.

The plants with $2n = 49$, which formed half of all the aneuploids among the offspring with an odd chromosome number, are particularly interesting. If appearance of these plants is considered to be a result of spontaneous hybridization between the octoploid and hexaploid forms, their largest number would have been in the progeny of octoploids, which was actually not observed. Several of them were offspring of plants with $2n = 55, 52$, and 51 , and two plants retained the chromosome number of the female parent, $2n = 49$.

The odd chromosome number in the plants was maintained over several generations by the unique behavior of the univalent chromosome at meiosis, very similar to the behavior of the univalents in the amphihaploids described by Maan and Sasakuma [14]. In this case, behavior of the univalents located within the metaphase plate is of organized type (Fig. 1). At AI the univalents are arranged on the equator and have distinctly visible chromatids, similar to the chromosomes of mitotic metaphase. They have equational division to the different poles, and subsequently behave as independent chromosomes. This mechanism can also ensure regeneration of the pair of homologous chromosomes, and the plants with chromosome number higher than in the initial plant appeared in the progeny, which was observed in the progeny of the heptaploid plant No. 11, in which two plants had $2n = 52$ and $2n = 54$. Splitting of the univalents into chromatids may increase the number of micronuclei leading to elimination of the univalent chromosomes. Thus, not only does the loss take place in the populations of octoploid Triticales, but one part of the high chromosomal plants is capable of restoring the octoploid number, while the other part maintains the balanced even number of homologous chromosomes from generation to generation and acts as euploids if, of course, the lost chromosomes did not control vital functions.

The comparative characteristics of the control euploid and aneuploid populations are given in Table 2. Large fluctuations in the productivity of the aneuploid plants is indicated by the coefficients of variation for grain number per spikelet and grain weight per spike, which were 1.5-2 times higher in the aneuploids as compared to the euploids. The coefficients of variation were very high in AD 734, since almost half of the plants in both types were sterile. Only in AD 595 were the euploids superior to the aneuploids in all the components of spike yield; plants of both groups were almost similar in AD 590 and AD 737, and in AD 874 higher productivity was observed in the aneuploids. Besides, the aneuploid plants with better productivity in these three strains were more productive than the corresponding best plants in the euploid groups.

It must be noted that the high yielding plants in the aneuploid groups were closer in chromosome number to the octoploid level than the hexaploid level and had even chromosome numbers.

TABLE 2. Meiosis and Yield Components of the Euploid and Aneuploid Triticales and the Best Plants in Each Group

Triticale line	Group, best plant in the group	No. of plants in the group	2n	Pairing configuration	Sterility of plants, %	length \bar{x}	number of spikelets \bar{x}	Main spike				1000-grain weight, g	
								grains per spike \bar{x}	grains per spikelet \bar{x}	grain yield per spike, g \bar{x}	V, %		
AD 590	Euploids	27	56	25,711+4,581	0,0	9,1	17,2	26,0	1,5	38,0	0,8	38,7	31,4
	Best plant	1	56	25,821+4,361	—	10,0	20,0	37,0	1,8	—	4,1	—	29,7
	Aneuploids	22	52	—	2,2	11,5	23,0	25,2	1,1	68,2	0,8	72,5	31,2
	Best plant	1	52	24,261+3,781	—	9,0	19,0	69,0	3,6	—	1,5	—	52,1
AD 595	Euploids	29	56	26,451+3,411	0,0	12,9	20,6	36,6	1,8	27,7	2,3	40,0	62,2
	Best plant	1	56	27,531+1,011	—	14,0	22,0	64,0	2,9	—	4,3	—	67,2
	Aneuploids	26	52	—	0,0	13,1	18,3	24,7	1,4	44,2	1,1	58,1	41,3
	Best plant	1	52	24,291+3,421	—	14,0	20,0	34,0	1,8	—	1,8	—	52,9
AD 737	Euploids	73	56	25,291+5,421	44,6	14,2	23,8	41,9	0,5	84,0	0,6	100,0	35,2
	Best plant	4	56	—	—	13,5	22,0	22,0	1,0	—	1,4	—	63,6
	Aneuploids	43	54	—	51,2	13,1	21,1	12,3	0,5	160,0	0,6	116,0	33,2
	Best plant	1	54	25,171+3,661	—	13,0	30,0	63,0	2,4	—	3,5	—	47,6
AD 874	Euploids	114	56	26,831+2,341	6,1	12,3	23,3	44,2	0,6	50,0	0,8	56,2	52,5
	Best plant	1	56	26,571+2,861	—	12,0	20,0	23,0	1,1	—	1,1	—	48,1
	Aneuploids	108	48	—	5,5	13,2	23,7	25,9	0,9	37,7	1,4	34,2	46,8
	Best plant	1	48	23,631+1,441	—	11,0	33,0	67,0	2,0	—	4,3	—	64,1

TABLE 3. Comparative Characteristics of Meiosis and Productivity of Main Spike in the Offspring of the Euploid and Aneuploid Sister Plants of AD 737

Initial sister plants			Characteristics of the offspring							
line	2n	pairing configuration	plant No.	2n	pairing configuration	productivity of main spike				
						number of grains		grain yield, g		
						per spike	per spikelet	per spike	1000 grains	
AD 737-5	56	25,54II+4,94I	1	52	21.45II+9.1I	Sterile	0	0	0	0
			2	56	26.49II+3.02I	10	0.4	0.4	40.0	
			3	56	25.41II+5.2I	9	0.4	0.6	66.6	
			4	52	22.51II+6.98I	Sterile	0	0	0	
			5	47	18.62II+9.76I	5	0.2	0.1	33.3	
			6	56	25.52II+4.96I	11	0.5	0.4	36.3	
			7	56	26.24II+3.51I	Sterile	0	0	0	
AD 737-10	56	26.0II+4.0I	1	56	26.65II+2.7I	Sterile	0	0	0	
			2	44	20.35II+3.3I	1	0.03	-	-	
			3	44	20.62II+2.77I	59	1.9	1.3	32.2	
			4	44	20.0II+4.0I *	13	0.5	0.8	61.5	
			5	52	25.83II+0.34I	44	1.5	2.3	53.2	
			6	42	19.14II+3.8I	Sterile	0	0	0	
			7	56	26.28II+3.44I	The same	0	0	0	
			8	56	25.58II+4.84I	6	0.2	0.3	50.0	
AD 737-1	52	24,05II+3,9I	1	46	18.5II+9.0I	Sterile	0	0	0	
			2	50	20.04II+9.92I	The same	0	0	0	
			3	50	22.5II+5.0I	"	0	0	0	
			4	48	17.33II+13.34I	24	0.8	0.8	33.3	
			5	48	18.15II+11.7I	1	0.03	-	-	
AD 737-6	52	22,33II+7,34I	1	48	17.92II+12.16I	Sterile	0	0	0	
			2	48	20.07II+0.03III+ +6.57I	3	0.1	0.2	66.5	
			3	48	21.0II+6.0I *	Sterile	0	0	0	
			4	46	21.5II+3.0I *	The same	0	0	0	
			5	50	17.0II+16.0I	"	0	0	0	
			6	50	22.0II+6.0I	"	0	0	0	

*Diakinesis

As regards meiosis, for example, in AD 874, the number of bivalents per cell over the entire population was slightly higher than in AD 595, and the productivity was three times less. This once again confirms the absence of a direct relationship between these characters and indicates independent action of the genetic factors in them [3, 15-17]. Of course, AD 874 is younger by three generations and there is reason to hope that subsequent selection will increase its yield level, and the balance achieved in the population will change the parameters of aneuploids and euploids in favor of the latter, as it happened in the AD 595 population. However, to achieve balance in the populations, the number of generations for each Triticale strain may vary.

AD 737 is distinguished by exceptionally low fertility of plants in both groups. The results of Table 3 give a more detailed characterization of this strain. Almost half (7 out of 15) of the offsprings of the euploid plants were found to be aneuploids and two plants among them (No. 3 and 5) in line AD 737-10 were most productive; the other plants in both the groups were either semisterile or completely sterile. As can be seen from Table 3, fertility of the plants in this case was not only associated with chromosome pairing at meiosis, but also with their total number. It is very clear that the reason for sterility of this Triticale strain is beyond the influence of the factors mentioned above. Maan [18], while studying *Aegilops*-wheat hybrids, reported that the critical chromosomes of *Aegilops* in the sporophyte tissue controlled mortality of the euploid as well as aneuploid gametes. He believes that the action of the sporophyte-controlled gametocyte system can explain the behavior of the interspecific and intergeneric hybrids from the genetic point of view, and this system may be common in them. Formation of spikes with gaps in the amphidiploid may be associated with cytological stability.

Therefore, cytological stability, fertility, and economic value of Triticales developed from a wheat-rye hybrid depend on the balance of genetic factors and their interaction in the hybrid plant even after chromosome doubling. Following colchicine treatment of several

TABLE 4. Cytological and Phenotypic Characteristics of the Offspring of the Aneuploid Plants with Hexaploid and Octoploid Types of Spike

Line	2n	Pairing configuration	Plant height, cm	Spike				Yield					
				type	density	shape	color	presence of awns	pubescence under the spike	grain num-ber in main spike	No. of grains per spikelet	grain yield per spike, %	1000-grain weight, g
AD 595-1/5-4	52	25,22II+1,56I	78	Octoploid	1,5	Spindle-shaped	White	Awnless	Weak	32	1,7	1,8	56,2
AD 737-4/1	52	24,04II+3,92I	105	Hexaploid	2,4	Cylindrical	the same	Short awns	The same	58	1,9	2,5	63,1
AD 595-4/13	52	24,21II+3,58I	85	Wheat like	1,5	Spindle-shaped	White with anthocyanin	Awnless	"	30	1,6	1,7	56,6
AD 590-4/11	52	24,26II+3,48I	60	The same	2,1	Erectoid	The same	The same	Without pubescence	69	3,6	4,5	21,7
AD 590-1/6	49	20,81II+7,4I	100	Octoploid	1,8	Spindle-shaped	White	Long awns	Weak	29	1,3	0,9	31,0
AD 874-12/12	49	21,67II+5,60I	95	Hexaploid	2,8	Cylindrical	Yellow	Awnless	The same	25	0,8	1,1	44,0
AD 874-12/13	48	21,41II+5,2I	90	Octoploid	1,8	Spindle-shaped	White	The same	Without pubescence	23	0,8	1,4	60,8
AD 874-12/9	48	23,43II+1,44I	96	Hexaploid	3,0	Cylindrical	The same	"	The same	67	2,0	4,3	64,1
AD 874-4/11	46	21,54II+2,92I	115	Octoploid	2,0	The same	"	"	Strong	56	2,0	3,2	57,1
AD 874-12/10	46	20,26II+5,48I	124	Hexaploid	2,2	"	"	"	Weak	75	2,1	4,1	54,6
AD 874-12/1	44	22,12II+3,76I	155	Octoploid, dense	2,2	"	"	"	Without pubescence	76	2,1	4,0	54,1
AD 874-12/11	44	20,67II+2,66I	84	Hexaploid	2,6	"	"	"	Weak	36	1,2	2,0	55,5
AD 874-15/12	42	18,62II+4,67I	75	Octoploid	1,7	Spindle-shaped	"	"	Strong	38	1,5	2,4	63,1
AD 874-4/3	42	20,21II+1,6I	112	Hexaploid	2,8	Cylindrical	"	"	Weak	32	2,3	1,8	56,1

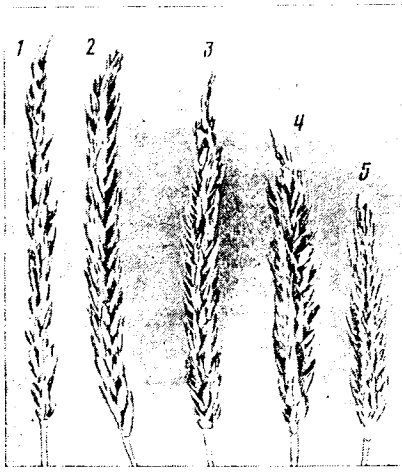


Fig. 2

Fig. 2. Spikes of the aneuploid plants of line 2AD 874-4. 1) Phenotypically typical plant of the octoploid population, semisterile ($2n = 46$); 2, 3) well-filled, compact, octoploid type ($2n = 46$); 4) well-filled semiwheat type ($2n = 42$); and 5) semisterile hexaploid ($2n = 42$).



Fig. 3

Fig. 3. Spikes of line 3AD 874-12. Plants with chromosome numbers: 1) semisterile octoploid type ($2n = 49$); 2, 3) dense with high grain filling, octoploid type ($2n = 46$ and $2n = 48$, respectively); 4, 5) semisterile hexaploid ($2n = 42$).

amphihaploid plants from the same cross-combination, progenies of each plant behave differently. For example, out of five plants producing seeds after colchicine treatment and giving rise to AD 737, normal fertile plants were selected in the progeny of only one of them; other plants gave rise to lines with semisterile plants.

It should be remembered that the hexaploid phenotype of a plant does not always correspond to the hexaploidy level. Table 4 contains cytological and phenotypic descriptions of seven pairs of aneuploid plants belonging to these two phenotypes but having equal numbers of chromosomes. Plants with octoploid as well as hexaploid phenotypes were obtained in all the chromosomal groups. At all chromosomal levels, many aneuploid plants were distinguished by good yield potential. As regards the phenotype, the suppressing effect of the D genome chromosomes is clearly manifested, which determine the phenotype of the octoploid Triticales. Even after loss of chromosomes to the hexaploid or a similar level, the aneuploid plants carrying chromosomes of this genome maintain the phenotypic properties of octoploid Triticales. Condensed spikes of the octoploids was the most frequent phenotype of the aneuploids. It has been repeatedly reported in literature that the octoploid Triticales have a tendency for reversal to wheat [19, 21]. In our experiment, five plants of wheat type (3.5% of the aneuploids) did not resemble the female wheat variety and differed among themselves on the basis of phenotype, chromosome number (from 46 to 52), and productivity. The appearance of plants of semiwheat and wheat types in the populations can hardly be called a simple reversion to wheat. The different phenotypes of the aneuploid plants are shown in Fig. 2-4.

Thus, establishment of an octoploid population is a complex process. The frequency of the aneuploid plants is not a qualitative index of a population. Individual high yielding aneuploid plants not only can compete successfully with the euploids, but can also compensate to a certain extent the shortfall in grain development on the other less productive plants. As a rule, the octoploid populations consist of plants with mixed chromosome composition which determines their different phenotype and productivity; therefore, its "purification" by chromosome counts in the root tips is not suitable for practical breeding. Involvement of the high-yielding aneuploid plants in hybridization can lead to elimination of the chromosomes carrying undesirable characters in succeeding generations.

Pieritz [22] reported that, through selection, plants can be obtained carrying incomplete wheat and rye genomes, but having such chromosome combinations that all the genes interact in the best manner. According to Biuthner and Mettin [23], the genetic poten-



Fig. 4. Spikes of line 5AD 737-4 with different levels of density phenotypically similar to the octoploid. The initial Triticale population AD-737 was awnless. 1, 2) $2n = 42$; 3) $2n = 52$; 4) $2n = 54$.

tial for compensation between the wheat and rye chromosomes in relation to the selection processes leads to creation of high yielding Triticale lines. Besides, the plants with mixed chromosomal sets are the source of different chromosomal substitutions which often lead to appearance of valuable Triticales. According to Merker [24], Giemsa staining of the chromosomes showed that most of the hexaploid Triticale lines of agronomic importance had mixed chromosomal composition.

Thus, occurrence of a larger number of homologous chromosomes from the different genomes in the octoploid Triticales, which control the same characters, makes it possible for them to maintain the phenotype and productivity even after loss of a few chromosomes, and sometimes interaction between the remaining genes improves, and the aneuploid plant is more productive than the euploid plant. Therefore, choice of plants for hybridization and selection in a Triticale population should be concentrated on the phenotypic homogeneity and high economic value of the plants, and their chromosomal constitution can be ignored.

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