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THE BIOLOGICAL METHOD OF OBTAINING HEXAPLOID TRITICALES AND THEIR CYTOGENETICS.

IV. COMPARATIVE STUDY OF MEIOSIS IN THE F_1 OF TRITICALES

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A comparative study of meiosis was carried out in 10 F_1 triticales obtained in two hybrid combinations. It was observed that the F_1 triticale plants had mostly 47 chromosomes and occasional plants had 43 chromosomes. Meiosis is strongly disturbed in these plants. The number of bivalents at metaphase I varied from 10 to 21. The average number of bivalents per cell, depending on the hybrid, varied from 14.7 to 16.1. Some F_1 triticales differed significantly in this respect. The major anomalies at meiosis were univalents, nonuniform distribution to the poles, laggards and their premature division into chromatids, formation of micronuclei in the dyads and tetrads, and formation of triads and polyads.

The plants of F_1 triticales obtained by the biological method had a lower seed setting in the spike, which varied strongly (8 to 45.9 grains) depending on their genotype [1]. Very little information is available in literature on such hybrids. The theoretically expected number of chromosomes in the F_1 triticales should be 49. However, only in one report it has been shown that such hybrids had 39-49 chromosomes, with the predominance of 49-chromosome plants [2]. In this context, it was interesting to determine the number of chromosomes in F_1 triticales and also to find out how meiosis takes place in the hybrids depending on the genotype of the parent components.

MATERIALS AND METHODS

Meiosis was studied in ten F_1 plants obtained in two cross combinations: (wheat × rye) × triticale amphidiploid 1 (AD 1) and (wheat × rye) × triticale amphidiploid 206 (AD 206), where wheat × rye were represented by the varieties: Bezostaya 1 (B 1) × Vyatka 2 (V 2), Mironovskaya 808 (M 808) × Saratovskaya 4 (S 4), Polukarlik 19 (P 19) × V 2, Polukarlik 808 (P 808) × S 4, and Khar'kovskaya 63 (K 63) × Saratovskaya Krupnozernaya (SK).

Young spikes were fixed in the Newcomer's mixture. Cytological analysis was carried out in temporary acetocarmine preparations. Meiosis was studied in 10-20 plants of F_1 triticale. The results obtained were subjected to analysis of variance.

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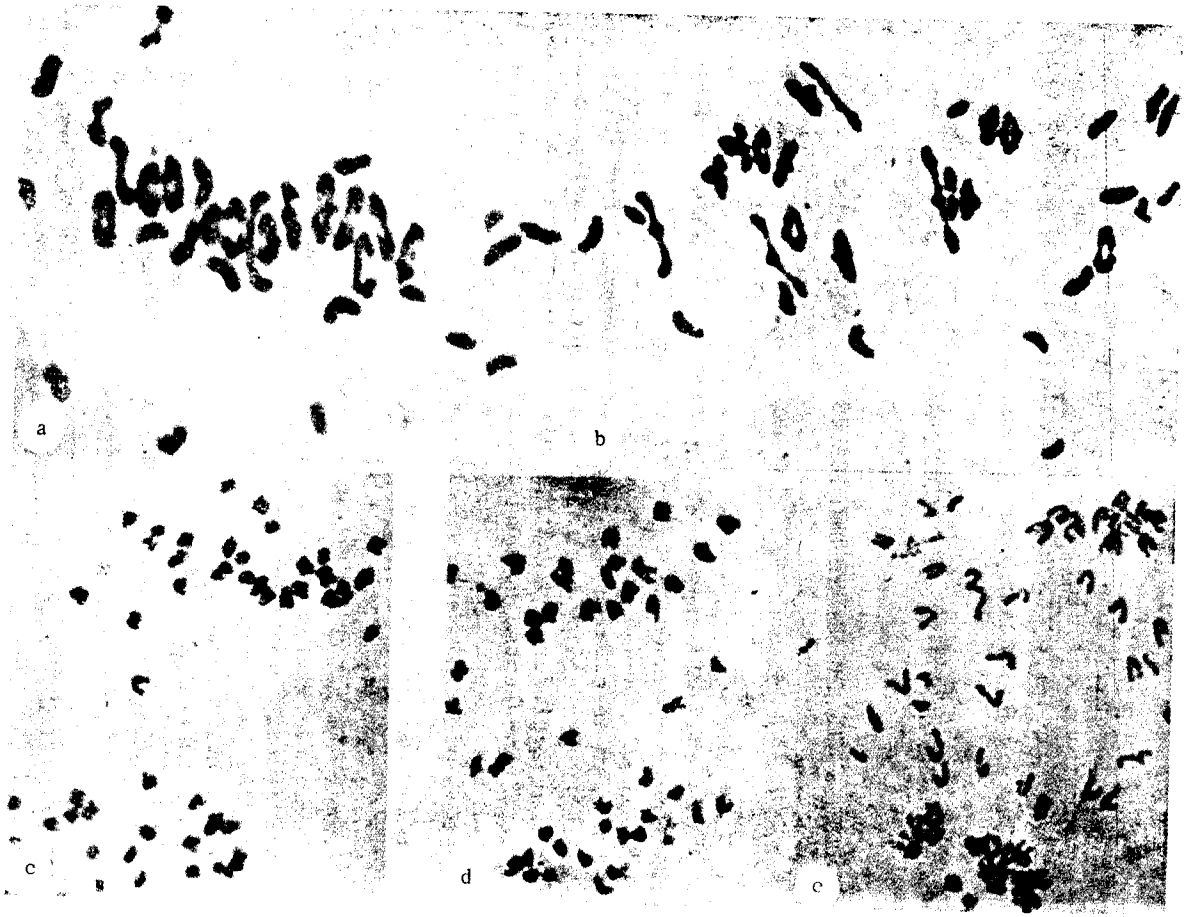

Fig. 1. Metaphase I and anaphase I in PMC of the F_1 triticale plants (500 ×): a, b) MI $14_{II} + 19_I$ and $16_{II} + 15_I$, some univalents appeared due to premature disjunction of bivalents; c, d) AI with different number of chromosomes at the poles and laggard univalents; e) AI with premature division of laggards into chromatids.

TABLE 1. Frequency Distribution of Cells at MI with Different Numbers of Bivalents in the F_1 (wheat × rye) × Triticale Plants

Hybrid	Number of cells studied	Cells with different number of bivalents								Number of bivalents per cell				
										total		open bivalents		
		10—13	14	15	16	17	18	19	20—21	$\bar{X}$	d	range	mean $\bar{X}$	mean d
F_1 hybrids (wheat × rye) × AD 1														
B 1 × V 2	19	–	–	15,8	15,8	47,4	10,5	10,5	–	15,3	–	3–9	5,4	–
M 808 × S 4	61	11,5	31,5	24,6	16,4	6,5	8,2	1,6	–	15,1	−0,2 *	2–9	4,9	−0,5
P 19 × V 2	31	3,2	32,3	22,6	22,6	6,5	9,6	–	3,2	15,1	−0,2 *	0–9	4,2	−1,2 *
P 808 × S 4	151	15,9	18,5	23,2	19,9	14,6	5,2	2,0	0,7	15,1	−0,2 *	0–11	3,6	−1,8 *
K 63 × SK	62	16,1	40,3	27,5	12,9	1,6	1,6	–	–	14,7	−0,6 *	1–7	3,8	−1,6 *
Mean	–	9,3	22,5	22,7	15,5	15,3	7,0	2,6	1,0	15,1	–	–	4,5	–
F_1 hybrids (wheat × rye) × AD 206														
B 1 × V 2	67	6,0	11,9	10,5	32,9	22,2	9,0	4,5	3,0	16,1	0,8 *	0–8	4,0	−1,4 *
M 808 × S 4	106	12,3	25,5	31,1	16,0	10,4	3,8	0,9	–	15,0	−0,3 *	1–8	4,0	−1,4 *
P 19 × V 2	29	6,9	27,6	20,7	20,7	17,2	3,5	3,5	–	15,8	0,5 *	0–9	4,1	−1,3 *
P 808 × S 4	92	7,6	19,6	21,7	21,7	13,1	9,8	5,4	1,1	15,7	0,4 *	0–6	3,9	−1,5 *
K 63 × SK	42	2,4	35,7	16,7	14,3	19,1	7,0	4,8	–	15,5	0,2 *	2–9	4,0	−1,4 *
Mean	–	7,0	24,0	20,1	21,1	16,4	6,6	3,8	1,0	15,6	–	–	4,0	–
$LSD_{0.05}$											0,2			0,3

*Differences significant at 5% level.

EXPERIMENTAL

The cytological analysis demonstrated that the plants of F_1 triticale mostly had 47 chromosomes, and only isolated plants had 43 chromosomes. Over the period of three years of investigation, 96% 47-chromosomal plants were obtained in the first combination (wheat × rye) × AD 1, and they were 90% in the second combination (with pollinator AD 206). The results of analysis of the 47-chromosomal plants are presented in the tables.

At metaphase I (MI) the main chromosomal associations were bivalents and univalents (Fig. 1a and b). Sometimes cells with one trivalent or tetravalent were also visible. The number of bivalents at MI varied from 10 to 21, and the corresponding univalents from 27 to 5 (Table 1). Depending on the male parent (the pollinator AD), a significantly higher number of bivalents (15.6) was recorded in the progeny obtained with AD 206 than with AD 1. The highest number of bivalents per cell (16.1) was recorded in (B 1 × V 2) × AD 206, and the smallest number (14.7) was in (K 63 × SK) × AD 1.

Ring bivalents of closed type were predominant, although in some cells 8-11 rod-shaped open bivalents were seen and their average number over the treatments was 4-4.5. In the hybrids with AD 1, cells with 9-11 open bivalents were found more frequently than in the offsprings from AD 206. On an average, a higher number of open bivalents (4.9-5.4) was recorded in the cells of the hybrids of M 808 × S 4 and V 1 × V 2 with AD 1, and a smaller number was recorded in (P 808 × S 4) × AD 1 (3.6). A significantly smaller number of open bivalents, on an average four per cell, formed in the progeny of AD 206 than that of AD 1. The lowest number of cells (3.6-4.8%) had 19-21 bivalents, they were significantly higher in number in the hybrids with AD 206. In the offsprings obtained from the amphihaploids B 1 × V 2, MI with $19\text{-}21_{II}$ were observed most frequently (Table 1). Not a single cell was observed where the MI had more than 21_{II}. Only in two progenies, (B 1 × V 2) × AD 206 and (P 19 × V 2) × AD 1, the number of cells with $20\text{-}21_{II}$ reached 3-3.2%, and in most of the F_1 triticales, cells with 15-17 univalents were found most frequently (19.4-24.8%), the average number per cell being 16.2.

As was expected, because of a large number of univalent chromosomes at MI, the anaphase I (AI) was strongly disturbed. One such disturbance was lagging behind of chromosomes in the center of the cell, numbering from 1 to 19 (Fig. 1c-e). The frequency of AI with all the chromosomes on the poles was only 3.9-6.7% over all the treatments. A significantly higher number of AI without laggards was recorded in the progeny obtained with AD 206. Most often, 10-11 chromosomes (13.3-12.1%) were found as laggards in the cross with AD 1 and 8-10 laggards (12.8-14.4%) in the hybrids obtained with AD 206, their average number per cell over the crosses was 8.6-9.7. In the F_1 plants of (P 19 × V 2) × AD 206, (P 19 × V 2) × AD 1, and (K 63 × SK) × AD 1, this parameter had the highest value, i.e., 10.3-11. The plants (P 808 × S 4) × AD 206 had a much lower number of laggards (7) per cell. In this hybrid and in (K 63 × SK) × AD 1, cells with 10 laggards occurred most frequently. Premature division of chromosomes into chromatids was observed in many laggards (Fig. 1e).

The second anomaly at AI was unequal distribution of the chromosomes of the poles, from 11 to 29 chromosomes. Chromosome disjunction to the pole was quite variable (Table 2). If one pole had 16 chromosomes, on the opposite pole the number varied from 17 to 29. In each treatment, about 40 different types of chromosomal disjunction were observed. The most frequent distributions to the poles were 18 + 19 and 19 + 20 chromosomes. The hybrids of AD 206 had 6-8% of such cells, and the frequency in the hybrids of AD 1 was 4.4-4.7%. A much smaller number of AI was found in which the poles had 21 chromosomes each (2.0-1.3% cells). The plants from the cross (P 808 × S 4) × AD 206 had 38.5% AI with 18 + 19 chromosomal disjunction. In the plants of (B 1 × V 2) × AD 206, the most frequent AI (15.4%) were those in which 19 + 20 chromosomes moved to the opposite poles.

In spite of univalent and laggard formation and unequal distribution of chromosomes to the poles, 36.7-28.0% normally developing cells (withoug micronuclei) were found in the terminal stage of the 1st division (dyads) (Table 3). In the hybrids (P 808 × S 4) × AD 206 and (K 63 × SK) × AD 1, their frequency was 53.5-54.6%. Other F_1 triticales had much smaller number of dyads without micronuclei. They were particularly fewer in number (15-18.9%) in B 1 × V 2 and P 19 × V 2 in crosses with AD 206. The main disturbance in the dyads was micronucleus formation, the number of which varied from 1 to 9, and the average number per cell was 1.2-1.6. More often, the dyads had 1-2 micronuclei(18.3-22.6%), less frequently, 7-9 (0.5-0.6%). The largest number of dyads with micronuclei (84.2%) was in the hybrid (B 1 × V 2) × AD 206, and the lowest number was in the plants of (K 63 × SK) × AD 1 × (44.5%).

TABLE 2. Chromosome Distribution to the Poles in the F_1 (wheat × rye) × Triticale Plants

Number of cells studied	Most frequent mode of chromosomal disjunction, %											
	16+17	17+18	17+20	18+18	18+19	18+20	19+20	19+21	20+20	20+21	20+22	23+24	others
F_1 hybrids (wheat × rye) × AD 1													
384	2.6	2.9	2.9	3.1	4.4	3.4	4.7	4.1	3.9	4.7	4.1	3.4	55.8
F_1 hybrids (wheat × rye) × AD 206													
151	4.0	4.6	4.0	3.3	6.0	2.0	8.6	2.0	2.0	1.3	2.7	2.0	47.5

The first division sometimes ended with formation of triads. Their number was significantly higher, on an average, in the progenies obtained with AD 206 than with AD 1 (Table 3). Very rarely (0.1-1.2%), triads were found in the plants having the genotype of the female parent P 808 × S 4. A particularly high percentage of such cells was observed in the hybrids of P 19 × V 2 and M 808 × S 4 with AD 206, which was 9.5-19.7%.

At the final stage of meiosis, i.e. tetrads, the number of disturbances in the hybrids was almost twofold that in the dyads. The percentage of normally developed tetrads without micronuclei, on an average, was 22.9-13.9 over the cross-combination (Table 3). They were in significantly higher numbers in the plants of the progenies obtained with AD 1 than with AD 206. The F_1 triticale obtained by crossing K 63 × SK and B 1 × V 2 with AD 206 had a smaller number of tetrads (micronuclei 2.9-3.6%). At the same time, their number was 41.3% in the plants of (M 808 × S 4) × AD 1.

The main anomaly in tetrads was micronucleus formation, the number of which varied from 1 to 14, and the number of micronuclei per cell, depending on the cross combination, was 2.6-2.9. A higher number of micronuclei (4.1-4.3) per tetrad was in the F_1 triticale having the genotype of the female parent K 63 × SK. The number (1.6 per cell) was 2.5 times less in the plants (M 808 × S 4) × AD 1. The number of cells with micronuclei varied from 56.1 to 91.2%, and their highest percentage was in the plants K 63 × SK, which was 90.7-91.2%. A much smaller number of tetrads with micronuclei (56.1-56.7%) was recorded in the progenies of M 808 × S 4 and P 19 × V 2 crossed with AD 1. Tetrads with two micronuclei were found more frequently (18.7-19.2%) and those with 7-14 micronuclei were rare (6.3-7.8%).

The microspores in the tetrads were arranged isobilaterally, but sometimes linear and T-shaped arrangements also occurred. The tetrads had micronuclei, irrespective of the arrangement of microspores.

The second division often ended with the formation of polyads: pentads, hexads, and sometimes heptads and octads. Among the polyads, the pentads were in highest percentage (3.1-3.7). Their numbers were significantly higher in the progenies from AD 206 than from AD 1. A particularly higher number of pentads (6.7-7.9%) was recorded in P 19 × V 2, and they were found very rarely (0.2-1.4%) in the plants from P 808 × S 4. Hexads were seen more rarely (0.5-0.7%) than pentads, and they were more often (2.1%) found in the progenies of (P 19 × V 2) × AD 1. The polyads also had micronuclei.

DISCUSSION

According to the theoretical estimates, the F_1 hybrids (wheat × rye) × triticale should have 49 chromosomes (21 wheat, 7 rye, and 21 triticale chromosomes). The triticale AD 1 has the genomic structure $A_1A_1B_1B_1RR$ (A_1 and B_1 are the genomes of hard wheat, R is the rye genome). The genomic composition of triticale AD 206 is AA_1BB_1RR, where A and B are the genomes of bread wheat, A_1 and B_1 are the genomes of hard wheat, and RR are the rye genomes. The genomes A and B of soft and hard wheats are homologous, but each of them has a genetic specificity depending on the species. Therefore, the genomes of hard wheat were designated by Shulyndin [3] as A_1B_1, and those of bread wheat as AB. In analysis of the hybrids, we will use these designations. Makhalin [4] proposed the designations A_1B_1 for the genomes of soft wheat and AB for hard wheat.

The F_1 hybrids of wheat × rye have the genomic formula ABDR (ABD are the genomes of bread wheat, and R is the rye genome). The genomic structure of F_1 hybrids (wheat × rye) × AD 1 is AA_1BB_1DRR, and that of the F_1 (wheat × rye) × AD 206 is AABBDRR and AA_1BB_1DRR. The studies of Merker [5] have demonstrated that many triticales are chromosome substitution lines

TABLE 3. Analysis of Dyads, Tetrads, and Polyads in F_1 (wheat × rye) × Triticale

Hybrid	Total number studied		Percentage of normal				Number of micronuclei in each		Percentage of				
			dyad		tetrad				triad		pentad		hexad
	dyad	tetrad	$\bar{X}$	d	$\bar{X}$	d	dyad	tetrad	$\bar{X}$	d	$\bar{X}$	d	
F_1 hybrid (wheat × rye) × AD 1													
B 1 × V 2	74	186	33,3	–	14,1	–	1,3	3,3	1,3	–	2,6	–	0,5
M 808 × S 4	319	1232	42,6	9,3 *	41,3	−27,2 *	1,3	1,6	5,1	3,8	2,5	−0,1	0,1
P 19 × V 2	287	672	30,2	-3,1 *	34,5	20,4 *	1,6	1,7	1,4	0,1	6,7	4,1 *	2,1
P 808 × S 4	1258	1601	23,0	−10,3 *	17,9	3,8 *	1,5	2,1	0,2	−1,1	1,4	−1,2 *	0,7
K 63 × SK	223	457	54,6	21,3 *	6,8	−7,3 *	0,6	4,3	0,9	−0,4	2,3	−0,3	0,2
Average	–	–	36,7	–	22,9	–	1,2	2,6	1,8	–	3,1	–	0,7
F_1 hybrid (wheat × rye) × AD 206													
B 1 × V 2	433	352	15,0	−18,3 *	3,6	−10,5 *	1,9	3,2	0,2	−1,1	2,4	−0,2	0,5
M 808 × S 4	567	435	32,8	−0,5	22,7	8,6 *	1,5	3,0	19,7	18,4 *	3,3	0,7 *	0,2
P 19 × V 2	350	646	18,9	−14,4 *	15,5	1,4	2,0	2,8	9,5	8,2 *	7,9	5,3 *	0,3
P 808 × S 4	1198	640	53,5	20,2 *	24,8	10,7 *	0,8	1,7	0,1	−1,2	0,2	−2,4 *	0,2
K 63 × SK	597	517	19,8	−13,5 *	2,9	−11,2 *	2,0	4,1	8,3	7,0 *	4,8	2,2 *	1,1
Average	–	–	28,0	–	13,9	–	1,6	2,9	7,6	–	3,7	–	0,5
$LSD_{0,05}$				3,0		2,3				4,0		0,6	

*Differences significant at 5% level.

of the R genome with the D genome chromosomes. Iordanskii et al. [6] have shown that the triticale AD 196, obtained by the biological method, carries only six pairs of rye chromosomes. The triticales AD 1 and AD 206 have not been studied for characterization of the individual chromosomes.

As was noted above, the plants of F_1 triticales mostly had 47 chromosomes, and only a few of them had 43 chromosomes. In the studies of Fedorova and Polenova [2], such hybrids had 38-49 chromosomes, with a predominance of 49-chromosomal plants.

Deviation from the 49-chromosome level originates, probably, due to a reduction in the number of chromosomes in female gametes. In most of the cases, the 26-chromosomal egg cells and occasionally 22-chromosomal egg cells of the amphihaploids pollinated with triticale pollen (n = 21) are capable of giving rise to viable progeny, which mostly has 47 chromosomes and rarely 43 chromosomes.

The chromosome number in 10 F_1 plants (wheat × rye) × wheat varied from 40 to 49, with a preponderance of 47 and 49 chromosomes, on the basis of which one author concluded that the 19-28-chromosome egg cells in the amphihaploids are viable [7]. Later, other investigators confirmed that the unreduced egg cells (2n = 28) or those having a slightly lower number of chromosomes are viable in the amphihaploids [8]. So are the plants having deviation of only one chromosome [9], and the minute aneuploid variations in the chromosome numbers in one or another direction are tolerated [10].

We have demonstrated significant differences in the number of bivalents in F_1 triticales depending on the male parent (the AD pollinator) and the female genotype of the wheat–rye amphihaploid. On an average, a significantly higher number of bivalents per cell was recorded in the progenies from the pollinator AD 206 (15.6%) than with AD 1 (15.1%). In the F_1 triticales from the female parent B 1 × V 2, in distinction from other combinations, the highest number of bivalents per cell (15.7) was recorded. In the studies of Fedorova and Polenova [2], this index was higher (19.2_{II}). It is interesting to note that the chromosomes of the ABR genomes of wheat–rye hybrid do not conjugate at all with those of the same ABR genomes of triticales. Only in isolated cells, $20\text{-}21_{II}$ formed, and in half of the hybrid combinations not a single MI with the above-mentioned index was found. Most probably, in these complex hybrids other factors are operating which manifest their effect so strongly that the homologous chromosomes do not form bivalents.

It is difficult to decide chromosomes of which genome, AB of wheat or R of rye, are represented in the univalents at MI in most of the cases. In $^1/_{10}$ fraction of the cells studied there were 10-13 univalents; a particularly large number of such MI was observed in the hybrid (K 63 × SK) × AD 1, whereas not a single cell with less than 15_{II} was noted in the plants (B 1 × V 2) × AD 1.

There are no reports in literature on distribution of bivalents over the cells in the F_1 plants of amphihaploids × triticales. Many cytologists have studied the F_1 hybrids of triticale × wheat and triticale × rye. In the former, the chromosomes of the AB genomes of triticale and AB genomes of wheat formed $13.5\text{-}14.8_{II}$ [11-13], and in the latter the chromosomes of the R genome of rye formed $5.8\text{-}8_{II}$ [13, 14]. Reduction in the number of bivalents in the former hybrids takes place because of multivalent formation by the homologous chromosomes of wheat and premature disjunction of the conjugated chromosomes at MI [11]. In our studies, multivalents were observed very rarely, but the cells with premature division of the bivalents at MI were found more frequently due to which the total number of bivalents might have been reduced to a certain extent.

An unexpected reduction in the synapsed chromosomes of AB genomes was also noted in the F_1 hybrid (wheat × rye) × wheat. In the process of synapsis, other factors also have an influence besides the chromosomal homology [15].

The AI in F_1 triticales was characterized by a uniformity in distribution of chromosomes to the poles, the number of which varied from 11 to 29. Depending upon the hybrid combination, AI with chromosomal distribution 21 + 21 were found very rarely (2-1.3%). Although there were cases among other types of disjunction, when one of the poles had 21 chromosomes. More often, the poles received 18 + 19 or 19 + 20 chromosomes. The highest numbers of such cells were recorded in (P 808 × S 4) × AD 206 and (B 1 × V 2) × AD 206, which were 38.5 and 15.4%, respectively.

The other anomaly at AI was lagging behind of 1 to 19 chromosomes at the center of the cells. Together with this, in spite of the fact that, on an average, there were 16.4-16.0

univalents per cell over the treatments in all the F_1 triticales with the exception of (B 1 × V 2) × AD 1, 3-18.1% AI were observed in which all the chromosomes were present at the poles. However, a higher frequency of AI with 21 chromosomes, at least in one of the poles, most probably, is favorable for the formation of 42-chromosomes progeny.

On the basis of the number of chromosomes at the poles it can be predicted what chromosome numbers the pollen grains would have. Most probably, the egg cells (n = 21) and the male gametes (n = 21) of F_1 triticales can give rise to 42-chromosome progeny. It is difficult to confirm whether the 21 chromosomes at the poles belong to the genomes ABR, as MI with 21_{II} were observed very rarely. Movement of the univalent chromosomes to the pole is random, and chromosomes of D genome may also be present instead of the univalents of ABR genomes.

The laggards may be considered to consist not only of the chromosomes of D genome, since, on an average, 51.3-65.1% AI had 9-19 univalent laggards. Disturbance was frequently observed in the laggards — premature separation of the chromatids.

In many cases, the first division of meiosis in F_1 triticale was completed with the formation of dyads without micronuclei. A particularly higher percentage (53.5-54.6%) was recorded in the F_1 plants (P 808 × S 4) × AD 206 and (K 63 × SK) × AD 1. However, the absence of micronuclei still does not mean that such dyads are favorably balanced in the chromosome composition, although they are normally developed. Most probably, the dyads in which at least one nucleus contained 21 chromosomes participate in the synthesis of hexaploid triticale. In all the F_1 triticales studied, the first division sometimes ended with the formation of triads. In the F_1 plants (wheat × rye) × AD 206, they were formed more frequently (7.6%) than in the F_1 (wheat × rye) × AD 1. Possibly, this was caused by the specific peculiarities of the male parent AD 206. Although, during the study of meiosis in triticales AD 1 and AD 206, significant differences were not recorded between them in the formation of triads [16].

The second division ended with the manifestation of a larger number of anomalies than the first one. The major disturbance of tetrads was formation of micronuclei. The number of tetrads without micronuclei varied strongly depending on the F_1 triticale (from 2.9 to 41.3%), and their average number was less in the progenies of AD 206. The second division ended with the formation of polyads. Pentads, hexads, were found rarely, and heptads and octads occurred frequently. All the polyads also had micronuclei.

Grain filling in the spikes of F_1 triticale did not depend on the number of bivalents, dyads, and tetrads without micronuclei.

As a result of these studies, it has been established that bivalent formation in F_1 triticale depends on the genotype of the male parent (the AD pollinator). On an average per cell, they were recorded in larger numbers in the hybrids obtained with AD 206. Open bivalents were also less in this hybridization schedule. The AI were characterized by unequal distribution and laggard formation. More often, 18 + 19 and 19 + 20 chromosomes were found at the poles. The hybrids with AD 206 had more such cells than the progeny of AD 1. In the F_1 plants (wheat × rye) × AD 206, the first and second meiotic divisions ended with the formation of a larger number of anomalies than in the hybrids obtained with AD 1.

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