MEIOTIC STABILITY OF TRITICALE (X TRITICOSECALE WITTMACK) AS AFFECTED BY BREEDING PROCEDURE

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CHAPTER I

INTRODUCTION

The increased population growth in the world today demands an increase in future food supplies. This increase includes a need for a greater supply of protein with a better essential amino-acid balance as well as an increase in total food volume.

Grains which provide the stable food in most countries are also the main source of protein, furnishing almost half the total supply. These cereals have a low protein percentage and a poor amino-acid balance. Triticale (X Triticosecale Wittmack), a man-made cereal produced by doubling the chromosome complement of wheat X rye F_1 hybrids, has the potential of partially providing this increase in protein percentage and amino-acid balance.

The nutritional quality of triticale grain is as good or better than wheat, both the protein percentage and amino-acid balance being significantly superior. The amino-acid lysine appears to be improved in particular (32, 35). Limited human and mouse bioassay tests indicate that the quality of triticale protein is superior to that of wheat protein (7). Small scale production from triticale grain of chapatis, injera, and tortillas, common foods of India, Ethiopia, and

Mexico, respectively, indicate that they are of acceptable appearance, keeping quality, and taste (35).

Triticale appears to have specific adaptation to areas where temperatures reach or approach freezing during the early growth period of cereals, to high elevation areas under high to moderate rainfall, and to sandy soils under moderate rainfall. It is adaptable to areas not suitable for wheat and outyields wheat in areas used for rye production.

Although triticale holds much potential, it is hampered by moderate to high sterility, varying degrees of grain shriveling, lack of winter hardiness, and poor adaptation to environmental conditions of the Great Plains of the United States. Therefore, grain yields are less than those yields obtained from wheat. The high sterility and grain shriveling could be caused by the meiotic irregularities which occur in triticale. This study was undertaken to determine if the breeding procedure used would influence the rate at which meiotic stability could be attained. A meiotically stable triticale would permit plant breeders to make improved varieties available much sooner to a protein-hungry world.

CHAPTER II

MATERIALS AND METHODS

This study was conducted from 1973 through 1976 and involved the use of three breeding procedures:

Procedure I: Hexaploid wheat (Triticum aestivum L.) X diploid rye (Secale cereale L.) - colchicine treatment,

Procedure II: (Hexaploid wheat X diploid rye) X hexaploid triticale,

Procedure III: Hexaploid triticale X hexaploid wheat (and reciprocal).

Each procedure was followed by successive backcrosses to hexaploid triticales. The entire study was conducted at the Agronomy Research Station Greenhouses, Stillwater, Oklahoma. Table I lists the cultivars used in the study along with their code number and places of origin.

In Procedure I, cultivars one through four were crossed with cultivars five through eight. Initial crosses were made in the greenhouse in 1973. The F_1 hybrids resulting from these crosses were treated with a 0.15% aqueous colchicine solution utilizing the capping technique as described by Bell (4). The fertile plants produced by

TABLE I

CULTIVARS USED IN THE THREE BREEDING PROCEDURES, THEIR CODE NUMBER AND PLACE OF ORIGIN

Code No.	Cultivar	Origin
	Wheat	
1	TAM Wheat 101	Texas
2	Blueboy	North Carolina
3	Scout 66	Nebraska
4	Danne	Oklahoma
	Rye	
5	Okema	Oklahoma
6	Bonel	Oklahoma
7	Elbon	Oklahoma
8	WR811	-
	Triticale	
9	OK72179	Oklahoma
10	T385	Jenkins Foundation
11	T131	Jenkins Foundation

this treatment were then crossed with cultivars nine through eleven in succeeding generations.

Cultivars one through four were crossed with cultivars five through eight in Procedure II. Initial crosses were made in the greenhouse in 1973. The F_1 hybrids resulting from these crosses were pollinated with cultivars nine through eleven. Succeeding generations were backcrossed to cultivars nine through eleven. Procedure II was similar to Procedure I except wheat X rye hybrids were not doubled with colchicine. I hoped to isolate a fertile female gamete from the wheat X rye hybrids by pollination with hexaploid triticale pollen.

Cultivars nine through eleven were crossed with cultivars one through four (and their reciprocals) in Procedure III. Initial crosses were made in the greenhouse in 1973. The F_1's resulting from these crosses were then crossed in succeeding generations to cultivars nine through eleven.

Analysis Procedures

Procedure I

1. Make initial wheat X rye crosses.
2. Grow F_1 progenies and double the chromosome complement with colchicine.
3. Grow the F_1 progenies, check cytologically for 2N = 28 II

chromosomes, and cross with hexaploid triticale cultivars nine through eleven.

4. Grow the F_1 progenies from the above crosses and check them cytologically for 2N = 21 II chromosomes.

Procedure II

1. Make initial wheat X rye crosses.
2. Grow the F_1 progenies and cross with hexaploid triticale cultivars nine through eleven.
3. Grow F_1 progenies from the above crosses and check them cytologically for 2N = 21 II chromosomes.

Procedure III

1. Make initial triticale X wheat crosses (and reciprocals).
2. Grow F_1 progenies of the above crosses, check them cytologically for 2N = 21 II + 14 I individuals, and cross to hexaploid triticale cultivars nine through eleven.
3. Grow F_1 progenies of the above crosses and check them cytologically for 2N = 21 II individuals.

Parental Selection

The parents used in the study were selected on the basis of their adaptability to the Central Great Plains. The maternal parents for each succeeding generation in each procedure were chosen on the

basis of closeness to a chromosome complement of 2N = 21 II except for Procedure I (step 3) and Procedure III (step 2). If no individuals could be found with a chromosome complement of 2N = 21 II then those with 21 II plus the least number of univalents were chosen. Paternal parents, for all except the first F_1 generation, were chosen on the basis of apparent fertility.

During each year of the study seedlings were started in flats in the greenhouse. After vernalization, the seedlings were transplanted to 5-inch clay pots and placed on benches in the greenhouse. The wheat X rye hybrids in Procedure I were transplanted to beds in the greenhouse for the colchicine treatment. The last year of the study, the seedlings were started as stated above and then transplanted to beds in the greenhouse after vernalization. The plants were watered and fertilized as needed throughout the growing season.

Collection of Pollen Mother Cells

Pollen mother cells were collected in the springs of 1975 and 1976 from those F_1 hybrids derived from the use of Procedures I and II, and in the springs of 1974 through 1976 from those F_1 hybrids derived from the use of Procedure III. Pollen mother cells were not collected in 1974 from F_1 hybrids derived from Procedures I and II because of the expected low seed set.

Fixation

The pollen mother cells were taken between 7 A. M. and 12 noon daily and fixed immediately in a 6:3:1 Carnoys solution. After 24 hours at room temperature, they were removed from the fixative and stored under refrigeration in 70% ethanol.

Staining and Squashing

Chromosomes were stained at the time squashes were prepared using McClintock's acetocarmine stain. Anthers from one floret were dissected out, placed on a microscope slide in a drop of stain and macerated completely. The slide was then rapidly examined under the microscope, without the cover slip, to check for chromosome stages. If the desired stages were found, a drop of Hoyer's solution was mixed with the acetocarmine, a cover slip added, and the material squashed by turning the slide upside down on blotter paper and pressing firmly over the cover slip with the thumb. Further spreading of the chromosomes was accomplished in the same manner.

Examination and Photography

After satisfactory spreading of the chromosomes, the slides were stored until examined and photographed. The slides were examined with a Nikon Model LBR-Ke microscope. Chromosome

counts were made at diakinesis, metaphase I, and anaphase I. A total of 50 cells of each experimental F_1 hybrid were analyzed during each year of the study. Photography was accomplished under oil emersion with a Pentax Spotmatic 35mm camera utilizing high-contrast copy film.

CHAPTER III

REVIEW OF LITERATURE

A Mr. Wilson, in 1875, reported to the Botanical Society of Edinburgh that he had succeeded in obtaining true hybrids between wheat (Triticum aestivum L.) and rye (Secale cereale L.) utilizing wheat as the female parent. The two hybrid plants that he produced were sterile. The American plant breeder Carmen published the first illustration of the hybrid in the Rural New Yorker in 1884. Other than in its morphological appearance, the hybridity was shown by its very low fertility and the characteristic rye pubescence on the peduncle which is present when wheat is used as the female parent (20).

The first amphidiploid, or allopolyploid, was discovered by Rimpau, a German plant breeder, in 1888, and described by him in 1891. The published report indicated that he probably discovered a doubled sector (chimera) on a diploid plant instead of an amphidiploid individual. Twelve out of 15 seeds produced offspring which resembled the hybrid parent. These amphidiploids are considered the first new species to be observed in origin (20). These hybrids between wheat and rye are now known as triticale (X Triticosecale

Wittmack) (3).

Muntzing (20) reported that the first triticales to be scientifically studied were the octoploid types developed at Saratov, Russia, by the Meister group, and that Lebedeff in 1934 was the first worker to report the occurrence of aneuploidy in triticale. According to Muntzing, Lebedeff pointed out that the reduced fertility and other meiotic disturbances of the amphidiploid were characteristic of inbred lines of rye and suggested that these characteristics might be avoided by the use of fertile and vigorous inbred lines of rye for the initial wheat-rye crosses. Studies conducted by Muntzing (19) and Sanchez-Monge (24) also showed that the use of outbreeding rye in triticale gives poor triticale from a standpoint of fertility and meiotic disturbances. This would appear to be true since triticale is self-fertilizing and homozygous like the wheat parent. All the weak points of the normally heterozygous rye genome would then show up in the triticale because of enforced homozygosity.

The variation in chromosome number in bulk populations of 27 advanced strains of hexaploid triticale obtained from cross combinations among seven primary types were studied by Tsuchiya and Larter (31). Euploids were found to average 81.5% and to range from 57.2 to 100% in these advanced strains. Tsuchiya and Larter (30) observed eight strains of hexaploid triticale which had undergone seven to eight generations of selection for improved agronomic characteristics. The mean frequency of aneuploids in the bulk populations was found to be

11.5% and to range from 9.9 to 14.9%. The immediate progeny of euploid plants from these bulk populations averaged 8.8%, varying from 3% in those strains involving T. turgidum L. var. dicoccum to approximately 11% in those strains with T. turgidum var. durum or T. turgidum var. carthlicum (persicum) as one parent.

Eight lines of hexaploid triticale investigated by Merker (14) had an aneuploid frequency ranging from 2.7 to 18%. At metaphase I, the number of euploids ranged from 24.72 to 60.61%. The number of univalents per cell were 2.33 and 1.01, respectively, with a range of 0 to 12. The frequency of euploid cells ranged from 15.52 to 58.30% at anaphase I while the number of laggards varied from 0.82 to 3.08 per cell with a range of 0 to 10.

Shkutina and Khvostova (26) cytologically investigated 16 hexaploid triticales, four of which were primary triticales and 12 were secondary triticales, and 15 octoploid triticales. They observed 21 and 28 bivalents, respectively, indicating that pairing was not disturbed. Meiotic disturbances, however, were found in all the triticales studied. The frequency of irregularities in the hexaploids varied from 12 to 87%. Disturbances included chromosomes outside the equatorial plate at metaphase I, lagging chromosomes and bridges at anaphase I and II, and micronuclei in telephases I, II and in polyads.

A comparative study of diakinesis and metaphase I was made by Baeva (1) in PMC's of F_1 hybrids between octoploid and hexaploid

triticale forms. The number of chromosomes in the hybrids ranged from 48 to 51 with an average of 49.09, which was the approximate expected number. The predominant number of cells at diakinesis had over seven univalents, indicating that the univalents are represented by more than the D-genome. The frequency of cells with more than seven univalents suggested that asynapsis was a regular phenomenon in F_1 hybrids.

The principal difference between diakinesis and metaphase I was the unequal ratio of the types of bivalents at the two phases. In metaphase I, there was a decrease in the average number of closed ring bivalents per cell, 12.86 to 6.15, and an increase in the number of rod bivalents per cell, 2.97 to 11.74. About 24% of the cells were found to have over seven open ring bivalents which indicates that the disturbances in the homology of the chromosomes most likely affects the R-genome primarily. However, in part of the cells the other genomes were also affected.

In a later study with three octoploid and three hexaploid triticales, Baeva (2) found no normal meiosis in any of the triticales. Disturbances were observed at diakinesis, metaphase I, anaphase I, and telephases I and II. The main disturbances at diakinesis appeared as incomplete pairing of part of the bivalents of both triticale types and as univalents in half of the types.

The most univalents at metaphase I occurred in those triticales which revealed the greatest number of open ring and rod bivalents at

diakinesis. A considerable number of univalents were observed at metaphase I in some triticales in which only bivalents were observed at diakinesis. This was explained by precocious separation, or desynapsis, of part of the open ring and rod bivalents. The univalents observed in some of the triticales at diakinesis were thought to result from asynapsis.

Six lines of hexaploid triticale investigated by Krolow (10) had an aneuploid frequency of 6.95% with a range of 3.3 to 11.43%. Progenies of euploids from these lines had an aneuploid frequency of 16.95%. The progenies of aneuploid plants had aneuploid frequencies ranging from 58.41 to 52.14%. Mean chromosome numbers in the progeny of aneuploid plants showed a reversion to the euploid number of 42.

Cytogenetic investigations were made by Merker (15) of meiosis and fertility in five F_1 combinations and two F_2 populations of hexaploid triticale. Meiosis was more unstable in the F_1's than in the parental lines. Four of the F_1 combinations had a lower fertility than did the parents. The F_2 populations showed a strong heterogeneity for meiotic disturbances.

The presence of univalents at meiosis is a characteristic feature of triticale. What causes these univalents to be present has been the subject of much speculation. Muntzing (19) found that meiotic lability in triticale was correlated with partial sterility, the percentage seed set and percentage of good pollen being reduced to varying degrees in

each triticale strain. He suggested this might be a direct consequence of meiotic disturbances which leads to formation of unbalanced aneuploid gametes or a non-selective sterility. Muntzing (18) suggested that the self-fertility of triticale led to an automatic inbreeding depression of the rye component. This could be the cause of meiotic instability, reduced fertility, and possibly poor vigor. If the univalents were the result of inbreeding depression, then the frequency of univalents would be expected to be lower in F_1 hybrids between different triticale strains. The F_1 hybrids are vigorous, however, and correspond with the fact that crosses between inbred lines of rye give vigorous F_1 hybrids.

Riley and Miller (22) found, by contrast, that in the hybrids of 'cereale' and 'montanum' triticales there were a maximum of 19 univalents and a mean number of 13.15 per cell. This high mean number of univalents can be interpreted to imply that the chromosomes of S. cereale and S. montanum rarely pair with each other against the background of the wheat genotype, although they pair fully at the diploid level.

Homoeologous wheat chromosomes are prevented from synapsing at meiosis by the genetic activity of the Ph locus on chromosome $5B^L$. Since the Ph activity also prevents the synapsis of homoeologous chromosomes derived from Triticum and Aegilops, Riley and Miller (22) considered that pairing between the chromosomes of S. cereale and S. montanum was similarly prevented.

Thomas and Kaltsikes (27) showed a durum wheat background to suppress the meiotic pairing of chromosomes of S. montanum with homoeologous chromosomes of S. cereale in hexaploid triticale. This was attributed to the activity of the $5B^L$ diploidizing system apparently active in tetraploid wheat. They found that the progeny of a pentaploid hybrid of triticale crossed with wheat gave little if any disruption of the pairing of wheat chromosomes. In hybrids of 'cereale' and 'montanum' triticales, however, there were significantly fewer ring bivalents per cell than in the pentaploid triticale X wheat hybrids. The $5B^L$ system may regulate pairing of chromosome sets whose ancestral affinities have been weakened by isolation but their findings indicated the meiotic behavior of disomic triticales require a change in some regulating system other than that on the $5B^L$ system.

Lelley (13) proposed desynapsis as the possible source of univalents in metaphase I of triticale. Meiotic analysis of three hexaploid triticale lines, crossed in all possible combinations, revealed a complete pairing in the F_1 hybrids and in the parents up to late diakinesis. In metaphase I, however, there were significant differences between the different genotypes with regard to paired chromosome ends and univalent frequency. He explained this as a genetically controlled decrease in chiasmata frequency, originating from the differences between the two parental genera, wheat and rye, as to their genetic adaptation for high chiasmata frequency.

Lelley (13) disagreed, as did Thomas and Kaltsikes (27), with

Riley and Miller (22) that the $5B^L$ system in wheat was primarily responsible for the pairing failure and univalent formation in triticale. He argued, that if the $5B^L$ system were operating, this would bring about suppression of the correct prealignment of the homologous chromosomes and the accurate functioning of the synaptinemal complex. If this happened, then univalents would be visible at early diakinesis. Chromosomes are held together only by the chiasmata after disappearance of the synaptinemal complex. These chiasmata represent the only physical linkage for the correct distribution of the half-bivalents during anaphase. In his material, the absence of unpaired chromosomes at diakinesis suggested that the previous steps of meiosis were not disturbed. After the synaptinemal complex disappeared the failure of chiasmata became apparent. Larter et al. (12) and Tsuchiya (28) also proposed desynapsis during late diakinesis as the cause of univalents being present in triticale. Both of these workers ascribed these univalents to the rye component in triticale.

Muntzing (20) believed that the univalents were exclusively or predominately rye and that they were eventually eliminated. Pieritz (21) confirmed the viewpoint of Muntzing (20) modifying it to the extent that, in rare cases, wheat chromosomes can also take part in the meiotic disturbances and eventual elimination. Researchers have since shown that the rye component alone is not responsible for the presence of univalents but that both the rye and wheat components contribute equally to univalence. Shigenaga et al. (25) working with

the triticale cultivar 'Rosner' showed that both the rye and wheat chromosomes contribute to aneuploidy. On the basis of karyotype analysis, 76 aberrant chromosomes were identified in 63 aneuploid plants. Out of a theoretical contribution to aneuploidy of 50.7 and 25.3 univalents, respectively, for wheat and rye, an actual number of 56 and 20 were obtained. This would indicate that both the parental genomes contribute about equally to misbehavior at meiosis. Rosner characteristically exhibits an average of 0.8 univalents per cell at metaphase I and approximately 10% of its progeny are aneuploids.

Further evidence by Larter and Shigenaga (11) indicates that approximately 70% of the PMC's of Rosner have 21 II's at metaphase I, the remaining cells exhibiting varying numbers of univalents. Careful measurement and classification of the univalents showed the range of univalent size to correspond to that obtained from measurement of the complete complement of univalents of a haploid of Rosner. This verified the earlier findings of Shigenaga et al. (25).

Merker (16) identified 39 monosomics and 15 trisomics cytologically in the progeny of euploid plants in a line of hexaploid triticale. He found that there were no significant deviations from a random distribution between the genomes of the two parental species. Later, Merker (17) investigated the chromosome complements of approximately 50 lines of hexaploid triticale and triticale-wheat intercrosses. A Giemsa technique was used which makes it possible to distinguish between rye and wheat chromosomes. He found the number

of rye chromosome pairs present in different lines to vary from one to seven. This revealed that the third genome of triticales can represent a wide range of rye and D-genome chromosomes. It would appear that most of the advances lines of triticale with good agronomic characteristics have a mixed chromosome composition.

Several workers [Krolow (8, 9, 10), Rupert et al. (23), Weimarck (33)] have proposed that an improvement in the meiotic behavior of triticale would enhance its fertility. There is evidence, however, that cytological instability and low fertility are two unrelated phenomena in both hexaploid and octoploid triticale. This was indicated by the low or negative correlations of univalent number and other cytological disturbances with fertility found in investigations by Weimarck (33), Gustafson and Qualset (5), Merker (14, 15), and Hsam and Larter (6). This seems to indicate that, in part, genetic factors determine fertility independently of meiotic irregularities.

The independence indicated between fertility and meiotic disturbances would have the result that lines with good fertility but with relatively disturbed meiosis might be selected for breeding purposes. These aneuploids are considered less fertile and vigorous than euploids and would most likely have a negative effect on agronomic properties of the lines. For this reason, Merker (15), Tsuchiya and Larter (31), and Larter et al. (12), have suggested that frequent cytological checking be undertaken in a triticale breeding program to prevent selection of individual aneuploid plants.

Lelley (13) suggested that the determining effect of outbreeding in rye and inbreeding in wheat was the upper limit to the improvement of fertility in triticale. Muntzing (19) stated that the properties of triticale depend on the parental strains, first the property of the rye and secondly that of the wheat. He suggested that selection for suitable gene combinations could ultimately overcome the possible occurrence of disharmony between the rye and wheat genomes. This would result in more vigorous and productive triticales.

The studies of Larter et al. (12) showed wide differences in fertility level to exist in the upper florets of each spikelet. Fertility based on the primary and secondary florets was found to be very uniform. They suggested that plant selections be made on the basis of fertility of the upper florets to improve the yielding ability of triticale.

Larter et al. (12), Tsuchiya (29), and Weimarck (34) found that the larger the triticale seed the less aneuploidy there is present. Screening for larger seeds could increase the frequency of euploids in populations and selected lines. Weimarck (34) did not think screening was practical, but Tsuchiya (29) thought screening would be of value if practiced yearly. They both found euploid frequency in populations derived from screened seed to be only slightly higher than in standard bulk populations. Hsam and Larter (6), by contrast, found a significant correlation between seed set and normal pollen percentage and a negative correlation of kernel weight with seed set. This could cause

difficulty in a breeding program when selecting for high fertility and improved kernel weight at the same time.

CHAPTER IV

RESULTS AND DISCUSSION

When taking immature cereal spikes for the purpose of obtaining pollen mother cells (PMC's) for analysis of the genetic products at meiosis, a good general guide is to take the immature head at the time when the flag leaf has begun to swell slightly from the growth and emergence of the spike. The immature spikes taken at this time should contain the optimum number of PMC's at diakinesis, the meiotic stage at which the number of chromosomes present can most easily be counted. At this stage of meiosis, synapsis, chiasma formation, and terminalization of the chiasmata should have taken place. Univalents, bivalents, and other pairing conditions should be readily apparent at diakinesis.

The general guide discussed above could not be depended upon in this study for selecting immature spikes for meiotic analysis in triticale. Immature spikes were first taken in the experimental F_1 hybrids of this study when swelling of the flag leaf could be detected. The spikes taken at this time, however, proved to have the larger number of their PMC's at late anaphase I or later meiotic stages. Because of the disappointingly low number of PMC's containing the

desired meiotic stage during the first year of the study, the selection procedure was modified in 1975. The spike was manipulated to locate the tip of the awns. When the awns were found to be at or slightly above the leaf collar, the spike was taken to provide PMC's for meiotic analysis. Observations revealed that slight swelling of the flag leaf became visible shortly after the awns reached this position in the flag leaf. The meiotic stages found with this modification in selection procedure were somewhat more desirable than in 1974, but still did not give a satisfactory number of PMC's at diakinesis.

As the meiotic stages found in 1975 were still unsatisfactory a more drastic modification in spike selection procedure was made in 1976. A greater change could be made in the selection procedure in 1976 because there was no longer a need to maintain the experimental F_1 hybrids and all of the spikes produced could be sacrificed. Spikes for meiotic analysis were taken from the time the spikes could be distinguished to that time at which swelling of the flag leaf could be detected. Approximately 350 heads were taken for meiotic analysis from all experimental hybrids. This compared to approximately 125 heads taken in 1974 and 200 taken in 1975.

The number of PMC's found at diakinesis in 1976 was no better than that found in 1974 although the number of PMC's at later stages of meiosis was lower. The number of cells at meiotic stages earlier than diakinesis increased.

Because of the difficulties encountered in obtaining PMC's at

diakinesis, most chromosome counts were made at metaphase I and anaphase I. At metaphase I, the PMC's exhibited a great amount of stickiness which in most cases prevented the number of bivalents from being determined. Most of the univalents were counted at metaphase I since they normally do not orientate themselves on the metaphase plate and remain scattered throughout the cytoplasm. Some error in the number of univalents determined at metaphase I could be present if bivalents have undergone precocious separation.

The number of bivalents present in the PMC's was largely determined at early anaphase I. At this stage of anaphase I, the chromatids have not yet exhibited the characteristic X-configuration of this meiotic stage and univalents are extremely difficult to identify if present. At later stages of anaphase I the characteristic X-configuration is exhibited by both the normal chromatids and those univalents present at metaphase I and again the univalents cannot be distinguished except as laggards. No laggards were found in this study and univalents were positively identified in only one instance in the course of this study at anaphase I.

Crossing Information

Procedures I and II

A total of 78 crosses was made in 1973. Danne was involved in 23 crosses, TAM W 101 in 33 crosses, Scout 66 in nine crosses, and

Blueboy in 13 crosses (Table II). The average number of seed per cross ranged from 0 to 15.7. All the seed produced was viable. Although the number of spikelets per spike was not recorded, average seed set ranged from slightly over 3% to approximately 52% with most hybrids exhibiting less than 30%.

The F_1 plants grown from seed produced in 1973 were either treated with colchicine or crossed with T385 or T131 triticale in 1974. Chromosome number in five plants were successfully doubled with colchicine, and they yielded a total of 23 viable seed (Table III). Three of these five F_1 hybrids survived in 1975. They were crossed with T131 triticale and produced a total of 126 seed (Table IV). The average number of viable seed/cross varied from 4.3 to 10. Three F_1 hybrids were pollinated with triticale and a total of 24 apparently viable seed were obtained (Table III). Of the four F_1 hybrids produced by pollination with triticale, three survived in 1975. Further crosses with triticale resulted in the production of 67 seed from seven crosses, none of which were viable (Table IV).

After locating seed produced by these two doubling techniques by fingering the spikes, the discarded heads were run through a head-thresher. This resulted in the recovery of 44 additional seed which had not been detected. Thirty of these seeds produced plants in 1975 and were designated Bulks 1 through 30 (Table IV). Pollination with triticale produced a total of 365 seed. Seven of these 30 plants exhibited wheat characteristics and accounted for 141 of the 365 seed

TABLE II

CROSSES MADE AND VIABLE SEED OBTAINED
IN 1973 FROM WHEAT X RYE CROSSES

PEDIGREE	Number Crosses Made	Number Viable Seed	
		Total	Average
Danne/Bonel	6	94	15.7
Danne/Elbon	7	35	5.0
Danne/WR811	7	53	7.6
Danne/Okema	3	30	10.0
	(23)		
TAM W 101/Bonel	9	56	6.2
TAM W 101/Elbon	3	8	2.7
TAM W 101/WR811	4	15	3.8
TAM W 101/Okema	17	84	4.9
	(33)		
Scout 66/Bonel	2	9	4.5
Scout 66/Elbon	2	26	13.0
Scout 66/WR811	3	25	8.3
Scout 66/Okema	2	-	-
	(9)		
Blueboy/Bonel	3	14	4.7
Blueboy/Elbon	4	28	7.0
Blueboy/WR811	2	18	9.0
Blueboy/Okema	4	17	4.2
	(13)		

TABLE III

CROSSES MADE AND VIABLE SEED OBTAINED IN 1974 FROM EXPERIMENTAL F_1 HYBRIDS OBTAINED BY USE OF PROCEDURES I AND II

PEDIGREE	* Number Crosses Made	Number Viable Seed
Danne/Elbon (8X)	94	2
Danne/Bonel (8X)	35	1
TAM W 101/Bonel (8X)	56	6
TAM W 101/Okema (8X)	84	13 (23)
Blueboy/Okema (8X)	17	1
Bulk (8X)	-	44 (44)
Danne/Bonel//962	1	2
Danne/Bonel//T385	1	6
TAM W 101/Okema//T131	2	9
Scout 66/WR811//T131	1	7 (24)

* or number plants treated

TABLE IV

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED IN 1975 FROM EXPERIMENTAL F_1 HYBRIDS OBTAINED BY USE OF PROCEDURES I AND II

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/Elbon (8X)//T131	3	57	19.0	30	10.0
TAM W 101/Bonel (8X)//T131	3	16	5.3	13	4.3
TAM W 101/Okema (8X)//T131	3	53 (126)	17.7	19	6.3
Danne/Bonel//T385/3/T131	5	47	9.4	-	
Danne/Bonel//T385/3/OK72179	1	4	4.0	-	
Scout 66/WR811//2*T131	2	16 (67)	8.0	-	
*Bulk 6E (8X)/T131	1	11	11.0	11	11.0
*Bulk 8E (8X)/T131	2	26	13.0	15	7.5
*Bulk 9E (8X)/T131	2	25	12.5	14	7.0
*Bulk 10E (8X)/T131	2	27	13.5	27	13.5

TABLE IV (Continued)

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
*Bulk 12E (8X)/T131	3	23	7.7	17	5.7
*Bulk 14E (8X)/T131	2	18	9.0	14	7.0
*Bulk 15E (8X)/T131	1	11	11.0	11	11.0
Bulk 21E (8X)/T131	7	71	10.1	71	10.1
#Bulk 22E (8X)/T131	2	30	15.0	24	12.0
Bulk 23E (8X)/T131	1	3	3.0	3	3.0
Bulk 24E (8X)/T131	1	8	8.0	8	8.0
Bulk 25E (8X)/T131	2	19	9.5	10	5.0
#Bulk 26E (8X)/T131	3	37	12.3	10	3.3
Bulk 27E (8X)/T131	1	1	1.0	1	1.0
Bulk 28E (8X)/T131	1	16	16.0	16	16.0
#Bulk 29E (8X)/T131	4	27	6.5	27	6.5
#Bulk 30E (8X)/T131	3	12	4.0	12	4.0
		(365)			

* wheat-like F_1 hybrids in 1975
# wheat-like F_1 hybrids in 1976

produced. Both the average number of seed/cross and average number of viable seed/cross for the triticale-like plants ranged from 1 to 16. The wheat-like plants had a seed-set of 7.7 to 13.5/cross and a range of 5.7 to 13.5 for viable seed/cross. Four of the ten bulk F_1 hybrids grown in 1976 exhibited wheat-like characteristics (Table IV).

Procedure III

Five F_1 hybrids from wheat X triticale crosses were obtained in 1973. These hybrids produced 181 seed with an average number of seed/cross that ranged from 2 to 19 (Table V). No viable seed was produced in three of the F_1 hybrids and 0.5 and 5.2 viable seed/cross were obtained from the other two F_1 hybrids which produced 17 viable seed. These two surviving F_1 hybrids produced 216 seed of which only 28 were viable in 1974. Seed/cross ranged from 6.0 to 13.7 and viable seed/cross from 0.7 to 4.7 (Table VI). Four F_1 hybrids of wheat X triticale were observed in 1975. These produced 103 seed from 24 crosses. The average number of seed/cross varied from 3 to 7. Three of the hybrids produced a total of 17 viable seed and averaged 0.5 to 3.5 viable seed/cross (Table VII).

The reciprocal cross, triticale X wheat, also produced five F_1 hybrids in 1973. The 12 crosses produced 180 seed of which 98 were viable. Seed set/cross ranged from 1.0 to 19.1 and the number of viable seed/cross from 8 to 19 (Table V). The crosses in 1973 produced four F_1 hybrids which were observed in 1974. They

TABLE V

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED IN 1973 FROM WHEAT X TRITICALE (AND RECIPROCAL) CROSSES

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/T131	5	53	10.6	16	5.2
Danne/T385	1	2	2.0	-	-
TAM W 101/OK72179	4	36	9.0	-	-
TAM W 101/T131	2	33	16.5	1	0.5
Scout 66/T385	3	57	19.0	-	-
		(181)		(17)	
T131/Danne	7	134	19.1	62	8.8
T385/Danne	1	19	19.0	19	19.0
OK72179/Danne	2	21	10.5	16	8.0
OK72179/Scout 66	1	1	1.0	1	-
OK72179/Blueboy	1	5	5.0	-	-
		(180)		(98)	

TABLE VI

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED IN 1974 FROM EXPERIMENTAL F_1 HYBRIDS OBTAINED BY USE OF PROCEDURE III

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/2*T131	15	169	11.3	12	0.7
Danne/T131//OK72179	3	41	13.7	14	4.7
TAM W 101/2*T131	1	6	6.0	2	2.0
		(216)		(28)	
T385/Danne//T385	11	14	1.3	2	2.1
T385/Danne//T131	1	2	2.0	1	1.0
OK72179/Danne//OK72179	6	14	2.3	6	1.0
OK72179/Danne//T131	1	-	-	-	-
		(30)		(9)	

TABLE VII

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED IN 1975 FROM EXPERIMENTAL F_1 HYBRIDS OBTAINED BY USE OF PROCEDURE III

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/T131//OK72179/3/T131	12	77	6.4	8	0.7
Danne/T131//2*OK72179	4	12	3.0	2	0.5
Danne/3*T131	6	-	-	-	-
TAM W 101/OK72179//2*T131	2	14	7.0	7	3.5
	(24)	(103)		(17)	
T385/Danne//2*T385	1	10	10.0	3	3.0
T385/Danne//2*T131	1	-	-	-	-
	(2)	(10)		(3)	

produced 30 seed from 19 crosses. No seed was obtained from one of the F_1 hybrids. The number of seed/cross varied from 0 to 2.3. Viable seed/cross varied from 0 to 2.1 with a total of nine being viable (Table VI). Only two F_1 hybrids of this cross combination were observed in 1975. Two crosses with them produced ten seed of which three were viable. No seed was obtained from one of the F_1 hybrids (Table VII).

Because of the low number of crosses and viable seed obtained in 1973, additional wheat X triticale (and reciprocal) crosses were made in 1974 (Table VIII). Three of the 39 crosses produced no seed. Out of 443 seed produced from the remaining 36 crosses, only 76 viable seed were obtained. The wheat X triticale crosses produced from 0 to 23 seed/cross for a total of 375 seed. Thirty of these seed were viable and the number of viable seed/cross ranged from 0 to 2. Eight wheat X triticale F_1 hybrids were observed in 1975. These produced 51 seed of which 16 were viable. Average number of seed/cross ranged from 1 to 10 and 0 to 4.3 viable seed were produced/cross (Table IX). The reciprocal crosses, triticale X wheat, produced 68 seed in 1974 of which 46 were viable. Total seed/cross ranged from 2 to 9 and viable seed/cross varied from 0 to 5 (Table VIII). Eight of these F_1 hybrids produced a total of 41 seed and from 0 to 9 seed/cross. Twenty of these seed were viable and averaged 0 to 7 seed/cross (Table IX).

The initial wheat-rye crosses, which produced the experimental

TABLE VIII

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED
IN 1974 FROM WHEAT X TRITICALE
(AND RECIPROCAL) CROSSES

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/T385	3	51	17.0	6	2.0
Scout 66/T385	5	78	15.6	7	1.4
Scout 66/T131	1	-	-	-	-
Scout 66/OK72179	1	-	-	-	-
TAM W 101/T385	7	113	16.1	5	0.7
TAM W 101/T131	3	17	5.7	-	-
TAM W 101/OK72179	1	3	3.0	2	2.0
Blueboy/T385	4	66	16.5	5	1.3
Blueboy/T131	2	24	12.0	3	1.5
Blueboy/OK72179	1	23	23.0	2	2.0
		(375)		(30)	

TABLE VIII (Continued)

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
T385/Danne	3	18	6.0	14	4.7
T385/TAM W 101	2	18	9.0	10	5.0
T385/Blueboy	2	9	4.5	9	4.5
OK72179/TAM W 101	1	2	2.0	-	-
OK72179/Scout 66	1	6	6.0	3	3.0
T131/Scout 66	2	15	7.5	10	5.0
		(68)		(46)	
		(443)		(76)	

TABLE IX

CROSSES MADE, SEED OBTAINED, AND VIABLE SEED OBTAINED IN 1975 FROM EXPERIMENTAL F_1 HYBRIDS OBTAINED BY USE OF PROCEDURE III

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
Danne/2*T131	3	16	5.3	13	4.3
Danne/T385//T131	1	3	3.0	-	-
Danne/T131//OK72179	1	6	6.0	-	-
TAM W 101//2*T385	1	2	2.0	-	-
Blueboy/2*T131	3	3	1.0	-	-
Blueboy/T131//T385	1	8	8.0	1	1.0
Blueboy/2*T385	1	3	3.0	1	1.0
Blueboy/T385//T131	1	10	10.0	1	1.0
		(51)		(16)	

TABLE IX (Continued)

PEDIGREE	Number Crosses Made	Number Seed Obtained		Number Viable Seed	
		Total	Average	Total	Average
T131/Scout 66//T131	8	4	0.5	2	0.3
T385/Danne//T131	6	1	0.2	-	-
T385/Danne//T385	4	3	0.8	-	-
T385/TAM W 101//T131	2	18	9.0	14	7.0
T385/TAM W 101//T385	2	9	4.5	4	2.0
T385/Blueboy//T131	6	5	0.8	-	-
T385/Blueboy//T385	1	1	1.0	-	-
OK72179/Scout 66//T131	1	- (41)	-	- (20)	-

material for Procedures I and II, had approximately the same range of viable seed/cross regardless of the parental material involved in the crosses. Procedure I was apparently less successful as a means of obtaining F_1 seed than was Procedure II. Twenty-four seed were produced from five crosses in 1974 as opposed to only 67 seed produced from 286 colchicine treated plants. The average number of seed/cross in 1975 was approximately the same for both Procedures I and II. No viable seed, however, was produced from crosses involving Procedure II. All crosses involving Procedure I produced viable seed.

In Procedure III, the same number of both wheat X triticale and reciprocal crosses were made initially. The range of seed/cross was also of the same magnitude. The number of viable seed produced, however, was less for the wheat X triticale crosses than for the reciprocal crosses. More seed was obtained from crosses with wheat X triticale than with the reciprocal crosses in 1974 and 1975. Numbers of viable seed obtained/cross were greater for the wheat X triticale crosses in 1974, but were approximately the same for both sets of crosses in 1975. The second set of wheat X triticale (and reciprocal) crosses begun in 1974 showed basically the same pattern as the first set.

When the crossing data are examined over the entire study period, it appears that all three breeding procedures will produce approximately the same amount of seed/cross. The number of viable seed/cross, however, are much greater for Procedures I and

II than for Procedure III. Procedures I and II are equal to each other and better overall than Procedure III when both total seed/cross and viable seed/cross are considered.

Meiotic Analysis

Procedure I

Chromosome counts were made on 11 experimental F_1 hybrids. Six of the 11 F_1 hybrids had counts made for two years while the other five F_1 hybrids were counted for only one year. No meiotic irregularities except univalents were observed in any of the 11 F_1 hybrids.

In the F_1 hybrid TAM W 101/Okema (8X)//T131 in 1975, 21 bivalents were counted in one cell. Univalents were counted in 57 cells in this F_1 hybrid (Table X). There was an average of 0.5 univalents per cell while the total number of univalents per cell ranged from 0 to 4. In 1976, countable bivalents were not found in any of the PMC's examined. Twenty-three cells were scored for univalents which averaged 2.96 per cell. Figure 1-1 to 1-4 shows typical meiotic configurations for this F_1 hybrid.

The number of chromosomes in the F_1 hybrid TAM W 101/Bonel (8X)//T131 averaged 28 II in 16 cells in 1975 and ranged from 25 to 28 (Table X). No univalents were found in 83 cells examined. This F_1 hybrid in 1976 had three fewer bivalents per cell based on two cells examined. The number of univalents, however, increased

TABLE X

NUMBER OF CELLS COUNTED AND AVERAGE NUMBER OF UNIVALENTS (I) AND BIVALENTS (II) OF EXPERIMENTAL F_1 HYBRIDS OBTAINED FROM PROCEDURES I AND II

	1975				1976			
PEDIGREE	No. cells	I	No. cells	II	No. cells	I	No. cells	II
TAM W 101/Okema (8X)//T131*	57	0.5	1	21	23	3.0		
TAM W 101/Bonel (8X)//T131	83	-	16	28	41	10.7	2	25
Bulk 6E (8X)	30	1.2	12	26				
Bulk 12E (8X)	4	2.5						
Bulk 15E (8X)	50	1.3						
Bulk 21E (8X)	44	2.1						
Bulk 22E (8X)/T131	54	1.5					1	22
Bulk 23E (8X)/T131	45	1.5			2	4.5	4	47

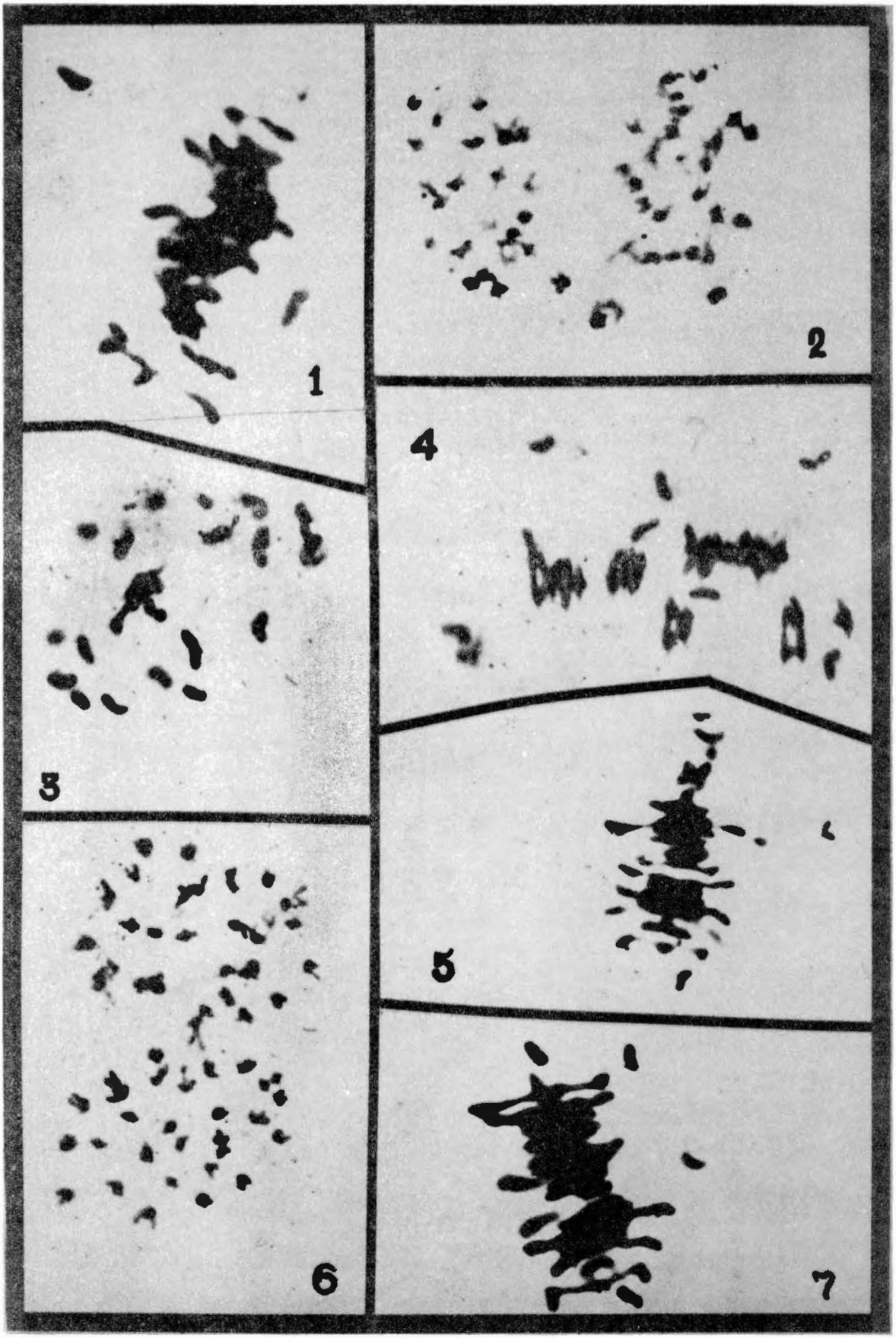
TABLE X (Continued)

PEDIGREE	1975 No. cells	1975 I	1975 No. cells	1975 II	1976 No. cells	1976 I	1976 No. cells	1976 II
Bulk 24E (8X)/T131	70	1.4					1	45
Bulk 25E (8X)	59	1.9						
Bulk 26E (8X)/T131					76	-	4	21
TAM W 101/Okema//2*T131	8	3.4	18	23	50	3.9		
Scout 66/WR811//2*T131					17	2.9		

* ex. - Pedigree for 1975 is TAM W 101/Okema (8X)
Pedigree for 1976 is TAM W 101/Okema (8X)//T131

1.	TAM W 101/Okema (8X)	Metaphase I	2 I
2.	TAM W 101/Okema (8X)	Anaphase I	24 II
3.	TAM W 101/Okema (8X)//T131	Diakinesis	21 II
4.	TAM W 101/Okema (8X)	Metaphase I	19 II 8 I
5.	TAM W 101/Bonel (8X)//T131	Metaphase I	2 I
6.	TAM W 101/Bonel (8X)	Anaphase I	28 II
7.	TAM W 101/Bonel (8X)//T131	Metaphase I	4 I

Figure 1. Photomicrographs of diakinesis, metaphase I, and anaphase I in different triticale F_1 hybrids from Procedure I.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greatly. Forty-one cells examined showed an average of 10.7 univalents per cell and ranged from 0 to 20. Figure 1-5 through 1-7 shows 28 II at anaphase I and univalents at metaphase I.

Nine bulk F_1 hybrids developed by use of Procedure I were also examined (Table X). The number of cells in which univalents were found varied from 4 to 70 in 1975. The number of univalents per cell averaged 1.2 to 2.5 with a range of 0 to 7. Bivalents were found only in BULK 6E (8X) in 1975. Twelve cells examined had an average of 26 II per cell and a range of 21 to 28 II.

Bivalents and univalents were examined in only four of these nine bulk F_1 hybrids in 1976 (Table X). Two cells of BULK 23E (8X) /T131 had an average of 4.5 univalents per cell while BULK 26E (8X) /T131 had no univalents in 76 cells examined. Anywhere from 1 to 4 cells were found to contain bivalents in these bulk F_1 hybrids. The average number of bivalents per cell ranged from 42 to 47 with an overall range of 42 to 49 with most being near the lower end of the range. Figure 2 shows several meiotic configurations in these bulk F_1 hybrids.

Procedure II

Two F_1 hybrids developed by the use of Procedure II were examined during this study. The F_1 hybrid TAM W 101/Okema//2* T131 in 1975 had an average of 3.4 univalents per cell in the eight cells counted (Table X). The number of univalents per cell ranged

1.	Bulk 25E (8X)	Metaphase I	2 I
2.	Bulk 24E (8X)	Metaphase I	3 I
3.	Bulk 25E (8X)	Metaphase I	6 I
4.	Bulk 24E (8X)	Anaphase I	28 II
5.	Bulk 23E (8X)/T131	Anaphase I	49 II
6.	Bulk 22E (8X)/T131	Anaphase I	24 II

Figure 2. Photomicrographs of metaphase I and anaphase I of different bulk populations from Procedure I.

1.	TAM W 101/OK72179//T131	Anaphase I	24 II 2 I
2.	TAM W 101/OK72179//T131	Metaphase I	25 II
3.	TAM W 101/OK72179//2*T131	Anaphase I	4 I
4.	TAM W 101/OK72179//2*T131	Metaphase I	12 I

Figure 3. Photomicrographs of metaphase I and anaphase I of different experimental F_1 hybrids from Procedure III.


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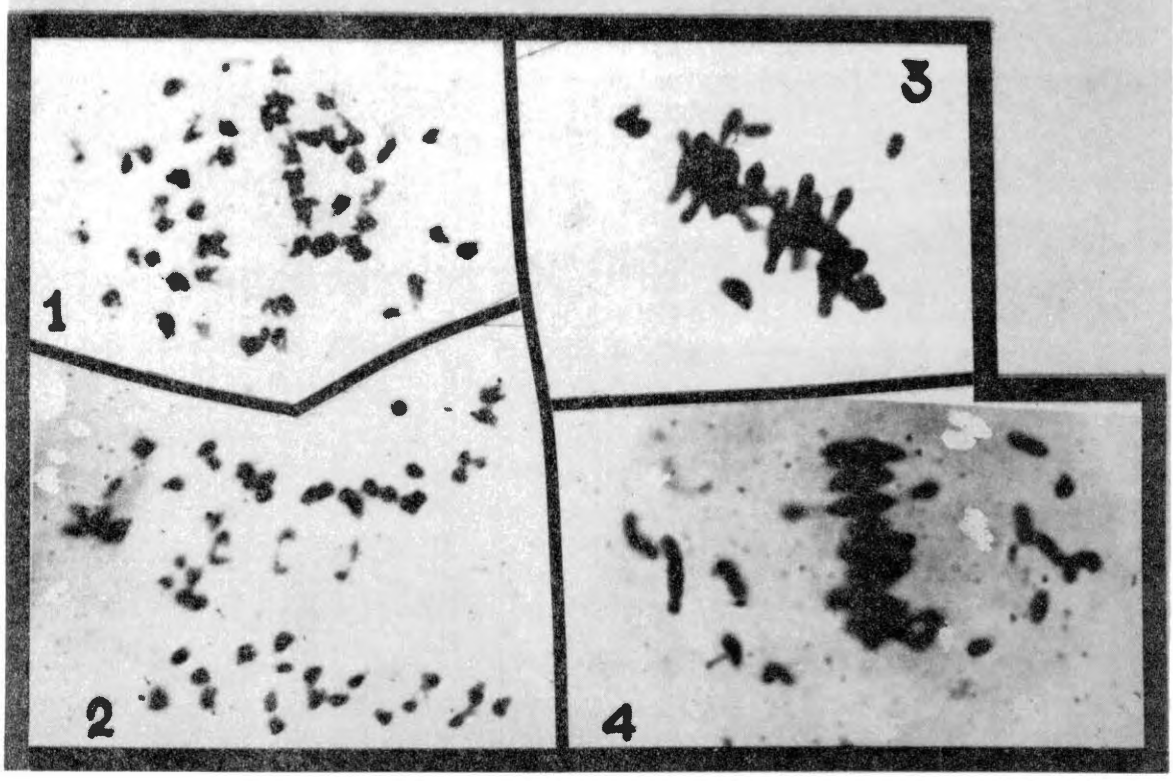
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from 1 to 8. Eighteen cells examined for bivalents showed an average of 23 II per cell and a range of 19 to 28. In 1976, 50 cells examined were found to have an average of 3.9 univalents per cell with a range of 2 to 7. No cells were found which contained countable bivalents (Table X). The F_1 hybrid Scout 66/WR811//2*T131 did not produce countable PMC's in 1975. An average of 2.9 univalents/cell were found in 1976 from the 17 cells scored. No cells were found in which bivalents could be counted (Table X). Photomicrographs of F_1 hybrids developed from use of Procedure II could not be obtained.

Procedure III

Five experimental F_1 hybrids of wheat X triticale were developed from the use of this procedure. Three of the five F_1 hybrids were examined cytologically for all years of the study, and the remaining F_1 hybrids were examined for one and two years, respectively.

The F_1 hybrid Danne/3*T131 (A) did not contain any univalents in the 40 cells examined in 1974 or in 1975 when 63 cells were examined. An average of 0.1 univalents/cell was found in 18 cells examined in 1976 (Table XI). Bivalents were found to average 21 II/cell in 23 cells examined in 1974 with a range of 19 to 21. The 40 cells examined in 1975 showed a range of 20 to 22 II and an average of 21 II/cell. Both cells examined in 1976 had 21 II/cell.

The F_1 hybrid Danne/3*T131 (B) showed essentially the same results as the F_1 hybrid discussed above. An average of 0.06 and

TABLE XI

NUMBER OF CELLS COUNTED AND AVERAGE NUMBER OF UNIVALENTS (I) AND BIVALENTS (II) OF EXPERIMENTAL F_1 HYBRIDS OBTAINED FROM PROCEDURE III

	1974				1975				1976			
PEDIGREE	No. cells	I	No. cells	II	No. cells	I	No. cells	II	No. cells	I	No. cells	II
Danne/3*T131 (A) #	40	-	23	21	63	-	40	21	18	0.01	2	21
Danne/3*T131 (B)	68	0.1	6	21	26	0.1	25	21	35	0.03	12	21
Danne/T131//2*OK72179	8	0.4	3	21	68	0.01	19	21	62	-	3	21
Danne/T131//OK72179/3/T131									45	0.13	5	21
TAM W 101/OK72179//2*T131					10	2.9	24	23	52	4.4		
T385/Danne			30	21								
T385/TAM W 101							4	20				

ex. - Pedigree for 1974 is Danne/T131, Pedigree for 1975 is Danne/2*T131, Pedigree for 1976 is Danne/3*T131

0.08 univalents/cell were observed, respectively, in 1974 and 1975. The number of cells examined was 68 in 1974 and 26 in 1975. The range of univalents in both years was 0 to 1. Thirty-five cells examined in 1976 gave an average of 0.03 univalents/cell (Table XI).

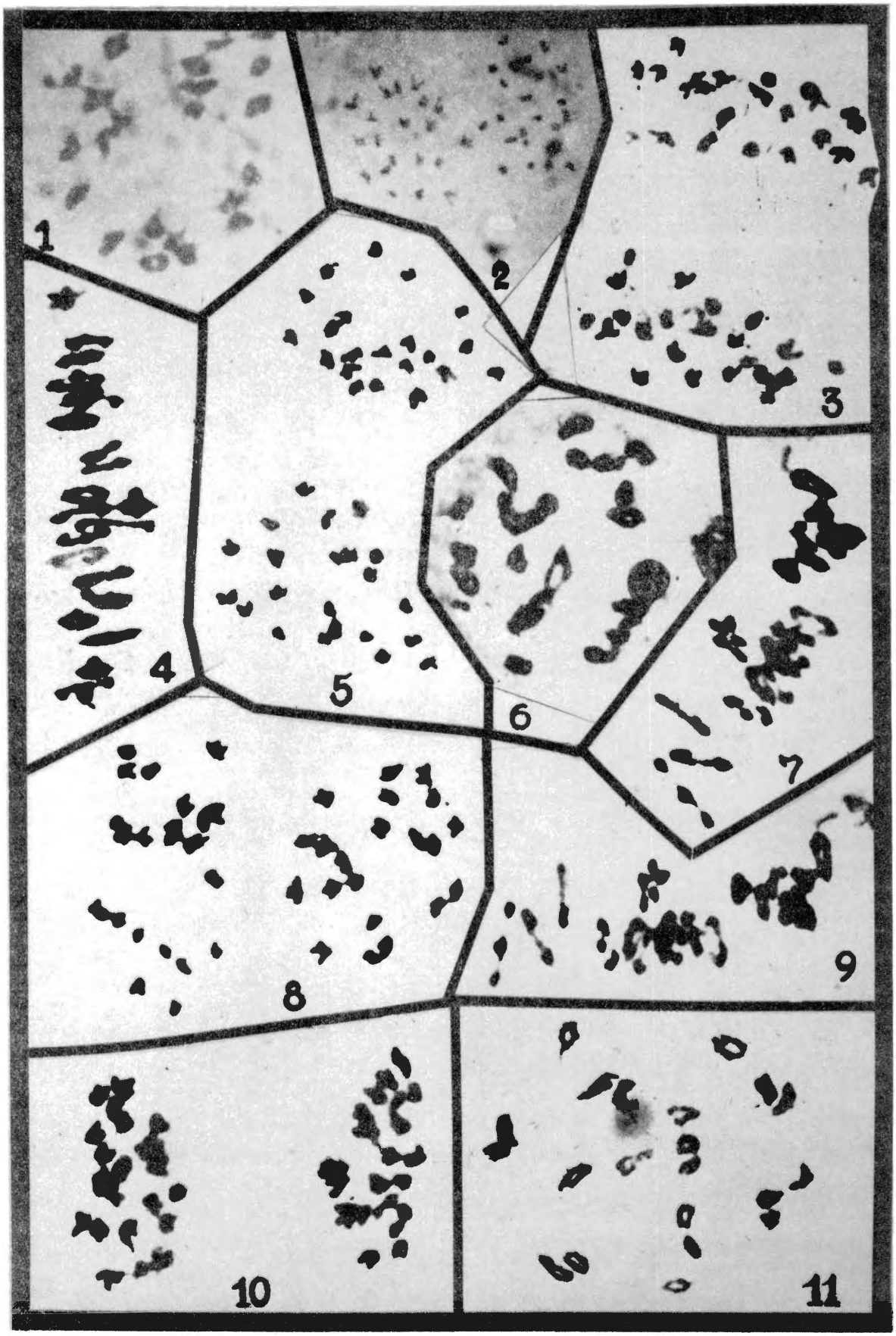
Bivalents were counted in six cells in 1974 and in 25 cells in 1975. These cells averaged 21 II/PMC with a range of 20 to 21 II. All 12 PMC's examined in 1976 had 21 II. Photomicrographs of the above two lines at diakinesis, metaphase I, and anaphase I are shown in Figure 4-1 through 4-5.

Fewer univalents/PMC were found in the F_1 hybrid Danne/T131 //2*OK72179. An average of 0.37 univalents/PMC were found in 1974 from eight cells which had from 0 to 2 univalents each. In 1975, 68 cells were examined which gave an average of 0.01 univalents/ PMC and a range of 0 to 1 univalents. There were no univalents in 62 cells examined in 1976. Bivalents were counted in three cells in 1974 and 1976, all of which had 21 II. Nineteen cells examined in 1975 had an average of 21 II/PMC and a range of 19 to 22 (Table XI). Photomicrographs of this F_1 hybrid at metaphase I are shown in Figure 4-6 through 4-9.

Meiotic counts were made in the F_1 hybrid Danne/T131// OK72179/3/T131 in 1976. Univalents averaged 0.13/PMC with a range of 0 to 3 in 45 cells. Twenty-one bivalents were present in all cells examined (Table XI). Photomicrographs of this F_1 hybrid at both diakinesis and anaphase I are shown in Figure 4-10 and 11. The

1.	Danne/T131	Diakinesis	21 II
2.	Danne/T131	Anaphase I	21 II
3.	Danne/2*T131	Anaphase I	21 II
4.	Danne/3*T131	Metaphase I	21 II
5.	Danne/3*T131	Anaphase I	21 II
6.	Danne/T131//OK72179	Diakinesis	21 II
7.	Danne/T131//2*OK72179	Metaphase I	21 II
8.	Danne/T131//OK72179	Anaphase I	21 II
9.	Danne/T131//2*OK72179	Metaphase I	21 II
10.	Danne/T131//OK72179/3/T131	Anaphase I	21 II
11.	Danne/T131//OK72179/3/T131	Diakinesis	21 II

Figure 4. Photomicrographs of diakinesis, metaphase I, and anaphase I in different triticale F_1 hybrids from Procedure III.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TAM W 101/OK72179//2*T131 F_1 hybrid was observed meiotically for two years. In 1975, an average of 2.9 univalents were found in ten cells which exhibited a range of 1 to 8 univalents. The average number of univalents increased to 4.38/PMC in 1976 from a total of 52 cells that had a range of 1 to 12 univalents. Counts in 24 cells gave a mean of 23 II and a range of 19 to 28 II (Table XI). Photomicrographs of this F_1 hybrid at metaphase I and anaphase I are shown in Figure 3.

Reciprocal crosses, triticale X wheat, gave PMC's in which meiotic counts could be made once in each of two years. The F_1 hybrid T385/Danne had an average of 21 II/PMC from 30 cells and ranged from 19 to 21 in 1974. The F_1 hybrid T385/TAM W 101 had four cells which had a mean of 20 II/PMC and a range of 20 to 21 (Table XI). No photomicrographs were obtained of these two F_1 hybrids because of improper squashing.

The F_1 hybrids developed by means of Procedure I supplied little information about their meiotic condition. Although in most of the hybrids approximately 50 cells were scored for univalents, these cells were scattered widely throughout the material examined. For this reason, the values given for these cells are not considered representative of the hybrids developed by use of this procedure. Values for univalents obtained the second year of the study were 3 to 10 times greater than those values obtained the previous year. This would seem to confirm the observation that the first year values were not representative of the material as selection was made each year

for those hybrids having the lowest number of univalents. Bivalents were scored on too few cells both years of the study to obtain reliable values/cell.

Information from Procedure II was obtained from only two F_1 hybrids. Cells were scored for two years and one year, respectively. The number of univalents/cell for the hybrid scored for two years was essentially the same both years and values obtained for the second hybrid were little different from the other. Only a few cells were scored for each hybrid. Bivalents were scored only on that hybrid observed for both years. The low number of cells scored for bivalents makes the value obtained questionable.

Procedure III provided more information than the other procedures, but the information was not considered to be of any greater reliability. Three hybrids were scored for each year of the study. Univalent values were less than 0.5/cell in most instances, but the cells scored were scattered widely throughout the material as they were for Procedure I. Although 21 bivalents/cell were scored in these three hybrids they were found in too few cells to be considered representative of the material examined. Information from the other four hybrids developed by this procedure differed very little from those examined each year of the study, although three of them were examined for only one year each.

CHAPTER V

SUMMARY AND CONCLUSIONS

Three different breeding procedures were employed to determine if the particular procedure used would influence the rate at which a stable meiotic product could be attained. Pollen Mother Cells (PMC's) were taken from each experimental F_1 hybrid and examined cytologically for meiotic abnormalities.

Considerable difficulty was encountered in obtaining PMC's at the correct physiological stage to determine the meiotic complement with any accuracy. In the majority of cases, the meiotic stages secured were too advanced to enable the meiotic complement and any meiotic abnormalities to be determined.

The examination of a minimum of 50 cells was attempted. The number of cells examined which contained univalents was fairly close to this number of cells. These cells, however, were not easily located and were generally in a metaphase I stage. Stickiness of the chromosomes at this stage prevented the number of bivalents from being determined with very few exceptions. Some error in the number of univalents in each cell could be present if any bivalents had undergone precocious separation.

Countable bivalents were generally found in fewer than 25 cells and most of these were in the early to mid-anaphase I stage. The presence of univalents could contribute to an error in the number of bivalents counted as the laggards would be difficult to identify at this stage.

The chromosome counts secured are not considered representative of the experimental F_1 hybrids examined because of the difficulty encountered in locating cells containing countable univalents or bivalents. The cytological information does suggest that there was little change in meiotic stability from one F_1 generation to another, and that the instability is of a minor nature.

This, however, does not appear to be true when one looks at the low seed-set/cross and the number of viable seed obtained from each cross. The majority of the crosses set an average of ten seed or less/cross and produced five or less viable seed/cross. This indicates that a high amount of meiotic irregularities should be present in the experimental F_1 hybrids examined.

The information secured in this study was not considered sufficient to reach a decision about which breeding procedure would result in an earlier stable meiotic condition. The information secured from Procedure III does suggest, however, that meiotic stability may result sooner from this breeding procedure than from Procedures I and II.

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