CYTOGENETIC ANALYSIS OF HYBRID STRAINS DERIVED FROM INTERSPECIFIC CROSSES OF *TRITICUM AESTIVUM* L. AND *T. TIMOPHEEVI* ZHUK

by

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INTRODUCTION

Sixteen advanced generation hybrid strains derived from seven different crosses involving a number of strains and varieties of Triticum aestivum L. (2n = 42) and T. timopheevi Zhuk. (2n = 28) have been studied with respect to their cytological stability and rust reactions. These strains came from breeding programs which were initiated about 25 years ago in different wheat growing regions in the United States and which were primarily aimed at transferring the rust resistance of T. timopheevi to common bread wheats. They have been tested and maintained in the wheat rust nurseries at the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, for a number of years and are known to carry the leaf and stem rust resistance of T. timopheevi to varying degrees. Now these have been studied more intensively in the greenhouse for their individual immature plant stage rust reactions against the more important representative leaf and stem rust races separately. For convenience in description, these were assigned line numbers.

The nature of rust resistance was found to vary considerably from line to line, thus indicating the possibility that different genes are involved. Besides rust resistance, these segregates have other less desirable characters which may be due to interaction of T. timopheevi genes with the T. aestivum genome. This has led to the belief that whole chromosomes or chromosome segments of T. timopheevi are either present or absent and that the rust resistance may not have been transferred by simple crossing over and genetic recombination.

Since T. timopheevi has 14_{II} chromosomes, only 7 of which could be expected to pair with 7 of the 21_{II} of T. aestivum, many chromosome irregularities

would occur in meiotic divisions in F_1 hybrids. Repeated back crossing to T. aestivum has resulted in bringing the chromosomes close to the genome of the recurring parents, i.e. to a number close to the 42 of T. aestivum. Selection for rust resistance has maintained at least a small portion from the T. timopheevi genome. So it is to be expected that the sixteen lines will differ chromosomally. In fact some of these lines were found to have unstable chromosome numbers and to be irregular in meiosis. In these, meiosis was studied in detail, records being made of chromosome numbers, presence or absence of micronuclei (m.n.) at tetrad (quartet) and dyad (interphase 1) stages, and various chromosome irregularities at other stages. Other lines, in spite of a normal chromosome number, showed extreme variability as to the number of PMC with micronuclei at dyad and tetrad stages. This variability was studied and analyzed statistically for plants within lines, samples within plants (different spikes of the same plant taken at the same time), spikes within samples (different spikes of the same plant taken at different times), and florets within spikes (different florets of the same spike). In order to obtain a statistical picture of chromosomal irregularities at successive stages of meiosis, correlations were made between the number of normal cells (lacking micronuclei or any irregular chromosome elements) at each stage with those at the five other meiotic stages. The pattern of meiotic irregularities points to the possibility that diverse types of chromosomal alterations are involved in different lines and that some of the lines have more than one type of structural alteration, which gave rise to highly variable and unpredictable chromosome behavior.

Since transfers of differing portions of T. timopheevi chromosomes may be involved, it is logical to expect that at least some of the lines may

differ from one another in their chromosome constitution and genetic expression. The primary aim of this study was to determine as much as possible about the nature of the genetic transfer that has presumably taken place from T. timopheevi to the segregates resembling common wheat and to select a line (or lines) that could be used as a donor of genes for rust resistance in a breeding program. From cytological observations made so far, it seems certain that in many of these lines structural alterations involving segmental translocations and/or inversions of varying sizes have taken place. It will be necessary to complete the study of F_1 hybrid progenies, that have been obtained by crossing these lines with a common wheat variety (Cheyenne), before much insight can be obtained into the nature of these genetic changes. Pairing relations at meiosis in these F_1 hybrids should indicate the presence in the segregates of any T. timopheevi chromosomes or segments which have no homologs in the T. aestivum genome.

One line has been selected as possibly the most desirable for the transfer of rust resistance. It has twenty-one pairs of chromosomes, normal meiosis and a high degree of rust resistance (0 type) against all the important races of leaf rust. This resistance is presumably determined by genes with varying degrees of dominance since resistance to the different races is present to different extents in the F_1 hybrid progeny obtained by crossing this line with Cheyenne. This line, like all the others, carries some undesirable characters, genes for which are probably located on the same chromosome or segment as the rust resistance and so are not likely to be lost by crossing over and segregation. In a further continuation of the study reported in this thesis, tips of young tillers of the F_1 hybrid progeny of this line with Cheyenne will be irradiated with x-ray and ultra violet in order to induce chromosome alterations. Among these may possibly be found a

translocation of a small segment of T. timopheevi chromosome to a chromosome of T. aestivum, thus making possible the eventual elimination of chromosome segments carrying genes for undesirable characters while still retaining the gene(s) for rust resistance (Sears, 1955).

REVIEW OF LITERATURE

Improvement of crop plants by hybridization with their wild relatives has proved to be more rewarding in some crops than in others. Related wild and semi-wild forms of the cultivated plants are often a valuable source of genes for disease resistance and for capacity to withstand adverse conditions, such as resistance to drought and extremes of temperature, and ability to grow in acid and alkali soils and under widely differing geographical locations.

Intergeneric Hybridization Involving Triticum

Perhaps the earliest intergeneric cross ever made in the grass family involved Aegilops ovata and Triticum aestivum (Gordon, 1853). The hybrid plants obtained from this combination were identical, both in morphological appearance and self sterility, with Aegilops triticoides Reg., which was collected by Requien in France in 1821-24 and by Gussone and Tenone in Italy and was first described by Bertolani (1833). This hybridization was attempted primarily to find an explanation for the occurrence of A. triticoides in and around wheat fields where A. ovata grew as a weed. Most of the subsequent early published reports of hybridization among Triticum and allied genera were attempts to obtain biological curiosities and slightly later ones were primarily for the purpose of elucidating the phylogenetic

interrelationships and genome homologies by morphological and cytological studies which were brief or fragmentary. Beside Aegilops, other genera viz., Secale (Wilson, 1876; Albert Carman 1884) and Agropyron (Tzitzin, 1936) were successfully crossed with Triticum.

True breeding strains of potential economic importance, derived from intergeneric hybridization in cereals, have been claimed by various workers from time to time (Rimpau, 1891; Miczynsky, 1905). Often such strains combined characteristics of the parents involved in the cross. In some cases cytological observations on such material revealed that their apparent stability could be attributed to their amphidiploid nature (Tiumiakov, 1928; Lewitsky and Benetzkaia, 1931; and others). Others were found to have normal chromosome numbers and regular or nearly regular meiosis; these probably had arisen from gene or chromosome transfer among the genomes of the species crossed. Chromosome transfer may involve substitution or addition of a chromosome or chromosome pair from one genome to another. Nearly wheat-like strains with substituated rye chromosomes and others with rye chromosome pairs have been obtained by Florell (1931), Kattermann (1938) and O'Mara (1940 and 1947), Jones and Jensen (1952) and Taylor (1934) found that such strains never did reach complete genetic homozygosity. Wheat lines, each with a different Hynaldia villosa chromosome or chromosome pair added to the wheat genome, have been obtained by Sears (1953) and Hyde (1953). Both cytologically and genetically stable wheat derivatives with normal chromosome number have been claimed by Tschermak (1929 and 1930) from wheat-rye combinations. In many cases, when there existed little or no homology between genomes of the species crossed, it has been observed that as soon as regularity in chromosome number and meiosis was attained, desirable characters

were lost along with the odd chromosomes from the nonrecurring parent. In such cases strict non-homology between the genomes was thought to interfere with normal genetic recombination (Kostoff, 1943 and Vishnu, et al., 1956). Now it is known that while lack of homology prevents transfer of genes by crossing over, translocation of chromosome segments may take place between genomes that have no synaptic homology. Reunion of broken chromosome ends is primarily determined by chance, so that any two chromosomes with broken ends may rejoin in a random manner (Sears, 1955 and 1956). Chromosome breaks are known to occur in nature and can be induced at a higher rate by treatment with x-rays and other mutagens.

Interspecific Hybridization in the Genus Triticum

Of the interspecific hybrids among Triticum species with different chromosome numbers, only those involving tetraploid and hexaploid combinations are self-fertile (Thompson, 1934) and have yielded strains of economic importance. Hayes, et al., (1920) predicted that rust resistance and presumably other desirable characters of T. dicoccum and T. durum could be transferred to common bread wheats. McFaddan (1930) fulfilled this expectation. He produced two hard red spring wheats, Hope and H_{44}, from a cross between tetraploid Yaroslov emmer (T. dicoccum) and a hexaploid winter wheat, Marquis. Both Hope and H_{44}, like the emmer parent, were immune under field conditions to then known races of stem rust in the United States. Another landmark in wheat breeding came in 1934 when Hayes and his co-workers (Hayes, et al., 1936) at Minnesota Agricultural Experiment Station released Thatcher, a stem rust resistant, non-lodging, good quality and high yielding wheat, which was selected from a double cross involving Marquis-Iumillo (also a

tetraploid-hexaploid cross) and Kanred-Marquis. Thatcher has since acquired world fame and is being used as one of the important sources of stem rust resistance all over the world. Earlier, Hayes and Amdot (1929) had produced Marquillo, a stem rust resistant, stiff strawed bread wheat from a cross involving Marquis and tetraploid Iumillo (T. durum). A number of other famous wheats have had similar origins. Coronation came from the tetraploid x hexaploid cross Pentad (T. durum) x Marquis. At Kansas Agricultural Experiment Station a cross involving Kawvale-Marquillo and Kawvale-Tenmarq has produced Ponca, a common bread wheat carrying a very high degree of Hessian fly resistance derived from the original durum parent of Marquillo, the tetraploid Iumillo (Laude, et al., 1952).

Interspecific Hybridization Involving T. timopheevi

Triticum timopheevi is known to have a high degree of disease resistance (Dickson and Shands, 1933). But unlike other tetraploid Triticum species, it crosses with difficulty with any of the other species and the few F_1 hybrid plants are usually sterile. Wheat breeders in Australia (Pridham, 1939) claimed to have obtained selfed progeny from a cross of T. aestivum (Steinwedel) and T. timopheevi, Timstine being a direct decendent of this cross. In other countries only back-crosses of the F_1 hybrids x common wheat have resulted in progeny (Shands, 1941). Kihara (1934) concluded that the second genome of T. timopheevi is not present in any of the other species of Triticum or Aegilops, since he obtained a maximum of seven pairs of chromosomes at meiosis in hybrids with these species. Other studies have suggested partial homology of this second genome of T. timopheevi with some of the T. aestivum chromosomes. Kostoff (1941) studied the meiotic behavior

of chromosomes in F_1 hybrids obtained from crosses between T. aestivum and T. timopheevi and found 8 to 14 bivalents. Love (1941) observed 4 to 13 bivalents in the F_1 hybrid plants from a cross between the same two species and an average of 9.5 bivalents per PMC was obtained. This amount of pairing suggested partial homology between the two genomes of T. timopheevi with two of T. aestivum, even though only one genome from each species is involved in bivalent formation most of the time. Consequently, genes, if located on pairing chromosomes, could be transferred by crossing over. If the genes for desirable characteristics were located on non-homologous chromosomes, then genetic transfer could only take place by transfer of whole chromosomes or by translocation of a chromosome segment.

Meiotic Stability of Derived Hybrid Strains

Wheats of hybrid origin have been found to vary in meiotic stability. Powers (1932a, 1932b) studied Thatcher and Marquillo, two wheat varieties derived from interspecific crosses, and Marquis, derived from an intervarietal cross of Red Hard Calcutta and Red Fife. He found that Marquillo was the least stable of the three wheats studied, judged by the frequency of micronuclei in microspores. In Marquillo, there was a direct significant correlation between the chromosomal irregularities at metaphase-I, the number of micronuclei in spore quartets and seed setting. Myers and Powers (1938) found that meiotic stability of the derived wheat strains was a heritable character and lines could be selected that differed significantly in frequency of micronuclei. Semeniuk (1947) observed that some of the wheat-like derivatives from a T. timopheevi - T. aestivum cross, those with winter habit, had on the whole comparatively less chromosome stability than those with

spring habit. Semeniuk worked with Pridham's selections and found highly significant correlations among all of the following: the metaphase I cells with univalents, the total abnormalities at anaphase I, metaphase II and anaphase II, micronuclei at dyad and at tetrad stages, and the amount of pollen abortion. All these showed high correlations, so that any one could be used as the index of meiotic stability or instability.

Genetic Exchange Between Genomes with Little or no Synaptic Homology

It is often difficult to determine the extent to which genetic transfer has taken place, particularly when meiotic pairing and irregularity are difficult to interpret. Thus, opposite conclusions have been reached as to the amount of rye chromosome material incorporated in some 29 vulgare-type lines derived from natural wheat-rye crosses obtained from Saratov (Meister, 1921). Bleier (1933) compared the behavior of F_1 hybrids obtained by crossing these derived lines with each of the following: T. aestivum (T. vulgare), T. durum, T. dicoccum and Secale cereale. All of the crosses were made without any unusual difficulty and plants of the derived lines produced F_1 populations similar to those resulting from comparable crosses with varieties of T. aestivum. These F_1 hybrids resulting from a cross of the derived lines x T. aestivum were the same in every way as offspring of the intervarietal crosses between any two common wheat varieties. Cytologically a few univalents and micronuclei were obtained in the F_1's but not a very high percentage. The F_1 hybrids obtained from crosses between the derived lines and rye also appeared the same as hybrids of T. aestivum x rye. This similarity of the derived lines to T. aestivum appears to negate the assumption that any

rye elements, chromosomes or chromosome fragments were retained by plants of derived lines. Kostoff (1943) and Liljefors (1936) believed that the few bivalents observed in PMC in F_1 wheat-rye hybrids were all the result of autosnydesis within the genomes of wheat and rye, and genetic exchange between the genomes of wheat and rye was considered unlikely. However, there were some indications that genetic elements of rye had been incorporated in at least some of the lines. Vaker and Erot (1934) studied the morphology and synaptic behavior of chromosomes in two of these same wheat-rye lines. They found evidence of segmental interchange between the wheat and rye sets of chromosomes which affected the regularity of meiosis and the production of functional pollen. Nondisjunction and scattering of bivalents at metaphase I and lagging at anaphase I were the chief irregularities observed.

In wheat-like segregates of certain other wheat-rye crosses, also, evidence shows incorporation of portions of the rye genome. Kattermann (1934, 1935) examined an F_2 plant obtained by backcrossing F_1 wheat-rye hybrids with wheat and found 22 bivalents in 7.81 percent of the 76 cells examined. Apparently some allosyndesis took place between rye and wheat chromosomes, since complete pairing of wheat chromosomes would be expected to produce only 21 bivalents. In these backcross plants pairing was comparable with that in the wheat parent. Counts of rod and ring bivalents showed chiasma frequency to be 3 percent to 34 percent lower in the hybrid. This was attributed to the structural alterations that presumably took place in intergeneric chromosome pairing. Such alterations were also assumed to produce an occasional trivalent and to be responsible for loose chromosome pairing in back-cross plants. However, meiotic irregularities may not always be due to obvious lack of synaptic homologies and to structural alterations.

Incomplete synapsis is known to occur in intervarietal F_1 hybrid plants of T. aestivum varieties each of which has regular meiosis (Elders, 1927; Hollingshead, 1932; Thompson and Robertson, 1930). Semeriuk (1947) also observed that "two F_1 hybrids between a Steinwedel x T. timopheevi derivative line with winter habit, and Premier and Merit were much more unstable than either parent." Myers and Powers (1938) found that meiotic stability was a heritable character.

Several instances are known of the substitution or addition of a whole rye chromosome or chromosome pair to the wheat genome. Kattermann (1938, 1939) found that speltoid derivatives from a wheat-rye cross (with 2n = 42) when back-crossed to rye, resulted in an F_1 genome which had only one chromosome pair morphologically that of rye. It had a conspicous constriction and was identical in appearance with the one in the derived speltoid line. Chiasma frequency was also found to be higher in this bivalent. In F_1 hybrids between speltoid and wheat this chromosome was the only one to remain unpaired. Obviously, the speltoid derivatives had 20 bivalents of wheat and one of rye. O'Mara (1940), by repeated back crossing of wheat-rye amphidiploids to wheat and selfing of the progeny for a number of generations, obtained plants with single chromosomes and chromosome pairs from Secale added to T. aestivum. Three different chromosomes or chromosome pairs were added to wheat. O'Mara (1947, 1950) substituted the pair of rye chromosomes carrying hairy neck for the speltoid chromosome IX pair of wheat.

From this brief review it is evident that in organisms with many small and indistinctive chromosomes, cytological evidence for genome transfer may be difficult to interpret and usually must be correlated with genetic information. That chromosomal interchanges involving segments of variable sizes

do take place among non-homologous genomes is supported by both cytological and genetical evidence. Such structural changes, partly due to the size of the segments involved and partly due to the polyploid nature of wheat, may not always be immediately detectable from their cytological appearance and genetical expression. Cytological evidence for their presence may not always be supported by genetical expression unless segmental interchange carrying genes with strongly contrasting characters are involved. This was conclusively proved by Sears (1955, 1956). He obtained wheat plants with a small intercalary translocation from an Aegilops umbellulata isochromosome carrying the gene for resistance to leaf rust race 9. The translocation was secured by pollinating normal untreated wheat plants with x-rayed pollen from plants with the added A. umbellulata isochromosome. This translocation was not cytologically detectable.

MATERIALS AND METHODS

Materials

Included in the present study are sixteen hybrid strains which originated from seven crosses of Triticum timopheevi with either T. aestivum or with derived aestivum - types from earlier interspecific crosses of Triticum species. A detailed listing of the derivation of each is given in Table 1. The two strains of cross I (1 and 3), are selections from Shands 473, a backcross progeny from T. aestivum and T. timopheevi crosses made by Shands (1941). Strains included under crosses II, VI and VII are derived from back-crosses of Shands 473 with Minturki, with Cheyenne and with T. timopheevi, respectively. Under cross III are included five strains which have been secured from back-crosses of derived strains with Cheyenne. Strain 7 in

Table 1. Derived T. aestivum strains studied in 1957-58.

Year (1)	Cross (2)	1957 Line (3)	1955 Row (4)	Series (5)	1956 Parents (6)	Cross
1938	I	1	2672	C.I. 13091	56-1	((111 no. 1 x Chinese) x T. timopheevi P. I. 94761) X Wis Ped. 2, Turkey
		3	2674	C.I. 13093	56-12	ditto
1941	II	2	2673	C.I. 12622	56-6	Minturki x (111 no. 1 x Chinese) X T. timopheevi P.I. 94761 X Wis Ped 2
		4	2677	C.I. 12661F	56-16	An out cross of cross II Turkey)
1942	III	5	2682	53 R197-2	56-28	Cheyenne x 1279 A-9-III (Derived strain from T. timopheevi cross)
		6	2696	53 R197-5	56-85*	x 1279 A-9-III - 16 "
		10	2681	53 R197-1	57-122	x 1279 A-9-III - 16 "
		13	2703	50 N1281	56-62	x 1279 A-9-III - 21 "
		21	2704	50 N1374	55R2704*	x 1279 A-9-III - 16 "
1942	IV	7	2697	53R201-4	56-36	1279-A-III-16x Nebred
1940	V	14	2707	3206-6	56-71	(Marquillo-Oro X T. timopheevi) X (Marquillo-Oro x Kawvale-Fultz) X
		15	2708	3206-7	56-78	(Merit-Thatcher) X) Early Black - Hull - Tenmarq X Hope - Turkey)
1942	VI	12	2695	C.I. 13005	56-56	Shands 473 (Cross I) x T. timopheevi
1942	VII	11	2687	504319	56-52	Shands 473 (Cross I) X Cheyenne
		8	2686	504317	56-47	Shands 473 (Cross I) X Cheyenne
		20	2685	504312	57-137	Shands 473 (Cross I) X Cheyenne
		16		H 193	Bulk	T. timopheevi
		17		7818	56-97	T. aestivum var. Cheyenne
		19		7831	56-99	T. aestivum var. Minturki

*These parental number (56-85 and 55R2704) are the only two which represent 1956 and 1955 field grown strains from which bulk seed was grown in 1957. All other strains are represented by single green house plants grown in 1956 and 1957, from which seed was grown in 1957-58.

**The column headings, left to right are: (1) year: of original cross, (2) cross: number assigned to each original cross, (3) line: number given to each strain in 1957 planting, (4) row: number of each strain in 1955 nursery plantings at the Kansas Agricultural Experiment Station, (5) series: number under which material is catalogued in Kansas Agricultural Experiment Station records, (6) parent: number of green house plant from which seed was grown in 1957, and (7) cross: the parental combinations from which the strains are derived.

Cross IV came from a back-cross between a derived strain from T. timopheevi crosses with Nebred. Strains 14 and 15 in Cross V represent selections from a very complex combination which was obviously made with the hope of combining the rust resistance of T. timopheevi with that from several rust-resistant T. aestivum genomes including Marquillo, Thatcher and Hope and with other desirable qualities of older wheats viz., Merit, Early Blackhull, Tenmarq, Turkey, Oro, Kawvale and Fultz.

These strains have been maintained, and new crosses and selections made over a period of some 20 years. They have been tested for rust reactions in the wheat nurseries for a varying number of years under the direction of Professor C. O. Johnston at Kansas Agricultural Experiment Station, Kansas State University, Manhattan. With the exception of two lines, (6 and 21) for which bulk seed was used, the plants were grown from seed of single plants. T. aestivum, varieties Cheyenne and Minturki, and T. timopheevi were studied as controls.

Methods

Ten plants each of Cheyenne and strain 8, and five plants each of the other 15 strains, Minturki and T. timopheevi were grown to maturity in five inch pots. All of these except T. timopheevi were kept out doors during winter months and moved into the greenhouse about the middle of February, 1958. Plants were healthy and tillered very heavily. They continued to tiller throughout the season as long as water and fertilizer supply was maintained at optimum, probably due at least in part to the removal of older tillers for cytological studies. Only two or three of the first few tillers were left for seed on each plant. Spike samples were taken for study of PMC

from time to time when these were ready, from March 12 to April 29. Spikes were fixed in freshly mixed Carnoy's solution (6 parts absolute alcohol: 3 parts glacial acetic acid: 1 part chloroform). Fixed material was immediately stored in a freezer and maintained at 0° F. Temporary acetocarmine smears were used for cytological study and a few of the more interesting slides were made permanent by the method developed by Sears (1941), and described by Smith (1947). This involves passing the slide through equal parts of acetic acid and tertiary butyl alcohol, then pure tertiary butyl alcohol and finally mounting in balsam.

A method was devised for counting various chromosomal irregularities and scoring them statistically. This is based on the meiotic index (or percentage of normal tetrads) proposed by Morrison and Unrau (1952) as a measure of chromosome regularity. They studied the frequency with which different monosomics of common wheat formed micronuclei in pollen tetrads. They observed that if the stage of tetrads was young, definite and reliable comparable counts could be made. In the 20 monosomics studied they found that all anthers from a floret had a similar frequency of tetrads with micronuclei, and the frequency of micronuclei formation was consistent for different florets of a plant and also for different plants of each particular monosome. Preliminary observations indicated that in the strains under investigation only some of the lines showed a similar consistency. A few lines had extreme meiotic variability even within the same spike. Some plants or lines with more or less regular tetrads and a high meiotic index (80% or more) were unexpectedly highly irregular at earlier stages. Therefore, in order to secure an adequate picture of meiotic irregularity, it seemed necessary to study the chromosome behavior at different stages of the meiotic divisions,

six successive stages being used. Usually for any one stage of meiosis 100 PMC were scored from each smear. The smears with less than a hundred cells in the right stage were either not counted or counted but not considered in computing the mean values. In a few cases when several counts of less than one hundred were made for one stage in one spike, these were added together and the percentage recorded as the mean value for that spike for that stage of meiosis.

Counts of irregularities included any abnormal chromosomes or chromosomal elements that (because of their structure or position or both at any stage) could be judged as capable of giving rise to micronuclei at dyad or tetrad stages. These are illustrated in plates I to X. They included micronuclei (Plate X), unpaired univalent chromosomes (Plate VIII), stray chromosomes or stray bivalents (Plate IIC), lagging chromosomes, cromatin bridges (Plates I, IIIC, IX), fragments (Plates VI, VIII), or any other chromatin structure that could possibly give rise to micronuclei.

EXPERIMENTAL RESULTS

Since the lines from different crosses differ from one another, both cytologically and in rust reactions, they can be grouped into categories determined chiefly by the degree of meiotic stability. With the exception of four lines (2, 8, 12, and 20), all the lines had a fairly high meiotic index. But some of these lines with high meiotic index showed considerable differences in the presence or absence of cytological irregularities at other stages of meiosis. In general, the lines from any one cross behaved more or less the same way. The only two exceptions were: line 11 which showed a very high degree of meiotic stability as compared to the other two sister strains

(lines 8 and 20) and line 2 which was less regular than the other line (4) of cross II.

The information leading to this conclusion is summarized in Table 2, which gives the over all mean (%) values of normal PMC at six stages of meiosis for all sixteen lines along with those for the three controls, T. aestivum varieties Minturki and Cheyenne, and T. timopheevi. The data in this table shows that there are some differences in meiotic regularity among the controls. T. timopheevi and Cheyenne have a meiotic index (percent of regular tetrads) of above 97 percent (97.39% and 99.19% respectively), while that of Minturki is 94.65 percent. Other stages of meiosis are correspondingly slightly less regular in Minturki. Several of the lines have overall mean values very close to those of the more regular controls, Cheyenne and T. timopheevi. These include the two lines of cross I, the five lines of cross III, and one of the three in cross VII. The two lines of cross V and one line of the two in cross II are slightly less regular, resembling the control Minturki in this respect. Line 7 of cross IV is similar, except for deviations in anaphase I and metaphase I. The remaining four lines were considerably more irregular than any of the controls. This irregular group includes one line (2) of the two in cross II, two lines (20 and 8) of the three in cross VII and the one line (12) of cross VI. It may be noted that meiotic regularity or irregularity is similar in all lines of some crosses (I, III), while the lines in other crosses (II, VII) may differ considerably from each other in this respect.

The data summarized in Table 2 apparently suffices to distinguish stable lines from those which have not yet attained meiotic stability, but tends to eliminate deviations from regularity which may have considerable significance.

Table 2. Mean and range* of normal PMC at various stages of meiosis in sixteen strains and three controls.

Cross	Line No. or variety	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
1. Controls													
	Cheyenne	99.19	100-98(27)**	98.36	100-94(11)	98.86	100-95(7)	98.44	100-95(9)	95.67	97-94(6)	96.88	98-94(8)
	T. timopheevi	97.39	100-93(23)	97.50	100-91(6)	97.86	100-95(7)	96.77	100-92(13)	98.00	100-97(8)	96.67	99-93(9)
	Minturki	94.65	98-88(23)	87.80	94-76(10)	96.83	99-94(6)	97.10	99-94(10)	96.40	99-95(10)	90.31	96-79(13)
2. Cross I	1	96.05	100-70(65)	95.43	100-87(23)	94.60	100-70(15)	96.83	100-87(30)	97.78	100-84(18)	94.30	99-79(30)
	3	96.28	100-79(57)	93.69	99-74(16)	94.94	99-92(18)	92.00	99-47(21)	93.78	99-82(19)	93.10	99-70(29)
3. Cross III	5	98.91	100-92(35)	98.44	100-94(16)	98.94	100-95(16)	99.39	100-97(23)	97.40	100-84(20)	97.44	100-82(25)
	6	98.78	100-95(36)	98.13	100-92(16)	98.79	100-96(14)	98.67	100-90(12)	98.60	100-97(15)	97.50	100-93(26)
	10	98.54	100-92(54)	98.13	100-92(16)	99.44	100-97(16)	98.93	100-97(16)	96.38	100-85(16)	98.35	100-94(20)
	13	97.77	100-83(56)	98.50	100-95(18)	98.77	100-95(13)	98.38	100-94(13)	98.40	100-92(13)	98.53	100-94(15)
	21	99.29	100-97(58)	99.35	100-98(14)	99.24	100-96(17)	99.32	100-98(22)	99.07	100-98(15)	97.48	100-92(21)
4. Cross II	4	94.55	99-90(50)	93.29	99-80(17)	98.57	100-95(14)	95.75	98-94(28)	88.42	99-43(19)	93.26	100-86(23)
	2	84.36	97-65(84)	82.71	82-71(31)	97.77	100-92(22)	92.56	99-85(32)	88.76	99-73(41)	85.85	96-68(27)
5. Cross V	15	95.65	100-90(62)	93.68	100-72(22)	96.79	100-92(14)	95.25	100-85(24)	93.14	99-79(14)	93.13	99-70(24)
	14	92.09	100-34(43)	97.83	100-95(18)	98.25	100-92(20)	95.67	100-79(15)	95.08	100-49(13)	96.12	100-62(17)
6. Cross IV	7	95.89	100-69(66)	98.40	100-97(10)	99.11	100-96(9)	96.33	100-93(14)	91.83	100-84(10)	91.83	100-84(12)
7. Cross VII	11	97.02	100-90(45)	93.90	96-80(21)	96.44	100-91(18)	94.44	100-80(16)	97.00	100-93(11)	94.85	99-91(13)
	20	85.50	100-59(105)	74.29	100-26(51)	65.66	90-24(32)	58.19	96-23(62)	52.26	97-2 (39)	88.12	100-69(64)
	8	65.56	99-23(146)	57.97	97-8 (38)	70.78	94-25(23)	50.34	97-0 (90)	34.24	96-2 (33)	75.51	99-26(73)
8. Cross VI	12	54.70	96-4(71)	60.79	92-15(24)	56.08	100-6 (12)	38.10	97-10(57)	40.39	94-0 (28)	87.12	100-56(64)

* Gives the range of normal PMC from different counts, followed by number of counts in parenthesis: each count was for 100 PMC per smear.

**99.19 100-98(27) means 27 counts of 100 PMC (2700 PMC) each from a single smear, with a maximum range between 100 percent and 98 percent normal PMC out of 27 counts from various plants, spikes and florets of variety Cheyenne which had a mean of 99.19 percent normal tetrads (Meiotic index).

A detailed cytological description of these irregularities (in stable as well as in unstable lines) might help in the understanding of the extent of various chromosomal alterations which have undoubtedly taken place in different lines.

Detailed Cytological Description and Analysis

Controls. A minimum of three spikes from each of two plants of the three controls, Cheyenne, Minturki and T. timopheevi was studied. In all, 21 spikes from these three varieties were examined and the data for normal PMC for these spikes is summarized in Table 3. On the whole, Cheyenne, which is a selection from Turkey, was more regular in meiosis than Minturki which was a derived wheat from a cross of Turkey (T. aestivum) and Mindum (T. durum). T. timopheevi occupied an intermediate place between these two with respect to meiotic index. Cheyenne on the whole was the most regular with a meiotic index of 99.19 percent (27; 100-96) i.e., 99.19 percent of the 2700 tetrads counted were normal and the extreme deviations from these 27 counts (of 100 tetrads each) were 100 percent to 96 percent. Next in order of regularity in meiosis was T. timopheevi with 97.39 percent (23; 100-93) as the meiotic index and third was Minturki with 91.65 percent (23; 98-88). It is evident from the range of meiotic indices given that variation from one spike or plant to the next for any one variety is slight.

A few minor irregularities were found in all three controls. One or more unpaired univalents were present in a small percentage of PMC at metaphase I. In Minturki, at least three end to end bivalents were present at metaphase I in most of the PMC and sometimes one or more of these either failed to pair or disjoined early. Occasionally a chromatin bridge at

Table 3. Percentage and range* of normal PMC at six stages of meiosis in two plants each of three controls, Cheyenne Minturki and T. timopheevi.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
17 Cheyenne	58-81	8-209	99.25	100-98(4)**	98.50	99-98(2)	100.00	100- (1)	99.50	100-99(2)	97.00	97- (1)	97.00	97- (1)
		8-354	99.00	100-98(3)	98.00	98- (1)	99.00	99- (1)	96.50	98-95(2)	95.00	95- (1)	98.00	98- (1)
		8-325	99.00	100-98(3)	98.00	98- (1)	99.00	99- (1)	98.00	98- (1)	96.00	96- (1)	94.00	94- (1)
		8-235	98.89	100-96(9)	98.67	100-97(3)	-	-	-	-	-	-	-	-
			+99.00	100-96(19)	98.43	100-97(7)	99.33	100-99(3)	96.00	100-95(5)	96.00	97-95(3)	96.33	98-94(3)
	58-84	8-158(a)	99.67	100-99(3)	-	-	100.00	100- (1)	98.00	98- (1)	-	-	96.50	98-95(2)
		(b)	99.00	99- (1)	99.00	99- (1)	100.00	100- (1)	99.00	99- (1)	97.00	97- (1)	98.00	98- (1)
		8-206(a)	100.00	100- (1)	100.00	100-100(2)	99.00	99- (1)	100.00	100- (1)	94.00	94- (1)	97.00	97- (1)
		8-304(a)	99.67	100-99(3)	94.00	94- (1)	95.00	95- (1)	99.00	99- (1)	95.00	95- (1)	98.00	98- (1)
			+99.63	100-99(8)	98.25	100-94(4)	98.50	100-95(4)	99.00	100-98(4)	95.33	97-94(3)	97.20	98-95(5)
			++99.19	100-96(27)	98.36	100-94(11)	98.86	100-95(7)	98.44	100-95(9)	95.67	97-94(6)	96.88	98-94(8)
19 Minturki	58-92	8-352	96.00	97-94(3)	94.00	94- (1)	95.00	95- (1)	96.00	98-94(2)	95.50	96-95(2)	94.00	96-92(2)
		8-380	96.00	96- (1)	92.00	92- (1)	98.00	98- (1)	96.75	97-96(4)	96.00	96- (1)	81.50	84-79(2)
		8-305	96.25	98-95(4)	81.00	85-77(2)	94.00	94- (1)	97.00	97- (1)	96.00	96- (1)	88.50	92-85(2)
			+96.13	98-94(8)	87.00	94-77(4)	95.67	98-94(3)	96.57	98-94(7)	95.75	96-95(4)	88.00	96-79(6)
		8-239	95.14	97-92(7)	85.00	85- (1)	97.00	97- (1)	99.00	99- (1)	98.67	99-97(3)	88.67	89-88(3)
		8-323	97.00	97-97(2)	93.67	97-91(3)	98.00	98- (1)	99.00	99- (1)	97.00	97- (1)	98.00	98- (1)
		8-383(a)	91.75	94-88(4)	88.00	88- (1)	-	-	-		95.00	95- (1)	92.50	95-90(3)
		(b)	90.50	91-90(2)	76.00	76- (1)	99.00	99- (1)	97.00	97- (1)	95.00	95- (1)	97.00	97- (1)
			+93.87	97-88(15)	88.33	98-76(6)	98.00	99-97(3)	98.33	99-97(3)	96.83	99-95(6)	92.29	98-88(7)
			++94.65	98-88(23)	87.80	98-76(10)	96.83	99-94(6)	97.10	99-94(10)	96.40	99-95(10)	90.31	98-79(13)
16 T. timopheevi	58-76	8-69	99.00	100-98(3)	99.00	99- (1)	100.00	100- (1)	99.00	99- (1)	98.00	98- (1)	98.00	98- (1)
		8-61	100.00	100- (1)	100.00	100- (1)	100.00	100- (1)	99.00	99- (1)	100.00	100- (1)	98.00	99-97(2)
		8-49	100.00	100-100(3)	100.00	100- (1)	100.00	100- (1)	99.50	100-99(2)	98.00	98- (1)	97.00	97- (1)
			+99.57	100-98(7)	99.67	100-99(3)	100.00	100-100(3)	99.17	100-98(6)	98.67	100-98(3)	97.75	99-97(4)
	58-77	8-62	95.67	97-93(6)	97.00	97- (1)	96.00	97-95(2)	93.50	98-90(4)	97.00	97- (1)	95.00	95- (1)
		8-50	96.00	97-94(4)	98.00	98- (1)	98.00	98- (1)	92.00	92- (1)	97.00	97- (1)	95.00	95- (1)
		8-77	97.50	99-95(6)	91.00	91- (1)	95.00	95- (1)	98.00	99-98(2)	98.50	99-98(2)	96.33	98-93(3)
			+96.44	99-93(16)	95.33	98-91(3)	96.25	98-95(4)	94.71	99-90(7)	97.60	99-96(4)	95.80	98-93(3)
			++97.39	100-93(23)	97.50	100-91(6)	97.86	100-95(7)	96.77	100-90(13)	98.00	100-96(8)	96.67	99-93(9)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**99.25 100-98(4) means 4 counts of 100 PMC (400 PMC) each taken from a single smear, with a maximum range between 100 percent and 98 percent normal PMC out of 7 counts for spike 8-209 which had a mean of 99.25 percent normal tetrads.

+Means for individual plants.

++Means for the varieties.

anaphase I could be observed in some of the PMC in all the three varieties. In Cheyenne up to three anaphase I chromatin bridges were present in some PMC (Plate I). However, the chromosomes involved in bridge formation did not often appear to lag at telophase I and so did not result in micronuclei.

Cross I: (111 no. 1 x Chinese) x T. timopheevi) x Wis. Ped. 2 of Turkey. This cross was represented by two lines, line 1 (C.I. 13091) and line 3 (C.I. 13093). Both of these lines had a normal chromosome number and comparatively regular meiosis. Metaphase I and anaphase I stages in three plants each of lines 1 and 2 clearly showed 42 chromosomes and regular formation of 21 bivalents. Mean values of normal PMC at different meiotic stages for the spikes studied from each of the plants are given in Table 4. Means for plants and lines are also given. Even though there were conspicuous deviations from the general mean of a line for any one meiotic stage, yet means for the two lines were very close. The mean for normal tetrads for line 1 was 96.05 percent (65; 100-70) as compared to 96.28 percent (57; 100-79) for line 3. Deviations from the means are more extensive than in the controls. In a few instances, means for individual plants of a line deviated rather strikingly from the means of the line. For the tetrad stage, for example, the mean for plant 58-11 in line 3 was 91.83 percent (6; 97-79) and that for plant 58-2 of line 1 was 99.53 percent (17; 100-70), as compared to an over all mean value of about 96 percent normal tetrads for the line. Also there were striking deviations of means for spikes from the same plant, at some stages and not at others. Even though the tetrad stage mean for all the 5 spikes of plant 58-2 was 99.53 percent (17; 100-70), spike 8-460 had a mean value of 75.0 percent (3; 83-70). Also, it was noticeable that two of the spikes studied (8-271, 8-310) from plant 58-11 had a consistantly

Table 4. Percentage and range* of normal PMC at six stages of meiosis in six plants of lines 1 and 3 of cross I. (111 no. 1 x Chinese) x T. timopheevi P.I. 94761 x Wis Red 2, Turkey.

Line No.	Plant No.	Spike No.	Tetrad Mean	Tetrad Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
1	58-2	8-221	96.71	99-97(7)**	89.50	96-83(2)	75.00	75- (1)	92.00	92- (1)	89.00	89- (1)	79.00	79- (1)
	(2n=42)	8-336	95.50	100-99(2)	99.00	99- (1)	92.00	92- (1)	90.00	90- (1)	84.00	84- (1)	98.50	99-98(2)
		8-460	75.00	83-70(3)	-	-	-	-	-	-	-	-	-	-
		8-371	96.67	100-94(3)	-	-	-	-	-	-	-	-	-	-
		8-306	95.50	100-99(2)	-	-	-	-	97.00	97- (1)	-	-	-	-
			+99.53	100-70(17)	92.67	99-83(3)	82.50	92-75(2)	93.00	97-90(3)	86.50	89-84(2)	92.00	99-79(3)
	58-3	8-292	98.00	99-97(3)	97.00	98-96(2)	92.00	92- (1)	99.40	100-98(5)	99.67	100-98(3)	96.50	98-95(4)
	(2n=42)	8-220(a)	97.14	99-95(7)	99.00	99- (3)	-	-	99.00	100-98(2)	99.00	100-98(3)	95.00	98-90(5)
		(b)	97.33	99-96(3)	-	-	99.50	100-99(2)	-	-	-	-	-	-
			+97.38	99-95(13)	97.67	99-96(3)	97.00	100-92(3)	99.29	100-98(7)	99.33	100-98(6)	95.67	98-90(9)
		8-291(a)	99.00	100-86(8)	98.60	100-97(5)	99.00	100-96(4)	97.33	100-93(6)	88.00	88- (1)	95.00	96-94(2)
		(b)	96.60	99-95(5)	-	-	-	-	-	-	92.33	97-89(3)	-	-
		8-308(a)	97.33	100-96(3)	-	-	91.50	92-91(2)	99.00	100-98(3)	94.00	94- (1)	94.00	94- (1)
		(b)	100.00	100-100(3)	93.00	93- (1)	100.00	100- (1)	-	-	-	-	-	-
		8-337(a)	96.89	100-92(9)	95.00	100-92(6)	92.00	92-92(2)	95.50	99-91(8)	100.00	100- (1)	93.67	96.91(3)
		(b)	92.57	96.90(7)	93.60	100-87(5)	98.00	98- (1)	95.33	100-87(3)	99.00	100-98(4)	93.40	99-90(5)
			+96.77	100-90(35)	95.53	100-87(17)	96.10	100-91(10)	96.55	100-87(20)	95.50	100-88(10)	93.82	99-90(11)
			++96.05	100-70(65)	95.43	100-87(23)	94.60	100-75(15)	96.83	100-87(30)	95.78	100-84(18)	94.30	99-79(23)
3	58-11	8-271	88.33	94-79(3)	93.00	93- (1)	94.00	94- (1)	70.00	93-47(2)	94.00	94- (1)	79.33	94-70(3)
	(2n=42)	8-310	94.50	96-93(2)	74.00	74- (1)	92.50	93-92(2)	92.00	92- (1)	82.50	83-82(2)	92.00	92- (1)
		8-339	97.00	97- (1)	99.00	99- (1)	98.00	98- (1)	-	-	99.00	99 (1)	95.00	96-94(2)
			+91.83	97-79(6)	88.67	99-74(3)	94.25	98-92(4)	77.33	93-47(3)	89.50	99-82(4)	86.67	96-70(6)
	58-12	8-248	97.29	99-94(7)	97.50	98-97(2)	94.00	98-90(2)	97.00	98-96(2)	88.00	88- (1)	97.00	97-97(2)
	(2n=42)	8-295(a)	98.00	99-97(7)	97.40	98-97(5)	97.00	99-92(6)	91.14	99-77(7)	99.00	99- (1)	93.40	96-90(5)
		(b)	-	-	-	-	-	-	-	-	-	-	96.25	99-95(4)
		8-341	95.00	97-92(5)	97.00	97- (1)	99.00	99- (1)	96.00	97-95(2)	95.00	97-94(3)	93.00	94-92(2)
			+96.95	99-92(19)	97.38	98-97(8)	96.56	99-90(9)	93.09	99-77(11)	94.40	99-88(5)	94.77	99-90(13)
	58-14	8-141	97.82	100-93(17)	90.75	95-88(4)	95.00	99-91(2)	98.50	99-98(2)	96.00	98-95(4)	93.00	96-88(4)
	(2n=42)	8-174	95.00	99-91(12)	-	-	91.00	91- (1)	97.00	98-96(2)	92.00	92- (1)	96.00	96- (1)
		8-287	97.00	99-96(3)	91.00	91- (1)	91.00	94-88(2)	95.00	98-90(3)	95.50	97-94(4)	92.60	98-88(5)
			+96.72	100-91(32)	90.80	95-88(5)	92.60	99-88(5)	96.57	99-90(7)	95.33	98-92(9)	93.10	98-88(10)
			++96.28	100-79(57)	93.69	99-74(16)	94.94	99-88(18)	92.00	99-47(21)	93.78	99-88(18)	92.52	99-70(29)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**99-97(7) means 7 counts of 100 PMC (700 PMC), each taken from a single smear, with a maximum range between 99 percent and 97 percent normal PMC out of 7 counts for spike 8-221 from plant 58-2.

+Means for individual plants.

++Means for lines.

lower percentage of normal PMC at tetrad, dyad and metaphase I stages than the 7 other spikes of this line.

A few deviations of individual spikes were based on single counts of 100 PMC from one smear of an anther, rather than on an average of more than one count. These could have been due to chance irregularities of various sorts. For example, some evidence has been found (in other lines) that mitotic irregularities may give rise to different chromosome numbers in somatic tissues, which could include any number of cells up to an anther, part of a spike or even a whole spike of a plant. As is evident from the mean numbers of normal PMC at various meiotic stages and the deviations from these means, there were minor irregularities which occasionally resulted in micronuclei in approximately 3-4 percent of PMC at dyad and tetrad stages. Occurrence of unpaired univalents at metaphase I could be directly correlated to irregularities at subsequent stages. Such univalents usually divided late at anaphase I, the half-univalents lagging and usually forming micronuclei (Plate IIE). On the other hand, if an undivided univalent was included in one of the telophase I nuclei, it divided regularly at anaphase II and no micronuclei were formed. Univalents at metaphase I were probably due both to asynapsis and to early disjunction of some of the paired chromosomes. Pairs held together by a single terminal chiasma, which occurred in about 20 percent of PMC in certain smears may have tended to disjoin early. Sometimes groups of PMC were found with a large number of unpaired chromosomes and a very few bivalents. Such chance groups might result in a comparatively low mean of normal PMC at metaphase I, and if this happened in the only smear obtainable for that spike (as in 8-221, for example) the spike would be classified as highly irregular. On the other hand, high mean values were

obtained in other spikes where the higher number of counts for normal PMC made up for the single deviations, which can be noticed from the range given. Such occasional deviations are of questionable significance and are usually ignored in making an estimate of the meiotic stability of the line as a whole. However, more frequent deviations (such as occurred in some other lines) are undoubtedly of more significance.

Frequently one or two chromatin bridges were observed at anaphase I, one of which usually broke fairly soon (Plate II, D), while the other sometimes persisted until anaphase II. The same chromosomes were apparently involved each time, and could be recognized from their shape, size, orientation and the very small size of the acentric fragment. In this line such chromosomes often were included in telophase I nuclei, but sometimes lagged and gave rise to micronuclei at the dyad stage.

Anaphase II chromatin bridges were seen in only a few cells, but one chromosome tended to lag irregularly and gave rise to micronuclei at the tetrad stage. This may have been a single chromatid from a univalent that divided at anaphase I and was included in one of the nuclei.

Cross III. Cheyenne x 1279A-9-III (derived strains from T. timopheevi crosses). Cross III was represented by five lines, each derived from the following backcrosses of derived strains to Cheyenne:

Line 5	Cheyenne x 1279 A 9-III	53-R-197-2
Line 6	Cheyenne x 1279 A 9-III-16	53-R-197-5
Line 10	Cheyenne x 1279 A-9-III-16	53-R-197-1
Line 13	Cheyenne x 1279 A-9-III 21	52-R-343
Line 21	Cheyenne x 1279 A-9-III 16	52-R-347

Some 58 spikes from 15 plants, 3 from each of the 5 lines, were examined

for meiotic stability and chromosome numbers. Chromosome number for the line as indicated by counts from more than one spike from each plant, was 42 at anaphase I and 21_{II} at metaphase I. All the plants showed highly regular meiosis at all the stages except for a few occasional minor irregularities at metaphase I and anaphase I. The summarized data for the five lines of cross III is given in Table 5. The meiotic index is as high as in the more regular of the controls, Cheyenne, and deviations from the means were slight. In a few of the spikes, groups of PMC with abnormal chromosome numbers were observed, but these presumably never produced viable gametes. In other spikes groups of cells with varying numbers of chromatin bridges at anaphase I were observed. Some of the cells in such smears had up to four chromatin bridges (one or more of which persisted until late anaphase stage) while there was some indication that one or two of these bridges in other cells had broken earlier in the anaphase. The cells at telophase I and dyad stages in the same smears did not show the micronuclei which might have been expected. Obviously most of the bridges did not result in lagging chromosomes or acentric fragments of visible size. As many as three end to end pairs at late metaphase were present in some of the PMC, but only one was more common in most of the cells.

Cross II: Minturki x (III. No. 1 x Chinese) x T. timopheevi x Wis. Ped. 2 Turkey) . Cross II consisted of a backcross of hybrid plants from cross I with Minturki, and was represented by two lines, Line 2 (C.I. 12662) and Line 4 (C.I. 12661-7). Line 4 was an outcross (53 R 365) of C.I. 12662. All plants studied in both lines had 42 chromosomes and fairly regular meiotic pairing. The mean for the meiotic index of line 4 was high (94.55%; 50; 99-90), that for line 2 being lower (84.36%; 84; 97-65), as

Table 5. Percentage and range* of normal PMC at six stages of meiosis in 15 plants of lines 5, 6, 10, 13 and 21 of cross III.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
5	58-22	8-228(a)	99.50	100-99(2)**	97.67	99-95(3)	97.00	98-95(3)	99.36	100-98(6)	98.33	99-98(3)	95.20	97-94(5)
	(2n=42)	8-251(a)	92.00	93-92(2)	98.00	98- (1)	100.00	100- (1)	99.00	99- (1)	92.00	92- (1)	96.00	98-94(2)
		8-250(a)	99.33	100-98(6)	99.00	99- (1)	100.00	100- (1)	99.75	100-95(4)	99.00	100-98(2)	99.00	99- (1)
			+97.90	100-92(10)	98.00	99-95(5)	98.20	100-95(5)	99.36	100-98(11)	97.50	100-92(6)	95.88	99-94(8)
	58-24	8-286(a)	99.33	100-98(3)	-	-	-	-	99.00	99- (1)	99.67	100-99(3)	98.00	98- (1)
	(2n=42)	8-286(b)	100.00	100- (1)	100.00	100-100(2)	99.00	99- (1)	97.00	97- (1)	94.00	94- (1)	100.00	100- (1)
		8-316(a)	97.50	100-97(6)	96.00	99-94(3)	98.00	100-95(3)	100.00	100- (1)	94.50	98-91(2)	98.50	100-95(4)
		8-342(a)	100.00	100-100(2)	100.00	100- (1)	100.00	100- (1)	98.50	100-97(2)	92.00	100-84(2)	98.67	100-98(3)
			+98.58	100-97(12)	98.00	100-94(6)	98.60	100-95(5)	98.60	100-97(5)	95.75	100-84(8)	98.67	100-95(9)
	58-25	8-275	100.00	100-100(6)	99.33	100-98(3)	100.00	100-100(3)	100.00	100-100(2)	98.00	98- (1)	100.00	100- (1)
	(2n=42)	8-285	100.00	100-100(6)	100.00	100- (1)	100.00	100- (1)	100.00	100-100(3)	99.00	99- (1)	99.80	100-99(5)
		8-315	100.00	100- (1)	99.00	99- (1)	99.50	100-99(2)	100.00	100-100(2)	100.00	100-100(4)	91.00	100-82(2)
			+100.00	100-100(13)	99.40	100-98(5)	99.80	100-99(6)	100.00	100-100(7)	99.50	100-98(6)	97.63	100-82(7)
			++98.91	100-92(35)	98.44	100-94(16)	98.94	100-95(16)	99.39	100-95(23)	97.40	100-84(20)	97.44	100-82(25)
6	58-26	8-150	97.33	98-97(3)	97.00	98-96(2)	100.00	100- (1)	98.50	98-98(2)	98.00	98- (1)	98.35	100-97(3)
	(2n=42)	8-170(a)	96.33	98-95(3)	-	-	-	-	-	-	-	-	96.50	97-96(2)
		8-170(b)	99.00	100-98(2)	97.00	97- (1)	98.00	98- (1)	99.00	99- (1)	95.00	95- (1)	95.50	96-95(2)
		8-230	100.00	100- (1)	-	-	99.00	100-98(2)	100.00	100- (1)	99.00	99- (1)	-	-
		8-253	97.00	99-95(3)	93.00	94-92(2)	96.00	96- (1)	90.00	90- (1)	97.00	97- (1)	97.00	97- (1)
			+97.50	100-95(12)	95.40	98-92(5)	98.40	100-96(5)	97.20	100-90(5)	97.25	99-95(4)	97.00	100-95(8)
	58-29	8-134(a)	97.00	97- (1)	99.00	99- (1)	99.00	99- (1)	99.00	99- (1)	98.00	98- (1)	93.00	93- (6)
	(2n=42)	8-134(b)	-	-	-	-	-	-	99.00	99- (1)	98.00	98-98(2)	96.50	98-93(6)
		8-181(a)	99.33	100-98(6)	99.00	99-99(2)	98.00	100-96(2)	100.00	100- (1)	100.00	100- (1)	98.00	98- (1)
		8-284(a)	99.00	99- (1)	99.00	99- (1)	100.00	100- (1)	100.00	100- (4)	100.00	100- (1)	97.00	97- (1)
			+99.00	100-97(8)	99.00	99-99(4)	98.75	100-96(4)	99.50	100-99(4)	98.80	100-98(5)	96.33	98-93(9)
	58-30	8-182(a)	100.00	100-100(4)	99.67	100-99(3)	99.67	100-99(3)	99.50	100-99(2)	100.00	100-100(3)	99.00	99- (6)
	(2n=42)	8-283(a)	100.00	100-100(3)	100.00	100-100(2)	98.00	98-	100.00	100- (1)	100.00	100- (1)	99.00	100-97(3)
		8-283(b)	99.33	100-98(9)	99.00	99-99(2)	99.00	99- (1)	100.00	100- (1)	98.00	99-97(2)	99.20	100-99(5)
			+99.63	100-98(16)	99.57	100-99(7)	99.20	100-98(5)	99.75	100-99(4)	99.33	100-97(6)	99.12	100-97(9)
			++98.78	100-92(36)	98.13	100-92(16)	98.79	100-95(14)	98.67	100-90(12)	98.60	100-84(15)	97.50	100-82(26)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**99.50 100-99(2) means 2 counts of 100 PMC (200 PMC), each taken from a single smear, with a maximum range between 100 percent and 99 percent normal PMC out of 2 counts for spike 8-228(a) which had a mean of 99.50 percent normal tetrads.

+Means for plants: 58-22, 58-24, 58-25, 58-26, 58-29 and 58-30.

++Means for lines 5 and 6.

Table 5. (cont.)

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
10	58-46	8-125(a)	97.33	98-97(3)	94.00	94- (1)	-	-	-	-	99.00	99- (1)	98.50	99-98(2)
	(2n=42)	(b)	98.00	98- (1)	97.50	99-96(2)	100.00	100- (1)	96.00	96- (1)	99.00	99- (1)	100.00	100- (1)
		8-190(a)	99.33	100-99(6)	100.00	100- (1)	100.00	100- (1)	-	-	-	-	92.00	92- (1)
		(b)	98.00	100-96(2)	97.00	97- (1)	100.00	100- (1)	100.00	100- (1)	99.00	99- (1)	100.00	100- (1)
		8-265(a)	98.00	98- (1)	97.00	97- (1)	99.00	99- (1)	100.00	100- (1)	97.00	97- (1)	98.00	98- (1)
			+98.46	100-96(13)	97.17	100-94(6)	99.75	100-99(4)	98.67	100-96(3)	98.50	99-97(4)	97.83	100-92(6)
	58-47	8-146	99.57	100-99(7)	99.50	100-98(4)	99.67	100-99(3)	97.00	97- (1)	96.50	100-94(4)	99.57	100-99(7)
	(2n=42)	8-297	98.90	100-92(10)	100.00	100-100(2)	99.50	100-99(2)	99.00	100-98(2)	99.00	99- (1)	99.50	100-99(2)
		8-347	99.36	100-98(11)	100.00	100- (1)	100.00	100-100(2)	98.50	100-97(2)	99.50	100-99(2)	99.00	99- (1)
			+99.25	100-92(28)	99.71	100-98(7)	99.71	100-99(7)	98.40	100-97(5)	97.71	100-94(7)	99.50	100-99(10)
	58-50	8-278(a)	99.00	99-99(1)	-	-	-	-	-	-	-	-	-	-
	(2n=42)	(b)	100.00	100-100(3)	99.00	99- (1)	99.00	99- (1)	99.50	100-99(2)	97.00	98-96(2)	99.00	99- (1)
		8-366	91.75	97-87(4)	92.00	92- (1)	98.00	99-97(2)	99.00	99-99(2)	89.00	93-85(2)	96.00	96-96(2)
		8-376	99.25	100-98(4)	98.00	98- (1)	99.50	100-99(2)	99.50	100-99(4)	92.00	92- (1)	94.00	94- (1)
			+97.08	100-87(13)	96.33	99-92(3)	98.80	100-97(5)	99.38	100-99(8)	92.80	98-85(5)	96.25	99-94(4)
			++98.54	100-87(54)	98.13	100-92(16)	99.44	100-97(16)	98.93	100-99(16)	96.38	100-85(16)	98.35	100-92(20)
13	58-61	8-127	99.00	99- (1)	98.00	98- (1)	99.00	99- (1)	100.00	100- (1)	97.00	97- (1)	99.00	99- (1)
	(2n=42)	8-148	91.75	100-83(4)	95.00	95- (1)	99.00	99- (1)	98.00	98- (1)	97.00	97- (1)	98.00	98- (1)
		8-202	99.00	99- (1)	98.00	98- (1)	98.00	98- (1)	99.00	99- (1)	97.00	97- (1)	100.00	100 (1)
			+94.17	100-83(6)	97.00	98-95(3)	98.67	99-98(3)	99.00	100-98(3)	97.00	97-97(3)	99.00	100-98(3)
	58-62	8-201	98.67	100-97(3)	99.00	99- (1)	100.00	100- (1)	99.00	99- (1)	96.00	96- (1)	97.00	97- (1)
	(2n=42)	8-244	99.67	100-99(3)	100.00	100- (1)	95.00	95- (1)	99.50	100-99(2)	97.33	100-92(3)	95.50	97-94(2)
		8-328(a)	99.00	100-98(2)	97.50	100-95(2)	100.00	100- (1)	98.00	98- (1)	98.00	98- (1)	99.00	99- (1)
		(b)	98.83	100-98(6)	-	-	-	-	-	-	-	-	-	-
			+99.00	100-83(14)	98.50	100-95(4)	98.33	100-95(3)	99.00	100-98(4)	97.20	100-92(5)	96.75	97-94(4)
	58-65	8-199(a)	98.29	100-95(7)	99.00	99-99(2)	99.00	99- (1)	98.00	98- (1)	-	-	99.00	100-98(2)
	(2n=42)	(b)	96.00	99-94(13)	98.00	99-97(2)	98.00	99-98(2)	94.50	95-94(2)	96.00	100-92(2)	98.00	98- (1)
		8-204(a)	-	-	-	-	-	-	-	-	-	-	100.00	100-100(2)
		(b)	98.88	100-88(8)	99.17	100-98(6)	99.67	100-99(3)	100.00	100-100(2)	100.00	100- (1)	100.00	100- (1)
		8-330(a)	96.63	100-98(8)	99.00	99- (1)	99.00	99- (1)	99.00	99- (1)	100.00	100-100(2)	99.00	99-99(2)
			+97.89	100-94(36)	98.90	98.90(11)	99.00	100-95(7)	97.67	100-94(6)	98.40	100-92(5)	99.25	100-98(8)
			++97.77	100-83(56)	98.50	100-95(18)	98.77	100-95(13)	98.38	100-94(13)	97.62	100-92(13)	98.53	100-94(15)

+Means for plants 58-46, 58-47, 58-50, 58-61, 58-62 and 58-65.
++Means for lines 10 and 13.

Table 5. (concl.)

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
21	58-131 (2n=42)	8-151	100.00	100- (1)	96.00	96- (1)	99.50	100-99(2)	99.00	99- (1)	99.00	99- (1)	95.67	99-92(3)
		8-231	99.85	100-99(6)	100.00	100-100(2)	100.00	100-100(2)	98.00	98- (1)	98.00	98- (1)	97.00	100-94(2)
		8-321	99.22	100-98(9)	98.00	98- (1)	99.00	99- (1)	99.50	100-98(4)	99.50	100-99(2)	94.00	94- (1)
			+99.50	100-98(16)	98.50	100-96(4)	99.60	100-99(5)	99.17	100-98(6)	99.00	100-98(4)	95.83	100-92(6)
	58-132 (2n=42)	8-133	99.00	100-98(3)	100.00	100-100(2)	97.00	98-96(3)	100.00	100-100(2)	93.00	93- (1)	100.00	100-100(3)
		8-232	99.00	100-98(3)	99.00	99- (1)	99.00	99-99(2)	99.00	99- (1)	99.00	99- (1)	93.00	93- (1)
		8-122	98.00	99-97(3)	100.00	100- (1)	100.00	100- (1)	100.00	100-100(3)	100.00	100- (1)	100.00	100- (1)
			+98.67	100-97(9)	99.75	100-99(4)	98.17	100-96(6)	99.83	100-99(6)	97.33	100-93(3)	98.60	100-98(5)
	58-134 (2n=42)	8-123(a)	99.89	100-99(9)	98.00	(1)	100.00	100- (1)	100.00	100- (1)	100.00	100- (1)	92.00	92- (1)
		(b)	99.00	100-97(6)	-	-	100.00	100- (1)	99.75	100-99(4)	99.60	100-98(5)	98.00	100-95(5)
		(c)	98.67	100-97(9)	-	-	-	-	-	-	-	-	-	-
		88-88(a)	100.00	100-100(7)	100.00	100-100(3)	100.00	100-100(2)	98.00	100-96(3)	100.00	100- (1)	97.00	97-97(2)
		(b)	100.00	100-100(5)	-	-	-	-	-	-	-	-	-	-
		8-122(a)	99.00	100-98(2)	99.00	100-98(2)	100.00	100- (1)	99.00	100-98(2)	100.00	100- (1)	100.00	100- (1)
			+99.36	100-97(33)	99.67	100-98(6)	100.00	100-100(5)	99.10	100-98(10)	99.75	99-75(8)	97.90	100-92(10)
			++99.29	100-97(58)	99.00	100-96(14)	99.24	100-96(17)	99.32	100-96(22)	99.07	100-98(15)	97.48	100-92(21)

+Means for plants 58-131, 58-132 and 58-134.

++Means for line 21.

shown in the summarized data of Table 6. The extent of deviation from the means at all stages of meiosis was also less in line 4. The only marked deviations in this line occurred at anaphase I in two spikes of plant 58-16. Spike 8-175b had a mean of 73.25 percent normal PMC with a range from 44 percent to 93 percent, while spike 8-149b had a mean of 76.00 percent and a range from 69 percent to 83 percent. These deviations lowered the anaphase I mean for the plant (58-16) to 76.86 percent (7; 93-44), a value considerably lower than the 95.17 percent (12; 99-93) mean for the other plant (58-18) studied in this line.

Line 2 plants had considerably lower means than those of line 4 and also showed noticeably greater deviations from these means. The two plants studied differed considerably from each other, but this difference was not entirely consistant from one meiotic stage to the next. Plant 58-7 had the higher number of normal PMC at tetrad and metaphase I than plant 58-8, but the latter had the higher percentage of normal PMC at anaphase I. In both the plants individual spikes showed considerable deviations from floret to floret and even within the three anthers of one floret. These deviations were so distributed that means for the spikes did not differ much and only the range within a spike pointed to this variability.

In both lines, the irregularities at anaphase II and tetrad stages were caused largely by late division of univalents and lagging of the resultant half-univalents at anaphase I. Up to four half-chromatids could be observed at anaphase II. Failure to disjoin was not uncommon, and occasionally one to two chromatin bridges were seen at anaphase I. A higher percentage of these irregularities were present in line 2 than in line 4. The metaphase I average of the means for the two plants of line 4 was 93.26 percent (23; 100-86)

Table 6. Percentage and range* of normal PMC at six stages of meiosis in 4 plants of lines 2 and 4 of cross II. Minturki x (111. No. 1 x Chenses) x T. timopheevi p.i. 9476 x Wis Ped. 2, Turkey.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
2	58-7 (2n=42)	8-165(a)	84.00	92-79(6)**	-	-	99.00	99- (1)	95.00	97-93(4)	83.33	95-70(3)	92.50	95-90(2)
		(b)	80.50	90-71(2)	-	-	95.00	95- (1)	94.00	94- (1)	72.50	75-70(2)	94.50	95-94(2)
		8-222(a)	90.00	97-81(6)	-	-	98.33	99-98(3)	93.00	98-88(5)	80.40	88-74(5)	87.00	94-73(3)
		(b)	-	-	93.00	93- (1)	99.00	99-99(2)	92.50	97-88(2)	88.67	96-77(3)	93.00	99-88(4)
		8-294(a)	91.55	95-87(11)	91.75	94-89(4)	94.67	96-92(3)	89.00	89- (1)	95.00	95- (1)	96.00	97-95(2)
			+88.48	97-71(25)	92.00	94-89(3)	97.10	99-92(10)	93.62	98-88(13)	82.71	96-70(14)	92.23	99-73(13)
	58-8 (2n=42)	8-143(a)	80.28	91-67(18)	55.00	79-36(3)	-	-	89.67	99-85(3)	92.00	95-89(5)	87.50	91-83(6)
		(b)	80.70	90-73(10)	74.00	92-58(5)	99.00	99- (1)	91.00	92-90(2)	90.75	93-87(4)	91.00	98-85(4)
		8-273(a)	80.67	87-65(9)	83.00	93-76(4)	-	-	88.25	96-82(4)	84.00	94-68(3)	88.17	91-82(6)
		(b)	81.17	88-76(6)	80.00	99-61(4)	97.67	99-96(3)	91.00	92-90(3)	-	-	84.00	90-76(9)
		8-223(a)	89.43	96-85(7)	92.00	92- (1)	98.50	100-97(8)	95.00	98-92(6)	-	-	-	-
		(b)	87.00	94-82(9)	91.00	96-82(9)	-	-	97.00	97- (1)	85.00	85- (1)	88.67	90-88(3)
			+82.61	96-65(59)	80.92	99-36(26)	98.33	100-96(12)	91.84	99-85(19)	89.23	95-68(13)	87.14	98-76(28)
			++84.36	97-65(84)	82.71	99-36(31)	97.77	100-92(22)	92.56	99-85(32)	85.85	96-68(27)	88.76	99-74(41)
4	58-16 (2n=42)	8-126(a)	98.00	98- (1)	88.00	88- (1)	-	-	-	-	-	-	97.00	97- (1)
		(b)	99.00	99- (1)	93.00	93- (1)	100.00	100- (1)	85.00	85- (1)	91.00	91- (1)	89.67	95-86(3)
		8-149(a)	91.50	93-91(2)	-	-	-	-	91.00	91- (1)	-	-	92.00	92- (1)
		(b)	97.00	97- (1)	-	-	-	-	93.00	94-92(2)	76.00	83-69(2)	87.00	87- (1)
		8-175(a)	96.00	96- (1)	92.00	92-92(2)	95.00	95- (1)	96.25	99-95(4)	73.25	93-44(4)	96.25	99-95(4)
		(b)	-	-	-	-	-	-	97.00	98-96(2)	-	-	-	-
			+ 95.50	99-90(6)	91.25	93-88(4)	97.50	100-95(2)	94.10	99-85(10)	76.86	93-44(7)	93.00	99-86(10)
	58-18 (2n=42)	8-176(a)	94.89	98-91(9)	-	-	99.00	99- (1)	94.67	95-94(3)	96.67	98-94(3)	93.50	99-88(2)
		(b)	93.67	99-91(9)	90.00	90- (1)	-	-	-	-	-	-	-	-
		(c)	95.88	99-92(8)	93.00	93- (1)	99.00	99- (1)	96.00	96- (1)	94.00	95-93(2)	96.50	97-96(2)
		8-313(a)	93.56	96-91(9)	96.33	98-95(3)	99.00	100-98(3)	97.13	98-96(8)	94.40	99-90(5)	92.78	100-87(9)
		(b)	94.22	99-91(9)	92.88	97-80(8)	98.57	99-98(7)	97.17	99-94(6)	96.00	97-95(2)	-	-
			+94.41	99-91(44)	93.92	99-87(13)	98.75	99-98(12)	95.60	98-94(18)	95.17	99-93(12)	93.46	100-88(13)
			++94.55	99-90(50)	93.29	99-80(17)	98.57	100-98(14)	95.75	98-94(28)	88.42	99-44(19)	93.26	100-86(23)

*Gives the range of normal PMC from different counts, followed by the number of counts in parenthesis; each count was for 100 PMC per smear made.

**84.00 92-79(6) means 6 counts of 100 PMC (600 PMC), each taken from a single smear, with a maximum range between 92 percent and 79 percent normal PMC out of 6 counts for spike 8-165(a) which had a mean of 84.00 percent normal tetrads (quartets).

+Means for individual plants; 58-7; 58-8; 58-16 and 58-18.

++Means for the lines 2 and 4.

while that for line 2 is 88.76 percent (41;99-73). From this it can be seen that an average of 6.74 percent of metaphase I cells in line 4 had one or more unpaired univalents, as compared to an average of 11.24 percent in line 2 and to a range in one spike as high as 27 percent. Although the means for normal PMC at metaphase I for the two plants of line 2 were different, 92.23 percent (13;99-73) for plant 58-7 as compared to 87.14 percent (28; 98-76) for plant 58-8, the range of deviations was similar. Of the 11.24 percent cells with univalents in line 2, 9.54 percent represents cells with one univalent, 1.51 percent with two, and .18 percent with three or more. By anaphase I, a total of 14.14 percent cells had extra chromosome elements, 7.96 percent with one such unit, 4.85 percent with two and 1.33 percent with three or more. The total increase is possibly due to univalents hidden at MI and to irregularities in disjunction, and the shift to higher numbers in individual cells to irregularities in disjunction and to premature divisions of univalents. The cells with irregular chromosome elements had decreased by dyad stage to 7.44 percent, as shown by the mean of 92.56 percent (32;99-85) normal dyads. Obviously some of the irregular chromosome elements were included in telophase I nuclei and did not result in the formation of micronuclei. By metaphase II a further decrease had taken place in the number of PMC with irregularities, the percentage being reduced to 2.23 percent, as shown by the mean of 97.77 percent (100-92) regular cells; presumably many of the irregular elements became obscured by development of the spindle figure. A great increase again appeared with disjunction difficulties at anaphase II, an average of 17.29 percent of cells having irregularities at this stage, as shown by the lowering of the mean of regular PMC to 82.71 percent (31; 99-36). Most of the irregular elements present at anaphase II

formed micronuclei at the tetrad stage, since an average of 15.44 percent of the cells were irregular and 84.36 percent (84; 97-65) regular. The number of irregular elements in one PMC increased or decreased correspondingly with the percentage of cells with irregularities. Thus, the number of PMC with three or more than three such irregular elements increased at anaphase I some ten to fifteen times over the number present at metaphase I; they decreased again by the dyad stage and still further decreased by metaphase II, but increased again several fold by anaphase II and tetrad stage.

Cross V. (Marquillo-Oro X T. timopheevi) X (Marquillo-Oro X Kawvale-Fultz) X (Merit-Thatcher) X (Early Blackhull-Tenmarq x Hope-Turkey) Cross V includes lines 14 and 15, both selections from C.I. 12803. Table 7 includes summarized data derived from 11 spikes of three plants of line 14 and 13 spikes of 3 plants of line 15. Both lines had 42 chromosomes and comparatively regular meiosis, as indicated both by the meiotic indices of 95.65 percent (line 15) and 92.02 percent (line 14) and by the rather consistent range of 90 percent to 100 percent normal PMC at the different meiotic stages. Means for individual spikes were also largely within this range, although two spikes showed noticeable deviations. Spike 8-229a of plant 58-75 in line 15 had a mean of only 80 percent regular PMC at anaphase I and 87 percent at metaphase I even though all other means for this spike fell in the range of 90 percent or above, as did all the means from spike 229b which was collected at the same time from the same plant. The second spike, 8-298, from plant 58-68 in line 14, showed extreme variation in different florets, even those at the same stages of meiosis. Three florets had a high meiotic index (tetrad stage) ranging from 98 percent to 100 percent, while 5 others ranged from 34 percent to 64 percent; one metaphase I floret

Table 7. Percentage and range* of normal PMC at six stages of meiosis in 6 plants of line 14 and 15 of cross V. (Marquillo-Oro x T. timopheevi) x (Marquillo-Oro x Kawvale-Fultz) x (Merit-Thatcher) x (Early Blackhull - Tenmarq x Hope-Turkey)

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
14	58-68	8-242	97.80	100-95(5)**	97.67	99-95(3)	99.00	100-98(6)	99.33	100-98(3)	100.00	100- (1)	99.50	100-99(2)
	(2n=42)	8-298i	99.00	100-98(3)	99.00	99- (1)	98.00	98- (1)	-	-	-	-	98.00	98- (1)
		ii	45.20	64-34(5)	-	-	-	-	74.50	79-70(2)	49.00	49- (1)	62.00	62- (1)
		8-388	98.75	100-97(8)	99.50	100-99(4)	99.25	100-99(4)	100.00	100- (1)	100.00	100- (1)	100.00	100- (1)
			+85.81	100-34(21)	98.75	100-95(8)	99.00	100-98(11)	91.17	100-70(6)	83.00	100-49(3)	93.17	100-62(6)
	58-69	8-200	97.50	99-96(2)	97.00	97- (1)	99.00	99- (1)	99.00	99- (1)	100.00	100- (1)	94.00	94- (1)
	(2n=42)	8-332	96.00	99-89(4)	97.00	97- (1)	98.00	98- (1)	100.00	100- (1)	95.50	96-95(2)	97.00	97-97(2)
		8-397	99.00	100-97(3)	95.00	95-95(2)	98.00	98-98(2)	97.00	97- (1)	100.00	100- (1)	94.50	98-91(2)
			+97.33	100-89(9)	96.00	97-95(4)	98.25	99-98(4)	98.67	100-97(3)	97.75	100-95(4)	95.40	100-91(5)
	58-70	8-162	98.20	99-97(5)	99.00	99- (1)	94.00	94- (1)	100.00	100- (1)	95.50	99-98(2)	99.00	99-99(2)
	(2n=42)	8-205(a)	98.33	99-98(3)	96.50	97-96(2)	92.00	92- (1)	97.00	97- (1)	-	-	-	-
		(b)	98.00	98- (1)	98.00	99-97(2)	98.50	99-98(2)	98.00	98- (1)	100.00	100-100(2)	100.00	100- (1)
		8-331(a)	99.33	100-98(3)	-	-	-	-	99.00	100-98(2)	99.50	100-99(2)	100.00	100-100(2)
		(b)	97.00	97- (1)	99.00	99- (1)	100.00	100- (1)	99.00	99- (1)	-	-	100.00	100- (1)
			+98.38	100-97(13)	97.83	97-83(6)	96.60	100-92(5)	98.67	100-97(6)	99.33	100-49(6)	99.67	100-99(6)
			++92.02	100-34(43)	97.83	100-83(18)	98.25	100-92(20)	95.67	100-70(15)	95.08	100-49(13)	96.12	100-62(17)
15	58-71	8-75	96.20	98-94(5)	95.00	97-94(2)	99.00	99- (1)	96.00	96-96(2)	98.00	99-97(2)	98.00	99-97(2)
	(2n-42)	8-159	98.40	99-98(5)	97.00	97-97(2)	98.00	99-98(2)	95.00	97-94(2)	92.00	92- (1)	79.50	89-70(2)
		8-360	95.89	98-93(9)	91.25	100-92(4)	100.00	100- (1)	98.33	99-97(3)	-	-	98.75	99-98(4)
			+96.63	99-93(19)	94.00	100-92(8)	99.20	100-98(5)	96.86	99-94(7)	96.00	99-92(3)	93.75	99-70(8)
	58-74	8-393	94.50	97-91(4)	90.50	91-90(2)	94.00	96-92(2)	95.00	99-90(3)	96.00	96- (1)	94.50	95.94(2)
	(2n=42)	8-128(a)	94.71	98-90(7)	96.50	97-96(2)	98.00	99-97(2)	96.00	96- (1)	97.00	97- (1)	88.00	88- (1)
		(b)	95.20	97-92(10)	98.00	98- (1)	94.60	94- (1)	99.00	99- (1)	95.00	95- (1)	92.00	92- (1)
		8-87(a)	93.50	97-90(4)	95.00	95- (1)	-	-	96.50	97-96(2)	96.50	99-94(2)	90.00	92-88(3)
		8-68(a)	93.75	98-91(4)	-	-	-	-	-	-	-	-	-	-
			+94.56	98-90(29)	94.50	98-90(6)	95.60	99-92(5)	96.14	99-90(7)	96.20	99-94(5)	91.25	95-88(7)
	58-75	8-229(a)	95.00	99-92(4)	91.33	99-85(3)	-	-	89.80	98-85(5)	80.00	81-79(2)	87.00	87- (1)
	(2n=42)	(b)	97.71	100-94(7)	94.00	94- (1)	92.00	92- (1)	94.00	94-94(2)	94.00	98-90(2)	93.00	98-86(3)
		8-362(a)	93.00	93- (1)	83.00	83- (1)	96.00	96- (1)	100.00	100-100(2)	93.50	97-90(2)	97.00	98-96(2)
		8-117(a)	100.00	100- (1)	98.50	99-98(2)	96.50	98-95(2)	98.00	98- (1)	-	-	96.00	96- (1)
		(b)	95.00	95- (1)	94.00	94- (1)	-	-	-	-	-	-	99.00	99- (1)
			+96.57	100-92(14)	92.75	99-83(8)	95.25	99-92(4)	93.50	100-85(10)	89.17	99-79(6)	94.38	99-87(8)
			++95.65	100-90(62)	93.68	99-83(22)	96.79	100-92(14)	95.25	100-85(24)	93.14	99-79(14)	93.13	99-70(24)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**97.80 100-95(5) means 5 counts of 100 PMC (500 PMC), each taken from a single smear, with a maximum range between 100 percent and 95 percent normal PMC out of 5 counts for spike 8-242 which had a mean of 97.80 percent normal tetrads.

+Means for individual plants.

++Means for two lines, 14 and 15.

had 62 percent normal PMC, while another had 98 percent. Florets at other stages had either a very high or a very low percent of normal cells. Evidently a very high degree of irregularity could occur at times in individual florets of plants otherwise highly regular, an irregularity which could not be connected with any obvious external environmental factors.

A few cytological abnormalities other than univalent formation occurred infrequently in plants of both lines. Occasionally chromosomes failed to disjoin. In some spikes, one or more bivalents lay out of the equatorial plate at metaphase I (up to 25 percent of PMC had this irregularity in spike 8-205b-3, plant 58-70, line 14), but disjunction apparently took place normally. Different spikes showed a noticeable difference with respect to presence or absence of chromatin bridges at anaphase I. Sometimes, when present, these appeared to break early so that their presence could not be detected after mid-anaphase. Others persisted until late telophase I. Not infrequently, two were present, one of which broke early and the other persisted.

Cross IV. 1279A-III-4 x Nebred. This backcross of a derived strain with Nebred was represented only by line 7 (53R-201-4). Three of the five plants studied, as data in Table 8 shows, had 42 chromosomes and were highly regular in meiosis, with a mean percentage of normal tetrads ranging from 93 percent to 100 percent. This percentage for plant 58-32 was 95.31 percent (13; 99-90), for plant 58-33, 98.50 percent (2; 99-98) and for plant 58-34, 97.35 percent (20; 100-93). All six spikes from these three plants had better than 90 percent regular PMC at all stages, and showed no great abnormalities.

A fourth plant, 58-35, had five spikes which also had 42 chromosomes and were as regular in meiosis as the three plants just described. A sixth spike

(8-116b) consisted of two more or less equal sectors, one of which was regular and the other extremely irregular in meiosis. One floret of the irregular sector is entered in Table 8 as 8-116bii and a second floret from this sector as 8-116biii. Exact chromosome counts from PMC of these florets could not be made, but the meiotic behavior strongly suggested that different chromosomal alterations had taken place in the two florets, resulting in variant chromosome numbers with consequent meiotic irregularities. One (8-116biii) was consistently more regular in meiosis with 65 percent, 48 percent and 50 percent normal PMC at dyad, anaphase I and metaphase I stages respectively, and the other had 37 percent (2; 40-34), 18 percent (2; 20-16) and 15.50 percent (2; 19-12) normal PMC at the corresponding stages. Presumably external environment was not involved, since anthers from a floret (8-116b-5) directly adjacent to this irregular sector had 95 percent, 85 percent and 69 percent normal tetrads, respectively. Counts from the irregular sector of this spike were not included in computing the means from plant 58-35, so that the meiotic index given in Table 8 as 95.03 percent (31; 100-69) is as high as that of the other four plants of the line.

The fifth plant of line 7, 58-31, had 43 chromosomes, a count confirmed in several PMC at both metophase I and anaphase I. Metaphase I pairing varied considerably, but the 7 spikes from the plant had a broadly similar meiotic pattern. Because of the variant chromosome number, data from this plant were not included in computing overall means for the line. It is possible that an aneuploid plant of this sort could arise in a highly stable line from a spike with aberrent sectors or florets, similar to the spike just described (8-116b) for plant 58-35.

Cross VI. Shands 473 x T. timopheevi. The single line, 12 (C.I. 13005),

Table 8. Percentage and range* of normal PMC at six stages of meiosis in 5 plants of line 7 of cross IV. 1279-A-III-16 (derived strain from T. aestivum x T. timopheevi cross) x Nebred.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
7	58-31** (2n=43)	8-256(a)	54.00	56-52(3)++	49.00	49- (1)	64.00	64- (1)	63.00	63- (1)	27.00	27 (1)	35.00	39-27(3)
		(b)	59.50	50-59(2)	-	-	-	-	54.00	54- (1)	22.50	25-20(2)	45.33	56-35(3)
		8-335(a)	54.00	61-51(2)	-	-	-	-	55.00	55- (1)	-	-	19.00	19-19(2)
		(b)	55.00	55- (1)	-	-	-	-	-	-	-		-	-
		8-365(a)	47.33	54-43(3)	35.00	35- (1)	-	-	39.00	40-38(2)	5.00	5- (1)	-	-
		(b)	55.00	55- (1)	29.00	29- (1)	79.00	80-78(2)	30.00	30- (1)	-	-	53.80	81-41(5)
		(c)	47.50	48-47(2)	-	-	82.00	82- (1)	54.00	54- (1)				
			+52.67	61-43(15)	37.67	49-29(3)	75.50	80-64(4)	47.57	62-30(7)	19.25	45-5 (4)	42.15	81-27(13)
	58-32 (2n=42)	8-183	93.33	96-90(3)	-	-	-		89.00	89- (1)	88.00	88- (1)	93.00	93- (1)
		8-257	95.90	99-91(10)	-	-	99.00	99- (1)	97.00	99-95(3)	-	-	95.00	96-94(2)
			+95.31	99-90(13)	-	-	99.00	99- (1)	95.25	99-89(4)	88.00	88- (1)	94.33	96-93(3)
	58-33 (2n=42)	8-145	+98.50	99-98(2)	-	-	-	-	-	-	-	-	-	-
	58-34 (2n=42)	8-144	98.40	100-95(5)	99.25	100-98(4)	99.75	100-99(4)	-	-	92.00	92- (1)	-	-
		8-184	98.00	100-96(3)	-	-	-							
		8-282	96.75	99-93(12)	96.50	99-94(2)	99.00		-	-				
			+97.35	100-93(20)	98.33	100-94(6)	99.60	100-99(5)	-	-	92.00	92- (1)	-	-
	58-35 (2n=42)	8-116(a)	95.50	99-90(12)	99.00	99- (1)	99.00	99- (1)	99.00	99- (1)	99.00	100-98(2)	100.00	100- (1)
		(b)i	90.78	96-69(9)	-	-	-		96.50	97-96(2)	93.33	97-90(3)	94.67	97-93(3)
		**(b)ii	-	-	14.00	14- (1)	-		37.00	40-34(2)	18.00	20-16(2)	15.50	19-12(2)
		**(b)iii	-	-	-	-	60.00	60- (1)	65.00	65- (1)	48.00	48- (1)	50.00	50- (1)
		(c)	-	-	-	-	96.00	96- (1)	95.33	97-93(3)	88.00	88- (1)	-	-
		8-185(a)	-	-	-	-	-		96.50	100-93(2)	84.00	84- (1)	95.67	98-92(3)
		(b)	98.86	100-98(7)	98.22	99-97(2)	100.00	100- (1)	95.00	95- (1)	90.00	90- (1)	96.50	97-96(2)
		(c)	97.00	98-96(3)	99.00	99- (1)	-		98.00	98- (1)	91.00	95-87(2)	94.00	94- (1)
			+95.03	100-69(31)	98.50	99-97(4)	98.33	100-96(3)	96.73	100-93(10)	92.20	100-84(10)	95.80	100-92(10)
			+++95.89	100-69(66)	98.41	100-97(10)	99.11	100-96(9)	96.33	100-93(14)	91.83	100-84(12)	95.46	100-92(13)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**Plant 58-31 and smears bii and biii from spike 8-116b of plant 58-35 are not considered in computing grand mean (***) for line 7 or means (+) for plant 58-35.

+Means for five plants: 58-31, 58-32, 58-33, 58-34 and 58-35, separately.

++54.00 56-52(3) means 3 counts of 100 PMC (400 PMC), each taken from a single smear, with a maximum range of 56 percent to 52 percent normal PMC out of 3 counts for spike 8-256(a) which had a mean of 54.00 percent normal tetrads.

of this cross was highly irregular as shown by data in Table 9. One plant (48-60) of the five studied had 41 chromosomes (Plate V, F and G), while the other four (58-56, 58-57, 58-58 and 58-59) had the normal 42. The monosomic plant (58-60) has not been included in determining means for the line. The mean for normal PMC at the tetrad stage was 54.70 percent (71; 96-4), at metaphase I 87.12 percent (64; 100-66), but only 38.10 percent (57; 97-0) at the dyad stage. (This observation becomes more meaningful when correlations for these stages are compared, Table 17).

A very great range of variation in regularity is evident at all stages, varying from about 92 percent (96-4) at the tetrad stage to 97 percent (97-0) at dyad stage. Considerable variation was also found between spikes and even in different florets of the same spike. One smear from a single floret (smear b-1 of spike 8-166b of plant 58-56) had 65 percent normal PMC at metaphase I in one anther, 1 percent in a second another and none (at dyad stage) in the third. Some of the irregularity may result from the apparently random occurrence of PMC or groups of PMC with widely aberrant chromosome numbers (Plates VI, VII and VIII C). In this smear, b-1 of spike 8-166b, 42 chromosomes could be counted in a number of the anaphase I PMC, but among them have been found metaphase I cells with as few as 15 chromosomes ($3_{II} + 9_{I}$). Another cell had 22_{II} + 6 small fragments, and a third had 17_{II} + 2_{I} + 4 fragments. In a different smear from a different plant (smear a-3 of spike 8-268a, from plant 58-57) were anaphase I cells with 35, 28 and lesser numbers of chromosomes and metaphase I cells with $20_{II} + 1_{I}$, $21_{II} + 1_{I}$ and 22_{II} chromosomes. Since none of these could have resulted from the meiotic division, they must represent aberrations which took place in the pre-meiotic sporocyte tissue.

Small fragments, in varying numbers up to 5 or 6, were observed in other

Table 9. Percentage and range* of normal PMC at six stages of meiosis in 5 plants of line 12 cross VI. Shands 473 (derived from T. aestivum x T. timopheevi cross) x Triticum timopheevi.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
12	58-56	8-116(a)	13.00	21-4 (3)**	38.00	38- (1)	6.00	6- (1)	0.00	0-0 (4)	0.00	0-2 (2)	89.13	93-85(8)
	(2n=42)	(b)	24.00	35-15(4)	-	-	-	-	0.50	1-0 (2)	-	-	83.00	88-69(4)
		8-194(a)	36.56	52-11(9)	65.00	65- (1)	51.00	51- (1)	17.89	64-0 (9)	4.00	4- (1)	68.00	79-64(6)
		(b)	69.50	70-69(2)	59.00	59- (1)	69.00	76-62(2)	38.25	53-20(4)	20.00	20- (1)	85.00	85- (1)
			+35.50	70-4 (18)	41.33	65-38(3)	48.75	76-6 (4)	16.58	64-0 (19)	6.00	20-0 (4)	80.95	96-64(19)
	58-57	8-195(b)	53.60	68-39(5)	52.50	68-37(2)	52.00	52- (1)	37.50	50-25(2)	24.00	48-0 (3)	84.50	91-80(4)
	(2n=42)	8-195(c)	66.00	74-58(2)	74.00	74- (1)	35.00	35- (1)	56.50	61-51(2)	8.00	12-6 (3)	70.00	85-56(3)
		8-147	83.50	96-65(12)	89.50	91-88(2)	100.00	100- (1)	85.50	92-79(2)	-	-	97.00	99-94(3)
		8-268	50.00	55-45(2)	-	-	61.67	73-42(3)	22.67	92-9 (6)	12.50	22-3 (2)	78.50	89-68(4)
			+71.52	96-39(21)	67.00	91-37(5)	62.00	100-35(6)	41.25	92-9 (12)	15.13	48-0 (4)	82.36	99-56(14)
	58-58	8-269(a)	61.38	79-28(8)	-	-	-	-	-	-	84.00	84- (1)	85.00	89-81(3)
	(2n=42)	8-269(b)	63.00	68-53(3)	87.33	95-79(3)	82.00	82- (1)	70.75	86-51(8)	52.00	55-9 (2)	90.13	100-74(8)
		8-269(c)	56.00	56- (1)	-	-	-	-	50.00	50- (1)	-	-	95.50	99-92(2)
			+61.33	79-28(12)	87.33	95-79(3)	82.00	82- (1)	69.00	86-50(9)	52.00	84-49(3)	89.77	100-74(13)
	58-59	8-196(a)	45.29	56-26(7)	15.00	15- (1)	-	-	56.00	56- (1)	45.00	45- (1)	83.75	91-77(4)
	(2n=42)	(b)	66.00	70-64(3)	41.33	55-18(6)	-	-	40.00	64-21(8)	41.40	73-23(5)	85.00	87-83(3)
		8-275	88.00	88- (1)	76.00	90-62(2)	-	-	71.40	97-47(5)	87.67	94-83(6)	79.70	91-66(10)
		8-334	48.89	70-28(9)	-	-	24.00	24- (1)	2.67	4-1 (3)	20.00	20- (1)	69.00	69- (1)
			+52.15	88-26(20)	46.11	92-15(9)	24.00	24- (1)	43.59	97-1 (17)	61.38	94-20(13)	80.89	91-66(18)
			++54.70	96-4 (71)	60.79	92-15(24)	56.08	100-6 (12)	38.10	97-0 (57)	40.39	94-0 (28)	87.12	91-66(64)
	58-60	8-167(a)	32.00	44-21(4)	12.00	12- (1)	-	-	0.00	0- (10)	-	-	38.00	41-35(2)
	(2n=41)	8-167(b)	41.33	47-38(3)	15.00	15- (1)	-	-	1.50	3-0 (2)	0.00	0- (1)	43.67	50-34(3)
		8-167(c)	37.00	54-20(2)	-	-	-	-	2.00	2- (1)	6.00	6- (1)	39.00	43.37(3)
		8-197	67.50	74-63(4)	30.00	30- (1)	-	-	6.33	15-0 (3)	1.00	1- (1)	16.00	16- (1)
		8-270	72.67	81-65(6)	54.00	54- (1)	78.00	78- (1)	55.00	55- (1)	20.00	20- (1)	39.33	44-35(3)
			+54.31	81-21(19)	27.75	54-12(4)	78.00	78- (1)	9.88	55-0 (8)	5.60	20-0 (5)	38.17	50-16(12)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**13.00 21-4(3) means 3 counts of 100 PMC (300 PMC), each taken from a single smear, with a maximum range between 21 percent and 4 percent normal PMC out of 3 counts for spike 8-166(a) which had a mean of 13.00 percent normal tetrads.

+Means for individual plants; 58-56, 58-57, 58-58, 58-59 and 58-60.

++Mean for line 12 does not include data from plant 58-60.

smears from all the plants, sometimes in as many as 10 percent of the PMC. They may have had an even greater frequency, but escaped detection because of their small size and close proximity to, or pairing with, other chromosomes. At least some of these were probably minute chromosomes with centromeres, since at least one small pair was seen. In another cell, such a minute chr mosome or chromosome pair formed a tiny bridge. It seems probable that the minute chromosomes or fragments also synapsed with the larger chromosomes, forming either a very unequal pair which resembled a univalent or a trivalent in which the one partner is very small (Plates VI A and B; VII, A and B; VIII, C).

Other anaphase I irregularities include bridge formation, division of univalents, lagging chromosomes and scattered bivalents. All of these were highly variable in occurrence. (Plate III, A, B, C).

Cross VII. Shands 473 x Cheyenne. The three lines studied in this cross, line 8 (53R456), line 11 (53R457) and line 20 (50 4312), differed considerably from each other. Line 11 was the only one to have attained a high degree of meiotic stability, as shown by summarized data in Table 10. The chromosome number of all three plants studied was 42, and all ten spikes from the three plants had a consistently high percentage of normal PMC at all stages of meiosis. The mean for the meiotic index of the line was 97.02 percent (45; 100-90), and means for the three individual plants were almost the same, 97.67 percent (12; 99-96) for plant 58-51, 97.33 percent (18; 100-90) for plant 58-54, and 96.13 percent (15; 98-90) for plant 58-55. Some irregularities were found, either few in number or of such a nature that micronuclei did not result. At metaphase I, 1-3 end to end bivalents were not infrequent and occasionally univalents were seen, presumably due either

Table 10. Percentage and range* of normal PMC at six stages of meiosis in 3 plants of line 11 of cross VII. Shands 473 (derived from T. aestivum - T. timopheevi cross) x Cheyenne.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
11	58-51 (2n=42)	8-226(a)	99.00	99-99(2)**	-	-	-	-	-	-	-	-	-	-
		(b)	97.00	97-97(2)	92.00	92- (1)	98.00	98- (1)	99.00	99- (1)	96.00	96- (1)	97.00	97-97(2)
		8-320	97.00	98-96(3)	98.00	98- (1)	100.00	100- (1)	99.00	99-99(2)	98.00	98- (1)	92.00	92- (1)
		8-363(a)	98.00	98-98(3)	86.00	86- (1)	94.00	94- (1)	99.00	99- (1)	96.00	96- (1)	89.00	89- (1)
		(b)	97.50	98-97(2)	96.00	96-96(2)	95.00	99-91(2)	97.00	97- (1)	99.00	99- (1)	96.00	96- (1)
			***97.67	99-96(12)	93.60	96-86(5)	96.40	100-91(5)	98.60	99-97(5)	97.25	99-96(4)	94.20	97-89(5)
	58-54 (2n=42)	8-192(a)	97.67	100-90(6)	95.40	98-88(5)	93.00	96-91(3)	86.00	90-80(3)	-	-	-	-
		(b)	95.33	99-90(6)	87.33	97-80(3)	98.75	100-98(4)	95.00	99-91(2)	-	-	-	-
		8-277(b)	99.00	100-97(6)	96.60	98-93(3)	97.33	98-97(3)	95.50	97-94(2)	100.00	100- (1)	97.00	97- (1)
			***97.33	100-90(18)	94.00	98-80(13)	96.60	100-91(10)	91.29	99-80(7)	100.00	100- (1)	97.00	97- (1)
	58-55 (2n-42)	8-276(a)	96.75	98-95(8)	94.00	94- (1)	99.00	99- (1)	97.00	97- (1)	95.50	98-93(2)	93.00	95-91(2)
		8-319(a)	95.17	98-90(6)	92.00	92- (1)	94.00	94- (1)	95.00	95- (1)	98.00	98-98(2)	96.50	99-94(2)
		8-375(a)	97.00	97- (1)	96.00	96- (1)	95.00	95- (1)	93.00	96-91(2)	95.50	97-94(2)	95.33	98-94(3)
			***96.13	98-90(15)	94.00	96-92(3)	96.00	99-94(3)	94.75	97-91(4)	96.33	98-93(6)	95.00	99-91(7)
			****97.02	100-90(45)	93.93	96-80(21)	96.44	100-91(18)	94.44	99-80(16)	97.00	100-93(11)	94.85	99-91(13)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each counts was for 100 PMC per smear made.

**99.00 99-99(2) means 2 counts of 100 PMC (200 PMC), each taken from a single smear, with a range between 99 percent and 99 percent normal PMC out of 2 counts for spike 8-266(a) which had a mean of 99.00 percent normal tetrads.

***Means for individual plants; 58-51, 58-54 and 58-55.

****Means for the line 11.

to asynapsis or early disjunction. In one spike (8-320 of plant 58-51), univalents present did not divide at anaphase I, and only seldom was there a bridge which invariably broke before mid-anaphase I. A single smear from another spike (363a) of the same plant had a number of cells with one anaphase bridge and several cells with two bridges. In this smear in some cells univalents divided at anaphase I.

The other two lines, 8 and 20, had a highly irregular meiotic behavior which closely resembled that of line 12 (cross VI), as is shown by data in Tables 11 and 12, respectively. All five plants of line 20 and six of the eight plants of line 8 had 42 chromosomes. The remaining 2 plants of line 8 (58-36 and 58-44) had 41 chromosomes and for this reason have been omitted in determining mean values of regular PMC for the line. Line 20 had consistently higher means, at all stages, than did line 8, but both showed wide variations which overlapped each other. Percent of normal tetrads in line 20 was 85.50 percent (105; 100-59) as compared to 68.47 percent (122; 99-31) in line 8. Normal PMC at metaphase I were 88.12 percent (69; 100-69) in line 20 as compared to 84.20 percent (56; 99-44) in line 8. In both lines, as in line 12 of cross VI, the percent of normal PMC at the dyad stage was very low, being 58.19 percent (62; 96-0) in line 20 and 53.07 percent (97-0) in line 8. Presumably, difficulties of disjunction at AI cause a great increase in irregularities which do not result in tetrad micronuclei. That this is a real difference and not a chance variation is indicated both by the large numbers of counts made at all these stages and by its consistent appearance in all plants and spikes studied in these lines.

Corresponding to the higher means of normal PMC at all stages, line 20 also had a somewhat lower range of deviations from the means. Since the

Table 11. Percentage and range* of normal PMC at six stages of meiosis in 8 plants of line 8, cross VII. Shands 473 (derived strain from T. aestivum - T. timopheevi cross) x Cheyenne.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase II Mean	Metaphase II Range*
8	58-36	8-259	68.25	7-65(4)**	65.00	70-61(2)	64.00	70-58(2)	30.00	34-26(4)	29.00	52-9 (3)	46.00	57-36(7)
	(2n=41)	8-346	53.50	59-45(4)	39.00	50-28(2)	70.00	75-65(2)	47.50	64-34(2)	2.00	2- (1)	-	-
		8-364	24.60	26-23(5)	25.25	42-13(4)	29.00	30-28(2)	4.50	7-0 (4)			46.33	50-40(3)
			+46.92	70-23(13)	38.63	70-13(8)	54.33	75-28(6)	23.30	64-0 (10)	22.25	52-2 (4)	46.10	57-36(10)
	58-44	8-348	62.00	80-48(4)	-	-	-	-	68.60	87-11(5)	62.00	70-54(2)	62.00	70-54(2)
	(2n=41)	8-369(a)	52.75	61-41(4)	54.00	54- (1)	-	-	40.50	49-32(2)	26.50	27-26(2)	26.50	27-26(2)
		(b)	50.00	54-48(3)	-	-	-	-	-	-	53.00	58-49(3)	53.00	58-49(3)
			+55.36	80-41(11)	54.00	54- (1)	-	-	60.57	87-32(7)	48.00	70-26(7)	48.00	70-26(7)
			++50.79	80-23(24)	40.33	70-13(9)	-	-	38.65	87-0 (17)	38.64	70-2 (11)	46.88	70-26(17)
	58-37	8-345	65.57	82-40(14)	-	-	-	-	96.00	96-96(2)	90.00	90- (1)	89.50	95-80(4)
	(2n=42)	8-186(a)	54.50	74-46(14)	31.71	51-8 (7)	29.00	33-25(2)	23.33	52-10(9)			88.83	96-79(6)
		(b)	50.33	60-41(6)	-	-	-	-	31.00	31- (1)	29.00	29- (1)	89.33	93-87(3)
			+58.32	82-40(34)	31.71	51-8 (7)	29.00	33-25(2)	36.08	96-10(12)	59.50	90-29(2)	89.15	96-79(13)
	58-38	8-187(a)	53.50	63-44(6)	-	-	-	-	8.00	14-4 (5)			-	-
	(2n=42)	(b)	51.67	79-35(9)	54.00	72-36(2)	-	-	3.83	8-0 (6)	1.43	80-0 (7)	80.43	90-70(7)
		8-261(a)	55.18	67-31(11)	30.00	36-24(2)	68.00	68- (1)	26.83	42-11(6)	0.00	0-0 (4)	79.40	89-68(5)
		8-317(a)	71.62	94-48(13)	82.25	89-72(4)	92.00	92- (1)	72.00	92-60(6)	66.00	66- (1)	67.50	91-44(2)
			+59.59	97-31(39)	62.13	89-24(8)	80.00	92-68(2)	28.52	92-0 (23)	6.33	66-0 (12)	78.21	91-44(14)
	58-39	8-281(a)	97.00	97- (1)	92.00	92- (1)	-	-	83.00	92-68(3)	78.00	96-60(2)	88.50	97-75(4)
	(2n=42)	(b)	88.00	99-71(10)	85.00	85- (1)	88.00	94-83(3)	71.00	90-58(10)			70.00	80-60(2)
		(c)	85.00	84-73(4)	86.50	88-85(2)	86.00	88-84(2)	49.50	64-35(2)	40.00	40- (1)	-	-
		(d)	88.20	93-82(5)	81.00	91-71(2)	87.00	88-86(2)	62.00	70-54(2)			82.50	94-59(4)
			+87.00	99-71(20)	85.43	92-71(7)	87.14	94-83(7)	69.65	92-35(17)	65.33	96-40(3)	82.40	97-59(10)
	58-40	8-344	63.71	94-77(7)	81.00	81- (1)	90.00	90- (1)	64.33	75-33(3)			70.00	70- (1)
	(2n=42)	8-280(a)	76.75	89-59(4)	90.00	90- (1)	85.33	88-83(3)	71.71	83-55(7)	5.00	5- (1)	69.50	80-55(4)
		(b)	-	-	-	-	-	-	84.33	90-74(3)			60.00	60- (1)
			+68.45	94-59(11)	85.50	90-81(2)	86.50	90-83(4)	72.92	90-48(13)	5.00	5- (1)	68.00	80-55(6)
	58-41	8-262(a)	88.33	89-87(3)	88.00	99- (1)	-	-	80.00	80- (1)			93.00	93- (1)
	(2n=42)	(b)	84.00	88-79(3)	-	-	48.00	48- (1)	84.00	84- (1)			93.00	94-92(2)
		8-189(a)	85.17	89-82(6)	28.00	28- (1)	-	-	72.00	72- (1)	54.00	54- (1)	92.00	92- (1)
		(b)	83.00	83- (1)	69.50	71-68(2)	80.00	80- (1)	53.00	53- (1)	78.00	78- (1)	89.00	89- (1)
			+ 85.46	89-79(13)	63.75	88-28(4)	64.00	80-48(2)	72.25	84-53(4)	66.00	78-54(2)	92.00	94-89(4)
	58-43	8-264(b)	80.00	80- (1)	-	-	-	-	84.00	84- (1)	82.00	82- (1)	96.17	99-95(6)
	(2n=42)	8-318(a)	90.50	95-86(4)	97.00	97- (1)	-	-	93.33	97-88(3)	95.00	95- (1)	96.00	97-95(2)
			+88.40	95-80(5)	97.00	97- (1)	-	-	91.00	97-84(4)	88.50	95-82(2)	96.00	99-95(8)
			++68.47	99-31(122)	63.45	99-8 (29)	76.59	94-25(17)	53.07	97-0 (73)	32.05	96-0 (22)	84.20	99-44(56)
			+++65.56	99-23(146)	57.97	99-8 (38)	70.78	94-25(23)	50.34	97-0 (90)	34.24	96-0 (33)	75.51	99-26(73)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**68.25 70-65(4) means 4 counts of 100 PMC (400 PMC) each taken from a single smear, with a maximum range between 70 percent to 65 percent normal PMC out of 4 counts for spike 8-259 which had a mean of 68.25 percent normal tetrads.

+Means for plants.

++Means for the plants with 2n=41 chromosomes and 6 plants with 2n=42 chromosomes.

+++Means for line 8.

Table 12. Percentage and range* of normal PMC at six stages of meiosis in 5 plants of line 20 cross VII. Shands 473 (derived from T. aestivum x T. timopheevi cross) x Cheyenne.

Line No.	Plant No.	Spike No.	Tetrads Mean	Tetrads Range*	Anaphase II Mean	Anaphase II Range*	Metaphase II Mean	Metaphase II Range*	Dyads Mean	Dyads Range*	Anaphase I Mean	Anaphase I Range*	Metaphase I Mean	Metaphase I Range*
20	58-96	8-154(a)	92.67	97-81(6)**	-	-	-	-	-	-	12.00	12- (1)	85.50	88-83(2)
	(2n=42)	(b)	82.00	87-77(2)	59.75	71-51(4)	80.00	80- (1)	48.50	73-24(2)	55.00	55- (1)	76.50	84-69(2)
		8-213(a)	77.33	90-65(3)	68.50	73-64(2)	68.00	68- (1)	65.00	75-55(2)	46.00	46- (1)	83.50	88-79(2)
		8-351(a)	84.20	88-79(5)	75.00	75- (1)	75.00	75- (1)	65.00	65- (1)	71.00	71- (1)	94.67	100-86(3)
			+85.81	97-65(16)	64.43	75-51(7)	74.33	80-68(3)	58.40	75-24(5)	46.00	71-12(4)	86.11	100-86(9)
	58-97	8-214(a)	96.50	98-96(4)	88.14	96-79(7)	75.00	80-65(3)	64.13	86-48(8)	48.00	60-35(4)	89.25	98-72(4)
	(2n=42)	8-214(b)	94.83	98-92(6)	-	-	-	-	96.00	96- (1)	84.50	93-75(4)	93.00	95-85(9)
		8-322(a)	73.00	87-59(5)	65.00	92-26(10)	51.25	78-24(8)	65.10	94-30(10)	37.57	66-15(7)	83.83	100-70(6)
			+88.00	98-87(15)	74.53	96-26(17)	57.73	80-24(11)	66.32	96-30(19)	52.87	93-15(15)	89.32	100-70(19)
	58-98	8-215(a)	89.67	94-80(6)	79.00	93-70(6)	62.00	82-34(5)	47.75	68-28(4)	74.50	80-69(2)	84.80	91-81(5)
	(2n=42)	(b)	94.50	96-93(2)	94.00	96-92(2)	88.00	90-86(2)	72.33	94-61(3)	-	-	89.25	95-84(4)
		8-155(a)	79.50	89-64(6)	56.67	79-45(3)	46.00	54-40(3)	27.38	57-0 (8)	13.60	25-2 (5)	94.00	92-84(8)
		(b)	-	-	-	-	-	-	-	-	-	-	99.33	100-99(3)
			+86.00	96-64(14)	75.64	96-45(11)	62.40	90-34(10)	41.80	94-0 (15)	31.00	80-2 (7)	91.55	100-81(20)
	58-99	8-156(a)	82.78	94-78(9)	69.00	69- (1)	75.00	75- (1)	48.00	63-32(6)	15.00	20-9 (3)	87.80	95-80(5)
	(2n=42)	8-216(a)	-	-	-	-	-	-	-	-	-	-	99.00	99- (1)
		(b)	88.13	93-80(8)	82.33	86-81(3)	82.00	82- (1)	64.33	85-54(3)	78.50	82-15(2)	86.00	86- (1)
		8-303(a)	90.22	94-86(9)	88.00	88- (1)	85.00	85- (1)	95.00	95- (1)	95.50	97-94(2)	91.20	95-88(5)
		(b)	85.56	94-74(9)	-	-	-	-	90.00	90- (1)	91.00	91- (1)	74.00	74- (1)
			+86.63	94-74(35)	80.80	88-69(5)	80.67	85-75(3)	60.63	95-32(11)	60.50	97-9 (8)	88.77	99-74(13)
	58-100	8-217(a)	83.69	90-74(13)	70.00	80-49(4)	73.00	80-64(3)	61.57	96-23(7)	58.00	88-28(2)	89.00	96-85(4)
	(2n=42)	8-217(b)	84.00	89-78(5)	75.33	80-70(3)	83.00	83- (1)	65.00	85-45(2)	80.00	80- (1)	91.00	91-91(2)
		8-333(a)	72.11	100-59(7)	82.25	100-49(4)	75.00	75- (1)	67.00	96-28(3)	82.00	84-8 (2)	83.50	84-83(2)
			+80.68	100-59(25)	75.91	100-49(11)	75.40	83-64(5)	63.50	96-23(12)	72.00	88-28(5)	81.92	96-83(8)
			++85.50	100-59(105)	74.29	100-26(51)	65.66	90-24(32)	58.19	96-0 (62)	52.26	97-2 (39)	88.12	100-69(69)

*Gives the range of normal PMC from different counts, followed by number of counts in parenthesis; each count was for 100 PMC per smear made.

**92.67 97-81(6) means 6 counts of 100 PMC (600 PMC), each taken from a single smear, with maximum range between 97 percent and 81 percent normal PMC out of 6 counts for spike 8-154(a) which had a mean of 92.67 percent normal tetrads.

+Means for 5 plants; 58-96, 58-97, 58-98, 58-99 and 58-100 separately.

++Means for Line 20 as a whole.

deviations were so great, however, the significance of this may be questioned. The tetrad stage of line 20 showed a deviation of 41 percent (100-59) in line 20 as compared to 68 percent (99-31) in line 8. Metaphase I in line 20 had a deviation of 31 percent (100-69) as compared to 55 percent (99-44) in line 8. Both lines had almost the greatest possible deviation at the dyad stage, ranging from 0 to 96 percent in line 20 and from 0 to 97 percent in line 8.

Both lines showed the same types of irregularities found in line 12 of cross VI. Scattered PMC and groups of PMC had widely deviating chromosome numbers, which must have arisen from aberrations in the pre-meiotic sporocyte tissue. Varying numbers of small fragments or minute chromosomes were found, together with other irregularities such as bridge formation, division of univalents at anaphase I, lagging chromosomes, and scattered bivalents (Plate III, D; Plate VIII, A and B; Plate IV). This scattering may have been due to variations in the cellular environment, as suggested by Pao and Li (1948), who found irregularities due to failure of spindle formation and paralysis of the centromere in normal wheat plants kept at 45° C. They attribute presence of univalents to the failure of synapsis, early disjunction and early terminalization due to a higher degree of chromosome contraction in plants kept at higher temperature.

Statistical Analysis and Interpretation

Meiotic data from the highly irregular lines, 8 and 20 (cross VII) and line 12 (cross VI) were analysed statistically. Line 20 was analysed separately, then data combined from these three lines were analysed collectively.

Analysis of Meiotic Variability in Line 20. Analysis of variance for

six meiotic stages in line 20 is given in Table 13. Variances were analysed for spikes taken on different dates from the same plant (samples within plants), for different spikes of the same plant taken at the same time (spikes within samples) and for different flowers in the same spike (flowers within spikes). At all stages of meiosis except anaphase I, one major source of variation was florets within spikes (i.e. the variation among florets of the same spike). This was significant at the 5 percent level at both metaphase I and metaphase II and highly significant 0.1 percent at dyad, anaphase II and tetrad stages. Samples (spikes) collected on different dates within plants (i.e. from the same plant) were another major source of variation. F values obtained for these at metaphase I were statistically significant (5%), rose to a higher degree of statistical significance at anaphase I (0.1%), were non-significant at the following stages until they finally became significant again (1%) at the tetrad stage. A third significant (5%) source of variation at anaphase I was spikes within samples (i.e., different spikes of the same plant collected on the same date), but this was non-significant at all other stages. Florets within spikes are then the major source of variation in meiotic regularity at all stages except anaphase I. Consequently, a reliable estimate of the general mean and the range of variation for the line for any one of the meiotic stages except anaphase I could be derived from a single spike of a single plant, if it were possible to make a sufficiently large number of counts. It is not necessary to have a large number of samples or a large number of plants. The reason for the non-significance of differences from plant to plant is probably that all plants have about the same range, and the recorded high and low mean values for plants are chance variations resulting from a low number of observations (counts) for individual plants. A large

Table 13. Analysis of variance for six meiotic stages for line 20 of cross VII. Shands 473 x Cheyenne series No. 504312 (1942).

Meiotic stages	Sources of variation	d.f.	MS	F	Sig.
Tetrad (quartet) stage	Plants	4	167.24	0.36	n.s.
	Samples : Plants	7	468.04	4.32	**
	Spikes : Samples	5	72.53	0.67	n.s.
	Flowers : Spikes	22	108.45	3.92	***
	Anthers : Flowers	63	27.66		
	Total	101			
Anaphase II	Plants	44	218.78	0.31	n.s.
	Samples : Plants	6	714.82	1.51	n.s.
	Spikes : Samples	3	173.20	0.36	n.s.
	Flowers : Spikes	13	474.89	7.92	***
	Anthers : Flowers	23	59.96		
	Total	49			
Metaphase II	Plants	4	543.53	1.52	n.s.
	Samples : Plants	7	358.41	0.85	n.s.
	Spikes : Samples	2	520.36	1.23	n.s.
	Flowers : Spikes	7	422.69	3.31	*
	Anthers : Flowers	11	127.70		
	Total	31			
Dyad	Plants	4	1422.10	1.43	n.s.
	Samples : Plants	7	966.94	1.09	n.s.
	Spikes : Samples	4	492.48	0.54	n.s.
	Flowers : Spikes	21	913.36	6.72	***
	Anthers : Flowers	25	135.85		
	Total	61			
Anaphase I	Plants	4	1454.43	0.51	n.s.
	Samples : Plants	7	2837.88	13.45	***
	Spikes : Samples	4	981.29	4.65	*
	Flowers : Spikes	10	211.06	0.65	n.s.
	Anthers : Flowers	13	326.53		
	Total	38			
Metaphase I	Plants	4	51.87	0.34	n.s.
	Samples : Plants	7	152.10	3.09	*
	Spikes : Samples	7	80.34	1.63	n.s.
	Flowers : Spikes	21	49.23	1.95	*
	Anthers : Flowers	29	25.25		
	Total	68			

number of counts would be expected to show a similar range of variation for all the plants and so to bring the individual means close to the general mean for the line.

The nonsignificance of variation at anaphase I stages for florets within spikes indicates that the rather large differences in means of normal PMC at this stage are mere chance variations. The mean of the line for this stage is 52.26 percent (39;97-2), as compared to means for the individual plants of 46.00 percent (4; 71-12) for plant 58-96, 52.87 percent (15;93-15) for plant 58-97, 31.00 percent (7; 80-2) for plant 58-98, 65.50 percent (8; 97-9) for plant 58-99, and 72.00 percent (5; 88-28) for plant 58-100. A larger number of counts would presumably have brought these means closer together. In conjunction with this, it might be noted that the plant for which the largest number of counts was made (15 counts for plant 58-97) had a mean (52.87%) which was closest to the mean for the line (52.26%).

Variations in external environmental conditions also undoubtedly contributed to these deviations, as shown by the statistical significance (at anaphase I; (5%) of variation of spikes within samples. As shown in Table 12, deviations from plant to plant at anaphase I were much smaller in spikes collected on the same day. Thus, means from five samples viz., 8-213 (46.00%), 8-214 (66.25%), 8-215 (74.50%), 8-216 (78.50%) and 8-217 (65.33%) collected on the same day from five different plants showed no greater deviations than spikes from any one of the plants collected on different dates. For example, plant 58-96 which had a mean value of 46 percent for anaphase I stage (4; 71-12) had spike means of 33.50 percent (spike 8-154), 46 percent (spike 8-213), and 71 percent (spike 8-351). In plant 58-99, means for three samples were 94 percent, 78 percent and 15 percent.

The effect of external environment which has been shown for anaphase I stage is apparently less for other stages of meiosis, since variation of spikes within samples at other stages for this line (20) is nonsignificant.

Analysis of Meiotic Variability in Lines 8, 12 and 20. Table 14 gives an analysis of the sources of variation at six meiotic stages in the three most irregular lines, 8 and 20 (of cross VII) and line 12 (of cross VI). Five points are of special interest.

1. The three lines did not differ significantly from each other at five of the six meiotic stages. Only at the tetrad stage did the lines differ at the 1 percent level of significance.

2. Samples (spikes taken on different dates) within plants were a significant source of variation at all the six stages. These differences were highly significant at all stages, metaphase II being significant at the 5 percent level and the other stages at levels varying from 0.1 percent to 1 percent.

3. Florets within spikes were another major source of variation at all stages except at metaphase II. At four stages (tetrad, anaphase II, dyad and metaphase I) the florets within spikes differed significantly at 0.1 percent level and at anaphase I the differences were significant at the 5 percent level only.

4. Differences within plants of a line were highly significant (0.1%) at metaphase I. These differences were probably obscured by more prominent sources of variation at later stages until at tetrad stage they were again significant at the 5 percent level.

5. Spikes within samples (spikes collected on the same day from any one plant) did not differ significantly except at anaphase I, at which

Table 14. Combined analysis of variance for six meiotic stages for lines 12 (cross VI), 8 and 20 (cross VII).

Meiotic stages	Sources	d.f.	MS	F	Sig.
Tetrad	Lines	2	23034.1410	8.40	**
	Plants : Lines	15	22741.3860	2.41	*
	Samples : Plants	23	1136.1209	4.37	***
	Spikes : Samples	21	181.2311	0.70	n.s.
	Flowers : Spikes	87	259.6863	4.13	**
	Anthers : Flowers	188			
	Total	336			
Anaphase II	Lines	2	4432.28	2.62	n.s.
	Plant : Lines	15	1693.97	1.89	n.s.
	Samples : Plants	18	895.79	2.89	**
	Spikes : Samples	11	243.41	0.79	n.s.
	Flowers : Spikes	34	309.48	2.65	***
	Anthers : Flowers	35	116.59		
	Total	115			
Metaphase II	Lines	2	704.81	0.71	n.s.
	Plant : Lines	13	998.65	1.52	n.s.
	Samples : Plants	15	656.81	3.05	*
	Spikes : Samples	6	234.34	1.09	n.s.
	Flowers : Spikes	18	215.32	1.98	n.s.
	Anthers : Flowers	13	108.55		
	Total	67			
Dyad	Lines	2	9275.87	1.93	n.s.
	Plants : Lines	15	4816.50	2.07	n.s.
	Samples : Plants	25	2332.01	4.76	***
	Spikes : Samples	16	296.96	0.61	n.s.
	Flowers : Spikes	65	489.42	4.96	**
	Anthers : Flowers	93	98.65		
	Total	216			
Anaphase I	Lines	2	3792.18	1.09	n.s.
	Plant : Lines	15	3479.49	1.92	n.s.
	Samples : Plants	20	1808.73	7.09	***
	Spikes : Samples	11	581.76	2.28	*
	Flowers : Spikes	27	255.12	1.61	*
	Anthers : Flowers	29	158.36		
	Total	104			
Metaphase I	Lines	2	4347.59	1.50	n.s.
	Plant : Lines	15	2890.09	13.48	***
	Samples : Plants	22	214.46	2.39	**
	Spikes : Samples	22	128.81	1.44	n.s.
	Flowers : Spikes	64	89.70	2.39	***
	Anthers : Flowers	92	37.51		
	Total	217			

stage these differences were just significant at the 5 percent level.

While this analysis of variance gives a general picture of the sources of variation in meiosis in these lines, the lines may have their own specific patterns which could be seen only if the data for the lines were analysed separately. Certain significant variations which might have existed at a comparatively low level in individual lines were probably enhanced in collective analysis, while others may have been cancelled out. Differences of this sort can be seen by a comparison with the analysis of variance for line 20 given earlier in Table 13. There, samples (spikes taken on different dates) within plants were significant only at tetrad, anaphase I and metaphase I stages, while in the collective analysis of the three lines this source of variation became significant at all six stages. Also in line 20 florets within a spike were the major source of variation at all the stages except anaphase I, while collective analysis of the three lines indicated significance at this stage as well. This analysis indicates that samples within plants and florets within spikes were the two major sources that contributed to variability at most of the meiotic stages. The different plants of a line did not differ significantly from one another in meiotic variations as shown by the nonsignificant F values at all the meiotic stages (in line 20, Table 13) and at four out of six stages in combined analysis of the three lines (Table 14). In the collective analysis, the three lines differed significantly only at the tetrad stage. Significant F values for samples (spikes taken on different dates) within plants at metaphase I, anaphase I and tetrad stages in line 20 and at all the six stages in the combined analysis for three lines plainly show the influence of external environment on meiosis at all the stages in these lines.

The highly significant variation of florets within a spike at all six meiotic stage when compared to nonsignificant F (except at anaphase I, which was significant at 5 percent) values obtained for spikes within samples (at five stages) clearly points to the fact that external environment, if if at all, is only a minor factor contributing to meiotic variability within spikes. The high degree of meiotic variability from floret to floret within a spike can be attributed to a high degree of genetic variability or to differences in internal environment (Pao and Li, 1948) or both. This conclusion from statistical analysis is supported by cytological observations of PMC with variable chromosome numbers, extra chromosomes and chromosome fragments, which indicated that any two PMC in any one anther could be different in their chromosome content.

Rust Reactions

During the spring of 1959 selfed and backcross (with Cheyenne) progenies of the plants, most of which had been studied cytologically, were tested against a few of the more important races of leaf rust (1, 5, 9, 11, 15, 122) and stem rust (11 and 15B). Rust tests were conducted in the immature plant stage by hypodermic inoculations made in the greenhouse from March 7 to April 4, about 6 to 9 weeks before heading took place. Rust reactions were recorded after 14 days of inoculation. At this stage of plant growth all the lines were completely susceptible to stem rust races 11 and 15B. However, some of these lines are known to have a fair degree of mature plant resistance against at least some races of stem rust under field conditions. While plants in most of these lines gave only completely susceptible reactions, all the plants in a few of the lines (13, 20) produced a few resistant

pustules among the numerous highly susceptible ones. This presumably indicates that the inoculum contained a slight mixture of spores from races other than the one being tested, and that resistant pustules resulted from a reaction to races other than 11 and 15B.

Lines differed considerably in degree of resistance against the different leaf rust races tested as shown in Table 15. Ten progeny plants from each of the two meiotically regular plants of line 7, cross IV, showed uniform and complete resistance to all the races (1, 5, 9, 11, 15, 122), with no pustules whatever developing on any of the plants. The uniformity of the reaction might be expected, since the meiotic index of the parent plants was very high, that of plant 58-33 being 98.50 percent (2; 99-98) and that of plant 85-35 being 95.03 percent (31; 100-69), with some spikes of the latter as high as 98.86 percent (7; 100-98). Different and slightly variable reactions against different leaf rust races were given by 55 F_1 plants of the backcross of these same two plants (58-33 and 58-35) to Cheyenne. They were highly resistant to races 1 and 9, mostly producing either just flaking or the 1-type of pustule which never developed further. However, some of the plants showed a difference in reaction depending upon location on the leaf, giving 0-type at the leaf base and 3-type at the tip (even on the same leaf). The F_1 plants showed somewhat less resistance to race 15, the pustules produced varying from 1 to 3 in type, dependent at least partly on position on the leaf. The plants were susceptible to races 5, 11, and 122, but the pustules formed were smaller than those of the susceptible control, Cheyenne. These reactions of the apparently uniformly heterozygous F_1 plants indicate that genes controlling resistance to races 1 and 9 are dominant, those controlling resistance to race 15 incompletely dominant, and those involved in races 5,

Table 15. Rust reactions of the 16 derived lines against leaf rust races 1, 5, 9, 11, 15, and 122.

Crosses	Line	No. Pl.	2n=	M. index	Leaf Rust Races					
					9	15	5	122	1	11
Cheyenne (control)		2	42(2)*	99.19	S	S	S	S	S	S
Cross I	Line 1	3	42(3)	96.05	S	S	—	S	—	—
	3	3	42(3)	96.28	S	S	—	—	—	—
Cross III	5	3	42(3)	98.91	S	S	—	S	—	—
	6	3	42(3)	98.78	S	S	—	S	—	—
	10	3	42(3)	98.54	S	S	—	S	—	—
	13	3	42(3)	97.77	S	S	—	S	—	—
	21	3	42(3)	99.29	S	S	—	—	—	—
Cross II	4	3	42(3)	94.55	S	S	—	—	—	—
	2	3	42(3)	84.36	S	S	—	—	—	—
Cross V	15	3	42(3)	95.65	S	R(2)	—	—	—	—
	14	3	42(3)	92.02	0	S	—	—	—	—
Cross IV	7	5	42(4)	95.89	0	0	0	0	0	0
			43(1)	52.67	—	—	—	—	—	—
Cross VII	11	5	42(5)	97.02	R	S	—	S	—	—
	20	5	42(5)	85.50	Seg.	S	—	—	R	S
	8	8	42(6)	68.47	R	S	S	S	R	—
			41(2)	50.79	Seg.	S	—	—	—	—
Cross VI	12	5	42(4)	54.70	Seg.	S	S	S	0	—
			41(1)	54.31	Seg.	S	S	—	—	S

0 High resistance
R Resistant
S Susceptible
Seg. Segregating
* Two plants of Cheyenne were examined and both had 2n = 42 chromosomes.

11 and 122 recessive (or with a very slight degree of dominance). Complete resistance is produced by all the genes when homozygous, but their effective expression appears somewhat variable when they are heterozygous. This variable expression may be affected by environment, including such factors as nutrient materials available (suggested by differing reactions on different portions of the same leaf). In this line (7) a number of genes for leaf rust resistance derived from T. timopheevi have obviously been incorporated into the genome and their transmission has reached stability.

All nine lines in crosses I, II and III were susceptible to races 9 and 15 of leaf rust (at the immature plant stage). These lines were characterized by comparative regularity and high meiotic indices (above 92 percent for all except line 2, where it was 84.36 percent). Genes for leaf rust resistance were obviously eliminated as the genomes became stabilized.

In some other lines, resistance to one leaf rust race became incorporated into a stabilized genome with a high meiotic index. Plants of line 15 from cross V (with a meiotic index of 95.05 percent) were susceptible to race 9 but resistant to race 15. This resistance was about the 1-2 type, and so different from the resistance of line 7 (cross IV) to race 15. However, the gene(s) concerned show partial dominance, since the F_1 hybrids with Cheyenne gave an intermediate reaction against race 15. The other line, 14, from cross V (with a meiotic index of 92.02 percent) was susceptible to race 15, but resistant to race 9. The F_1 hybrids of this line with Cheyenne were also resistant, indicating dominance of the gene(s) concerned and possible identity with the gene(s) in line 7 (cross IV) for resistance to race 9. The one meiotically stable line (11) (with a meiotic index of 97.02 percent) of cross VII was also susceptible to race 15 and resistant to race 9,

but the F_1 hybrids of the backcross to Cheyenne gave an intermediate type of reaction. The gene(s) concerned have incomplete dominance and so differ from the completely dominant gene(s) for resistance to race 9 in lines 7 and 14.

The meiotically very irregular lines 8 and 20 of cross VI were susceptible to race 15, and lines 8 and 12 were susceptible also to races 5 and 122. As shown in Table 16 they showed resistance or variable segregation for resistance to race 9 of the same type just described for line 11 of cross VII. In line 8 selfed progeny of 15 plants and backcross progeny of 77 plants from three 42-chromosome plants showed a resistant or intermediate reaction. But one plant 58-36 (2n = 41) with a meiotic index of 46.92 percent gave 2 susceptible and 15 resistant or intermediate type backcross progeny plants although all the five selfed progeny were resistant. Backcross progeny of the 42 chromosome plants of line 8, showed the same intermediate type of reaction found in line 11 of cross VII. In line 20, with a meiotic index of 85.50 percent, one of the 39 offspring from three 42-chromosome plants was susceptible, the other 38 being resistant. Presumably, the chromosomes on which the resistance is located usually segregate regularly (most of the aberrations being produced by other chromosomes), but the one susceptible plant presumably resulted from a failure of disjunction or other irregularity of the usually regular chromosome carrying the resistance. This interpretation is borne out by the appearance of 2 susceptible plants among the 152 F_1 hybrids of the backcross of these same plants to Cheyenne, the remaining 150 showing the expected intermediate type of resistance. The two susceptible F_1 plants were both derived from the backcross of the same plant 58-100, but a different plant from the one (58-97) which produced the single susceptible

Table 16. Reactions of the selfed and backcross progeny of individual plants of meiotically unstable lines, 8, 12 and 20, against leaf rust race 9.

Cross	Line (Meiotic index)	Plant No.	2n	M. index (%)	No. of progeny plants: Selfed R* or X**	Selfed S	Backcross R or X	Backcross S
VI	Line 8 (68.47%)	58-36	41	46.92	5	-	15	2
		58-37	42	58.32	5	-	42	-
		58-38	42	59.59	5	-	19	-
		58-42	42	—	5	-	16	-
		Total			20	-	92	2
	Line 20 (85.50%)	58-96	42	85.81	5	-	30	-
		58-97	42	88.00	16	-	33	2
		58-100	42	80.68	17	1	87	-
		Total			38	1	150	2
VII	Line 12 (54.70%)	58-56	42	35.50	4	-	47	4
		58-57	42	71.52	5	-	20	3
		58-58	42	61.33	4	-	15	1
		58-59	42	52.15	5	-	21	-
		58-60	41	54.31	3	2	7	19
		Total			21	2	110	27

*R or X, resistant or intermediate.
**Susceptible.

offspring.

All 18 progeny of 42-chromosome plants in line 12 were resistant to race 9, again suggesting a comparatively regular segregation of the chromosomes carrying the resistant gene. But the appearance of 8 susceptible plants among the 103 with intermediate resistance in the 111 hybrids of the backcross of the same plants to Cheyenne suggests either that the chromosome carrying resistance is subject to irregularities (presumably pairing difficulties) when combined with the Cheyenne genome or that this irregularity occurs at low frequency and could be picked up only in backcross progeny. This in turn strongly suggests that either a whole chromosome or a large chromosome segment is involved. The single monosomic plant (58-60) segregated

in a manner suggesting that it was monosomic for the chromosome carrying resistance, although the number of plants involved is too small to give dependable ratios. Of the five selfed offspring, 3 were resistant and 2 susceptible, while of the 26 backcross progeny, 7 had intermediate resistance and 19 were susceptible.

Correlations

In order to see how irregularities at one stage of meiosis were correlated with those at other stages, total correlations were worked out from data on the highly irregular lines 8, 12 and 20. Table 17 gives the correlations of the spike means for these three lines separately, the correlations obtained thus being pooled within spike correlations. Highly significant correlations were obtained between irregularities at all the stages, except anaphase I, in all the lines. In line 20, irregularities at anaphase I were also highly correlated with those at other stages. In line 8, anaphase I irregularities had a significant but low (0.45*) correlation with metaphase II irregularities, but had highly significant correlations with all other stages. In line 12 irregularities at anaphase I had nonsignificant correlations with those at metaphase I, metaphase II and anaphase II, but a high correlation (0.64**) with those at dyad stage and a significant correlation of 0.31* with those at tetrad stage.

A possible explanation for non-significant or low correlations of irregularities at anaphase I with those at metaphase I in line 12 is that anaphase I irregularities may have resulted primarily, not from lagging or division of unpaired univalents, bivalents off the spindle, etc., but from difficulties in disjunction of apparently normally paired chromosomes. These

Table 17. Correlations between total abnormalities at six meiotic stages in lines 8, 12 and 20.

		Anaphase I	Dyad	Metaphase II	Anaphase II	Tetrad
Line 8	Meta-I	0.78***	0.86***	0.83***	0.48***	0.96***
	Anap-I		0.81***	0.46*	0.56***	0.69***
	Dyad			0.75***	0.82***	0.87***
	Meta-II				0.92***	0.95***
	Ana-II					0.96***
Line 20	Meta-I	0.78***	0.87***	0.94***	0.96***	0.97***
	Ana-I		0.94***	0.83***	0.82***	0.80***
	Dyad			0.87***	0.88***	0.92***
	Meta-II				0.98***	0.95***
	Ana-II					0.96***
Line 12	Meta-I	0.25n.s.	0.39**	0.76***	0.80***	0.81***
	Anap-I		0.64***	0.26n.s.	0.31n.s.	0.31*
	Dyad			0.80***	0.73***	0.51***
	Meta-II				0.88***	0.91***
	Ana-II					0.91***

Pooled within spike correlations.

*Probability 0.05

**Probability 0.01

***Probability 0.001

might include chromatin bridge configurations and consequences there of, scattering of disjoined and non-disjoined bivalents and undivided univalents (Plate III, A, B and C), all of which would result in a high percentage of abnormalities at the dyad stage, and so would result in the highly significant correlation (0.64**) actually shown between these two stages.

It is likely some of the irregular chromosomes and chromosome pairs which formed micronuclei at dyad stage rejoined the rest of the chromosomes and behaved more or less regularly so that nonsignificant correlations were obtained between irregularities at anaphase I and those at anaphase II and metaphase II. Some of the univalents that divided at anaphase I would be irregular at anaphase II and result in a higher percentage of micronuclei at the tetrad stage. This behavior is similar to that reported by Sanchez-Monge and Mackey (1948) that micronuclei formed by chromosomes left out of the daughter nuclei at telophase I may later reform into chromosomes and participate normally in the second meiotic division. Sears (1952) also concluded "evidently some of the chromosomes excluded at TI either are included in one of the TII groups or participate in the second division as laggards."

Differences in correlation relationships between the lines show that even if these three lines are broadly similar in meiotic instability, there are significant differences, probably in the kind of structural alterations that make the anaphase I correlations variable (within certain limits) from line to line. Also the range of variability within lines at anaphase I indicates that this is the most sensitive stage to changes in external environment. For both these reasons, which differ in their effects on different lines, irregularities during successive stages may differ in degree

of correlation. In one line, irregularities at anaphase I and dyad stages may appear to decrease at later stages, while in others the number may remain more or less unchanged.

DISCUSSION

Most of the previously reported studies on the meiotic behavior of wheat varieties or lines have concluded that the pattern and range of variation were more or less constant for a particular genotype. Morrison and Unrau (1952) found that the meiotic behavior was constant in each of 20 monosomics of wheat and that there were no significant differences between different plants of a monosomic line or different florets of a single plant. This constancy in range of variation has often been assumed, without testing, although it may not hold true for all types of variations and under all environmental conditions. Blier (1930), as early as 1930, studying plants kept at different temperatures, found a higher percentage of chromosome irregularities in the plants kept at higher temperatures.

In this study, statistical analysis of the meiotic behavior of the three highly irregular lines (8, 12, 20) showed that meiotic variability was affected both by external and internal environmental or genetic factors. The effect of external environment is shown by the highly significant variations found in different spikes from the same plant taken at different times (samples within plants). The highly significant variation found in different florets of the same spike (florets within spikes) shows the effect of internal environment or of genetic instability. Similar significant variations were found by Pao and Li (1948) in their studies of the effect of high temperature on meiosis in common wheat. Highly significant variations found between

spikes of the same plant were attributed to external temperature differences, and equally highly significant differences between PMC of the same anthers to the non-homogeneous flow of heat to different cells and to differences in sensitivity of the cells to heat.

Detailed study revealed evidence that somatic aberrations were occurring in some of the lines and were operating against selection for meiotic stability. Aneuploid plants with 2n = 41 and 43 chromosomes were observed, both in lines with a normally high meiotic index and in others with irregular meiosis. Such aneuploid plants apparently arose from both somatic and meiotic abberations in which whole chromosomes were gained or lost. If the gain or loss happened to involve whole chromosomes from T. timopheevi or chromosomes with translocated segments from T. timopheevi carrying genes for rust resistance, segregation for rust resistance would be expected to result. Such segregates were found in the selfed and backcross progenies of certain plants from lines 8, 12 and 20.

Variations in chromosome number and presence or absence of chromosome fragments of variable size even within a smear from an individual anther, suggest that some of these chromosomal abnormalities were arising during mitosis. Some of these were probably similar to the irregularities which Morrison (1954) observed to arise from a dicentric chromosome in an F_2 interspecific hybrid of wheat. The dicentric originated from breakage and fusion of two nonhomologous univalent chromosomes. In somatic cells of the root tip, anther wall and ovary wall, few bridges were observed, evidence that the dicentric must be able to survive in the somatic tissue because of the parallel separation of chromatids. Aberrations other than bridges were observed in root tip cells. At meiosis the dicentric usually synapsed with the two

pairs of partial homologue, forming a chain or ring of five. In one spike, however, loss of one chromosome arm caused trivalent formation. Usually the dicentric formed a bridge which broke at anaphase I, but sometimes it broke up into small chromosomes, without having formed a bridge. Irregularities of this sort would account for some of the variability in the number of cells with chromatin bridges at anaphase I and anaphase II in some plants or spikes. Other structural alterations were undoubtedly caused by heterozygous inversions of variable size which produced bridges and acentric fragments.

In a number of lines end to end metaphase I pairing of a number of chromosomes indicated reduced chiasma frequency, presumably the consequence of reduced homology which may have resulted from translocations involving chromosome segments from T. timopheevi. Some of these structural alterations are probably self-prepetuating, while others may be arising spontaneously and irregularly from some sort of genetic instability, some of which may be especially sensitive to changes in external environment. Deficiencies or duplications of somatic origin might make meiosis in the cells affected more sensitive to environment. Viable gemetes produced by such PMC might give rise to aneuploid plants of various sorts. Some of the plants with 2n = 42 chromosomes in lines 8, 12 and 20 might not be true disomics, but instead monosomic for one and trisomic for another chromosome, and still another plants with 2n = 42 chromosomes could represent different aneuploid combinations. Such plants have actually been obtained by Person (1956) in wheat. Plants of this sort would be highly irregular in meiosis, with low meiotic indices in the general range found for 15 of the plants with 2n = 42 chromosomes in these three lines. Thus in line 12 the meiotic index of four plants with 2n = 42 chromosomes was 54.70 percent (71; 96-4) as compared to 54.31

percent (19; β1-21) for a monosomic plant. Thus the degree of irregularity in the apparent disomic plants is comparable to that in the monosomic, lending some support to (or at least not disproving) the suggestion that some might actually be complex aneuploids. The monosomic itself could in fact be a varient combination of this sort and not a true monosome.

Only tentative conclusions can as yet be made about the nature of the genetic transfer that has taken place in these lines. Probably more than one type of transfer is involved in different lines. The usual gene exchange by crossing over probably takes place between chromosomes of the A genome of T. timopheevi and their respective homologues in the A genome of T. aestivum so that incorporation of genes for rust resistance into the T. aestivum genome should take place readily if these genes are located on chromosomes of the A genome. Transfer of genes for rust resistance by crossing over and recombination is less likely if they are located in the G (or B?) genome of T. timopheevi, since very little, if any, pairing takes place with the more or less corresponding G genome of T. aestivum. It could still take place, however, if even occasional pairing occurs. Undesirable T. timpheevi characteristics also incorporated into the genomes by crossing over should be gradually eliminated by repeated back crossing. Therefore, if genes for rust resistance have been transferred into T. aestivum by crossing over, backcrossing and selection for T. aestivum characteristics might be expected to have already eliminated most of the undesirable T. timopheevi characteristics which were also transferred into these lines in the same way. There is some question, however, as to what extent the undesirable characteristics present in these lines have come from T. timopheevi but they may be the result of an interaction between the genomes of the two species. The long lax spikes in

these lines may well result from a complimentary effect of the genes producing the normal compact head of T. aestivum and those for the small compact heads of T. timopheevi. A similar sort of interaction accounts for the occurrence of both spring and winter types among T. aestivum-like segregates studied by Semenuik (1947) from a cross of Steinwedel and T. timopheevi, where both parents are spring wheats.

Genome transfer could also have taken place by the substitution of one or two T. timopheevi chromosome pairs, so that a line may have 19_{II} or 20_{II} of T. aestivum and 2_{II} or 1_{II} of T. timopheevi. Chromosome substitutions between different species have been obtained by several workers. Kattermann (1938) and O'Mara (1947) substituated a rye chromosome pair, which carried a gene determining hairy-neck character, for chromosome IX of wheat. Wheat plants with the substituted pair of rye chromosomes bred more or less true for the hairy-neck character because all chromosomes had homologues for synapsis. But Taylor (1934) found occasional asynapsis or faulty disjunction of the rye chromosome pair, so that a small percentage of the progeny always segregated for hairy-neck character. A similar situation may be involved in lines 8, 12 and 20 in which plants with 42 chromosomes produced selfed and backcross progenies with a small percentage of susceptible plants. Possibly a substituted T. timopheevi pair of chromosomes undergoes occasional irregularities to cause this segregation.

Stable line 7, with a high degree of T. timopheevi type of resistance to several races of leaf rust, probably carries one or more whole chromosome pairs of T. timopheevi (which behave regularly in meiosis) or chromosomes carrying translocations of large or small segment(s) from the T. timopheevi genome. Depending on the size of the chromosome or segment and the number

of genes that are located on it (besides the one(s) for rust resistance), other T. timopheevi characters might be linked with it.

A study of the F_1 progeny of a backcross of these to Cheyenne wheat is now in progress, to obtain evidence from pairing relationships of the genomes as to structural alterations or chromosome substitutions in these lines. Identification of the particular chromosomes involved in these changes may later be possible by monosomic analysis of these lines.

CONCLUSION

One line 7, from cross IV (1279A 9-III-16 x Nebred) was found to combine a high degree of leaf rust resistance with an equally high degree of meiotic stability. It was completely resistant to leaf rust races 1, 5, 9, 11, 15, and 122 and had a meiotic index of 95.89 percent (66; 100-69). Presumably a chromosome substitution or translocation of a chromosome segment from T. timopheevi was involved.

The remaining eleven lines with reasonably high meiotic stability (meiotic index 90% to 100%) had lost much or all of the leaf rust resistance of T. timopheevi, suggesting a loss of most or all of the T. timopheevi genome. The five lines (5, 6, 10, 13 and 21) with meiotic regularity comparable to that of the T. aestivum variety Cheyenne (meiotic index 99.19%) were susceptible to both leaf rust races 15 and 9. Presumably little or none of the T. timopheevi genome remained to cause irregularity. The five lines (1, 3, 4, 14, and 15) with somewhat lower meiotic stability, comparable to that of Minturki (meiotic index 94.65%), which is a variety derived in part from a tetraploid-hexaploid cross, have retained resistance to one race of leaf rust; race 9 for four of the varieties (1, 3, 4, 14) and race 15 for

the other one (15). The association of leaf rust resistance in these lines with a slightly lowered meiotic stability suggests that the transfer from T. timopheevi may involve at least segments of T. timopheevi chromosomes, which result in some degree of meiotic irregularity. Unlike other three lines from two crosses involving Shands 473, line 11 was equal to Cheyenne in Meiotic regularity and appeared to breed true for resistance to race 9 of leaf rust.

Of the four lines with irregular meiosis, three (8, 12 and 20) segregated for resistance against leaf rust race 9. Lines 8 and 12 were also unstable in chromosome number. In all the three lines it was found that external environment and internal environment or genetic factors influenced the meiotic irregularities. In general, meiotic irregularities at different stages were highly correlated.

SUMMARY

Sixteen hybrid strains derived from seven different crosses of Triticum timopheevi with either T. aestivum or with derived aestivum-types from earlier interspecific crosses were studied for their rust reactions, chromosomal stability and meiotic behavior. T. aestivum varieties Cheyenne and Minturki, and T. timopheevi were included as controls. Rust reactions of some of these lines were correlated with their meiotic behavior and chromosome numbers. Meiotic irregularities were studied and recorded at six stages, viz., metaphase I, anaphase I, dyad, metaphase II, anaphase II and tetrad stage. Means were computed for different florets of the same spike (florets within spikes), for different spikes of the same plant (spikes within plants), for different plants of the same line (plants within lines) and for each line

as a whole. Thus over all mean values for the sixteen lines and three controls could be compared at all the six meiotic stages.

Six lines (lines 5, 6, 10, 13 and 21 from cross III and line 11 from cross VIII) were comparable in meiotic regularity with the more regular of the controls, Cheyenne, which had a meiotic index of 99.19 percent (27; 100-98). Six lines (1 and 3 of cross I, line 4 of cross II, line 7 of cross IV and lines 14 and 15 of cross V) were at least as regular as the less regular of the controls, Minturki, with a meiotic index of 94.65 percent (23; 98-88). The remaining four lines (line 2 of cross II, line 12 of cross VI and lines 8 and 20 of cross VII) were all irregular in meiosis.

In lines that had not yet attained a stability comparable to that of Cheyenne, the range of variability in meiosis was rather wide. Some irregularities were, probably, due to instability in preceding mitotic divisions.

Lines with less regular meiosis had meiotic indices ranging from 54.70 percent (in strain 12, cross VI) to 85.50 percent in strain 20, cross VII. The range of variability in the lines was very great (from 4 to 96% in one instance), which tended to minimize the differences between the lines. Statistical analysis showed that only at tetrad stage were these differences between the lines significant. The same lack of significance applied to differences between plants in the same line. Different spikes of the same plant taken at different times (samples within plants) in these three lines (8, 12 and 20) showed significant differences at most stages, thus indicating that in these lines meiosis was under the influence of the external environment. Different spikes taken from the same plant at the same time (spikes within samples) did not differ significantly. The effect of internal environment or of genetic instability was shown by the significant differences found

between different florets of the same spike (florets within spikes). Highly significant correlations were obtained in lines 8 and 20 between irregularities at any one stage of meiosis with those at the other five stages. The same was also true in line 12, except that anaphase I irregularities had non-significant correlations with those at metaphase I, anaphase II, and metaphase II. In this line, anaphase I irregularities may have resulted primarily, not from lagging or division of unpaired univalents, bivalents off the spindle, etc., but from difficulties in disjunction of apparently normally paired chromosomes. These were regular in subsequent behavior, but gave a non-significant correlation between anaphase I and metaphase I irregularities. It is likely some of the disjoined or non-disjoined chromosomes and chromosome pairs which as a result of scattering at anaphase I formed micronuclei at dyad stage, rejoined the rest of the chromosomes and then behaved more or less regularly so that nonsignificant correlations were obtained between irregularities at anaphase I and those at anaphase II and metaphase II.

One line (7) with a high meiotic index (95.89%) was highly resistant to all the six races of leaf rust (1, 5, 9, 11, 15 and 122) against which it was tested. Presumably this line carried a chromosome pair or translocated segment from T. timopheevi. Leaf rust reactions of selfed and backcross progenes of this line (with Cheyenne) indicated that genes controlling resistance to races 1 and 9 were dominant, those controlling resistance to race 15 incompletely dominant, and those involved in races 5, 11 and 122 of leaf rust were very slightly dominant. In homozygous condition these genes resulted in complete resistance, but in heterozygous condition their expression was variable.

All other lines (except line 11) which had attained the highest degree

of meiotic stability had lost resistance to all the races of leaf rust against which they were tested. Other lines with a slightly lower meiotic index (comparable to Minturki), had retained resistance against one of the leaf rust races, but none were resistant to both races 9 and 15.

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APPENDIX

EXPLANATION OF PLATE I

Triticum aestivum var. Cheyenne, plant 58-84, spike 8-158(a)

A. smear a-2: Diakinesis with $18_{II} + I_{III} + I$ multivalent. (I= univalent; 2=trivalent; 3= multivalent).

B. smear a-4: Diakinesis with $18_{II} + 1_{I} + I_{V}$ (I= univalent; 2= pentavalent)

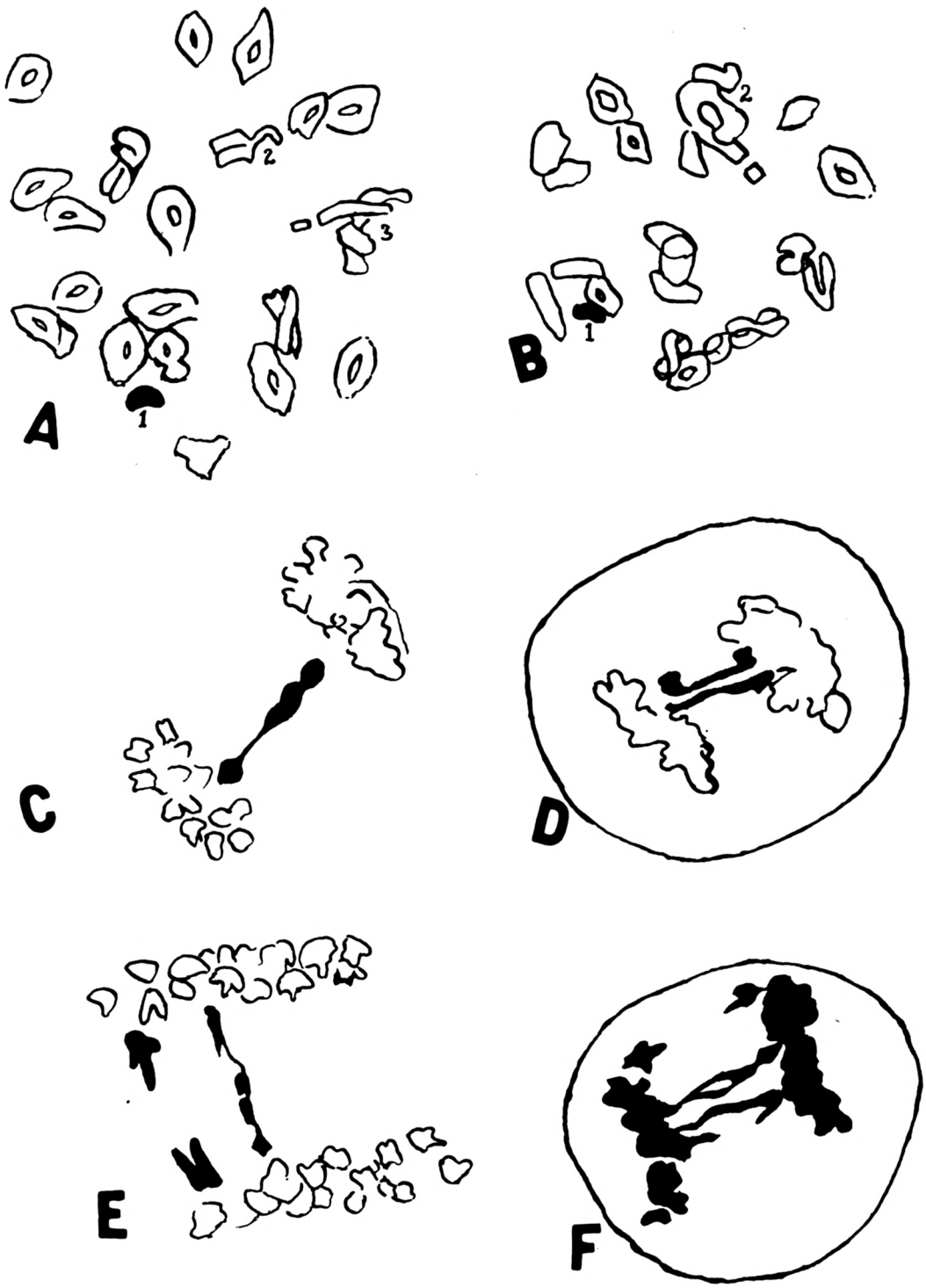
C. smear a-3: Late anaphase I with one chromatin bridge probably from the multivalent in A and B.

D. smear a-3: Anaphase 1 with 2 intact bridges, probably the 4 in (C) above make two separate bridges.

E. smear a-1: Anaphase 1 with one intact bridge involving four chromosomes and second bridge(?) broken at early anaphase 1

F. smear a-1: Anaphase 1 with two intact bridges and a third which has broken early.

PLATE I



EXPLANATION OF PLATE II

A. Line 1 A. Plant 58-2, spike 8-221, smear a-4: Diakinesis showing 21_{II}.

B. Line 1 B. Plant 58-2, spike 8-336, smear a-3: Prometaphase showing 21_{II}.

C. Line 3. Plant 58-11, spike 8-271, smear a-2: Metaphase I showing one end to end bivalent off the metaphase plate.

D. Line 1. Plant 58-2, spike 8-371, smear a-5: Anaphase I showing chromosomes delayed in division and one broken bridge with a fragment.

E. Line 3. Plant 58-11, spike 8-271, smear a-2: Late anaphase I showing a late dividing univalent chromosome.

PLATE II

EXPLANATION OF PLATE III

Line 12

A. Plant 58-59, spike 8-334: Anaphse I withscattering of non-disjoined bivalents, divided univalents, and undivided univalents.

B. Plant 58-59, spike 8-334: Anaphase I showing scattering of chromosomes.

C. Plant 58-60, spike 8-167(c) smear c-2: Anaphase I with two intact chromatin bridges.

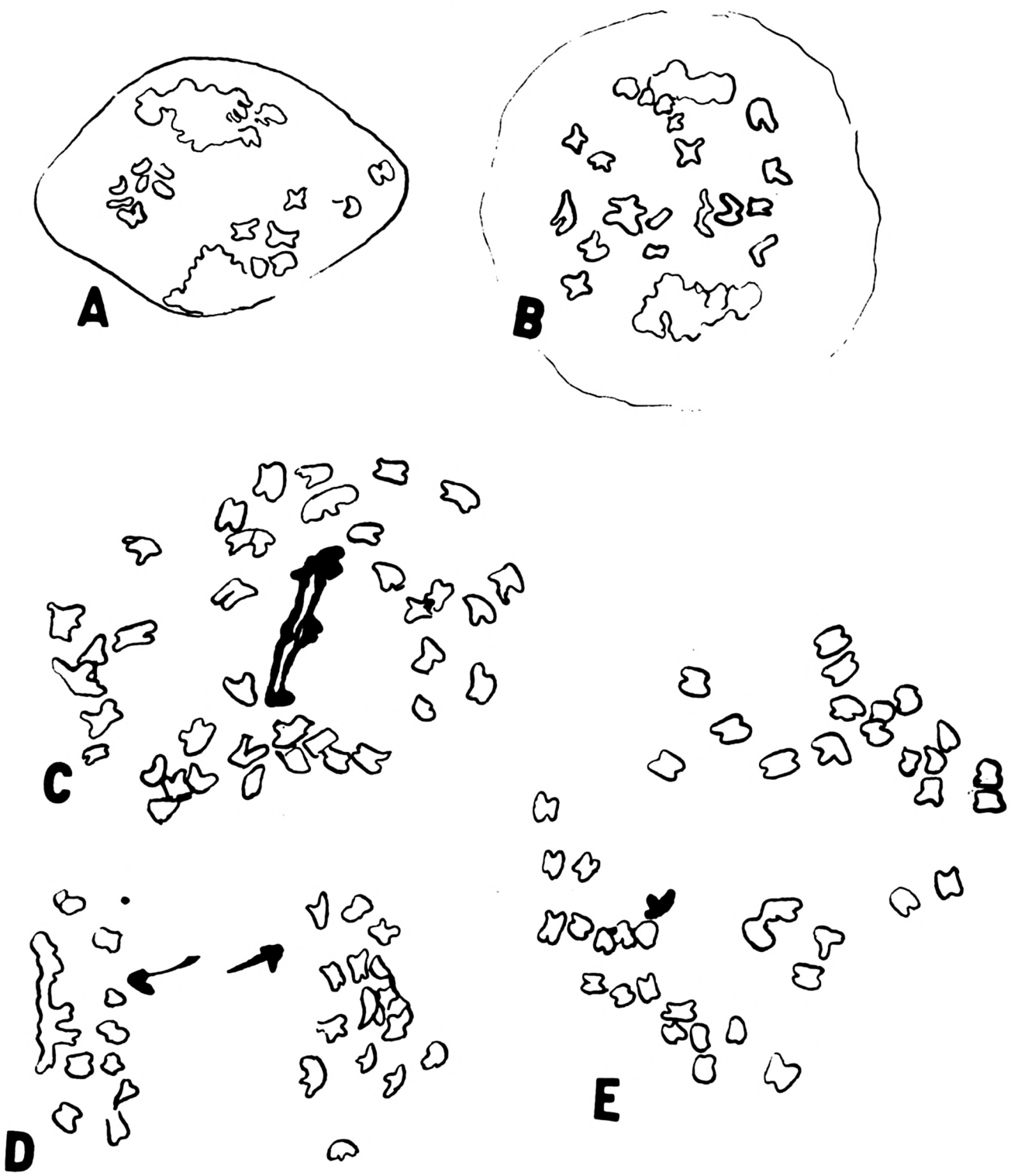
Line 8

D. Plant 58-40, spike 8-280: Anaphase I with one broken bridge and bridge and an acentric fragment.

Line 12

E. Plant 58-60, spike 8-167, smear a-5: Anaphase I of a monosomic plant with an undivided univalent.

PLATE III



EXPLANATION OF PLATE IV

Line 20, plant 58-99

A. spike 8-216(a) smear a-1: Diakinesis showing 20_{II} plus 2 small univalents or fragments.

B. spike 8-216(a) smear a-2: Metaphase I with 21_{II}

C. spike 8-216(b) smear b-2: Metaphase I with 21_{II} including 2 end to end bivalents.

D. spike 8-156(a) smear a-5: Metaphase 1 with 6_{II} + 10_{I} = 22 chromosomes.

E. spike 8-156(a) smear a-5: Metaphase I with 8_{II} + 12_{I} = 28 chromosomes.

F. spike 8-196(a) smear a-1: Metaphase I with 22_{II} = 44 chromosomes including three end to end pairs, one disjoining early.

PLATE IV

EXPLANATION OF PLATE V

Line 12

A. plant 58-57, spike 8-195(c), smear c-1: Metaphase I with 21_{II}.

B. plant 58-57, spike 8-195(c), smear c-1: Metaphase I with a number of unpaired univalent chromosomes and a chain of (3?).

C. plant 58-57, spike 8-195(c), smear c-1: Metaphase I with about 10 univalents.

D. plant 58-59, spike 8-196(a), smear a-2: Metaphase I with only $20_{II} = 40$ chromosomes.

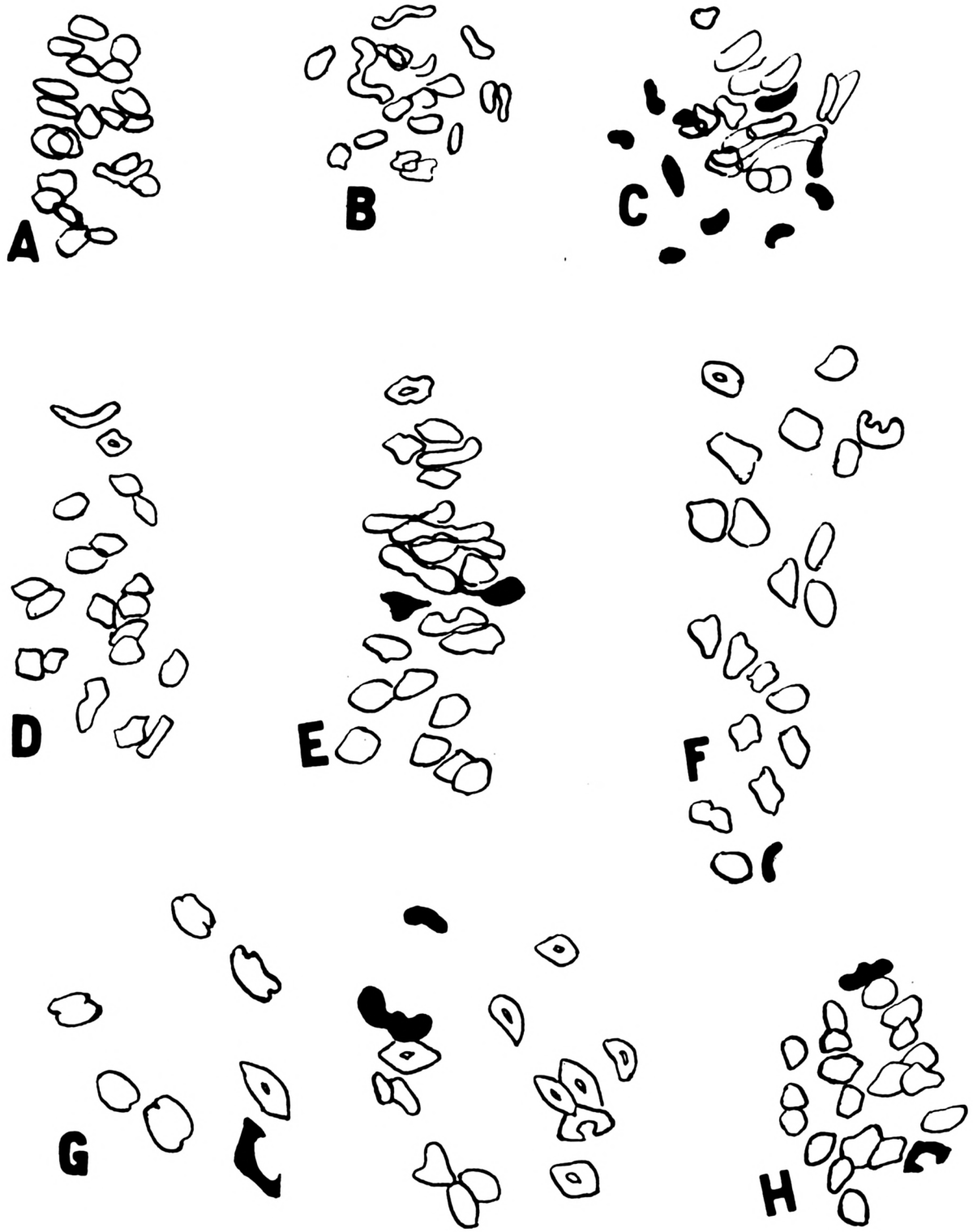
E. same as (D) but a different floret: Metaphase I with $20_{II} + 2_{I}$ (probably one pair disjoined early).

F. plant 58-60, spike 8-167, smear a-5: Metaphase I with $20_{II} + 1_{I}$, including one open bivalent. (a monosomic plant).

G. same as (F): Metaphase I with $20_{II} + 1_{I}$, including 3 open bivalents.

H. plant 58-59, spike 8-334, smear a-4: Metaphase I with 21_{II}, including 2 open bivalents.

PLATE V



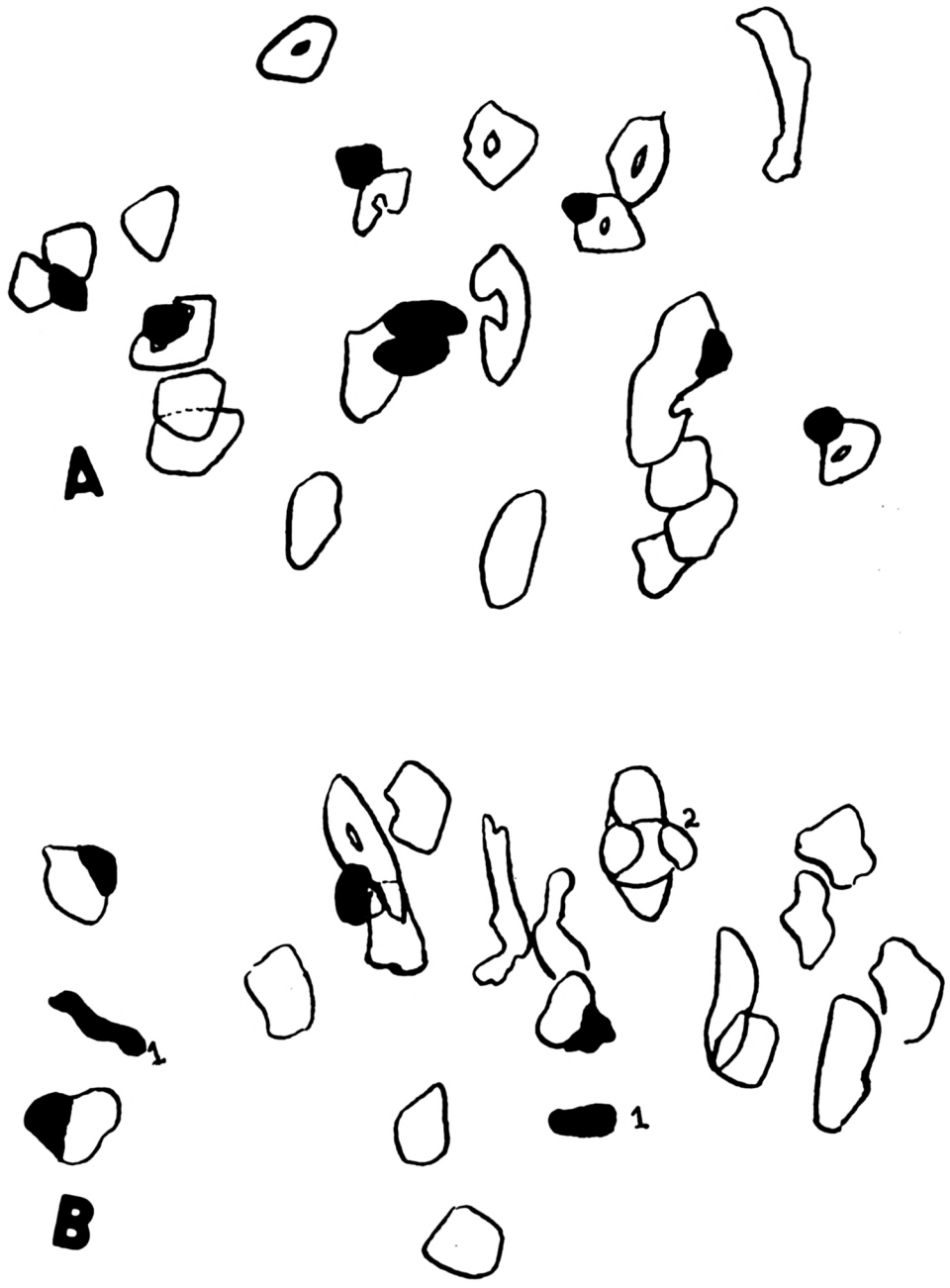
EXPLANATION OF PLATE VI

Line 12, plant 58-56, spike 8-166b and smear b-1:

A. Prometaphase with 20_{II} + 8 extra chromosomes or chromosome fragments of different sizes associated with some of the bivalents.

B. Prometaphase with 17_{II} + 2_{I} + 1_{IV} + 4 fragments (1 = univalents: 2 = quadrivalent).

PLATE VI



EXPLANATION OF PLATE VII

Line 12, plant 58-56, spike 8-166(b) smear b-1:

A. A 42-chromosome plant showing metaphase I with $18_{II} + 2_{I} + 3$ fragments; one bivalent, two fragments and two univalents off the plate, one fragment possibly associated with another chromosome pair.

B. same smear as (A), metaphase I with $20_{II} + 2_{I} + 4$ fragments; univalents from an early disjoining pair, fragments associated with other bivalents.

PLATE VII

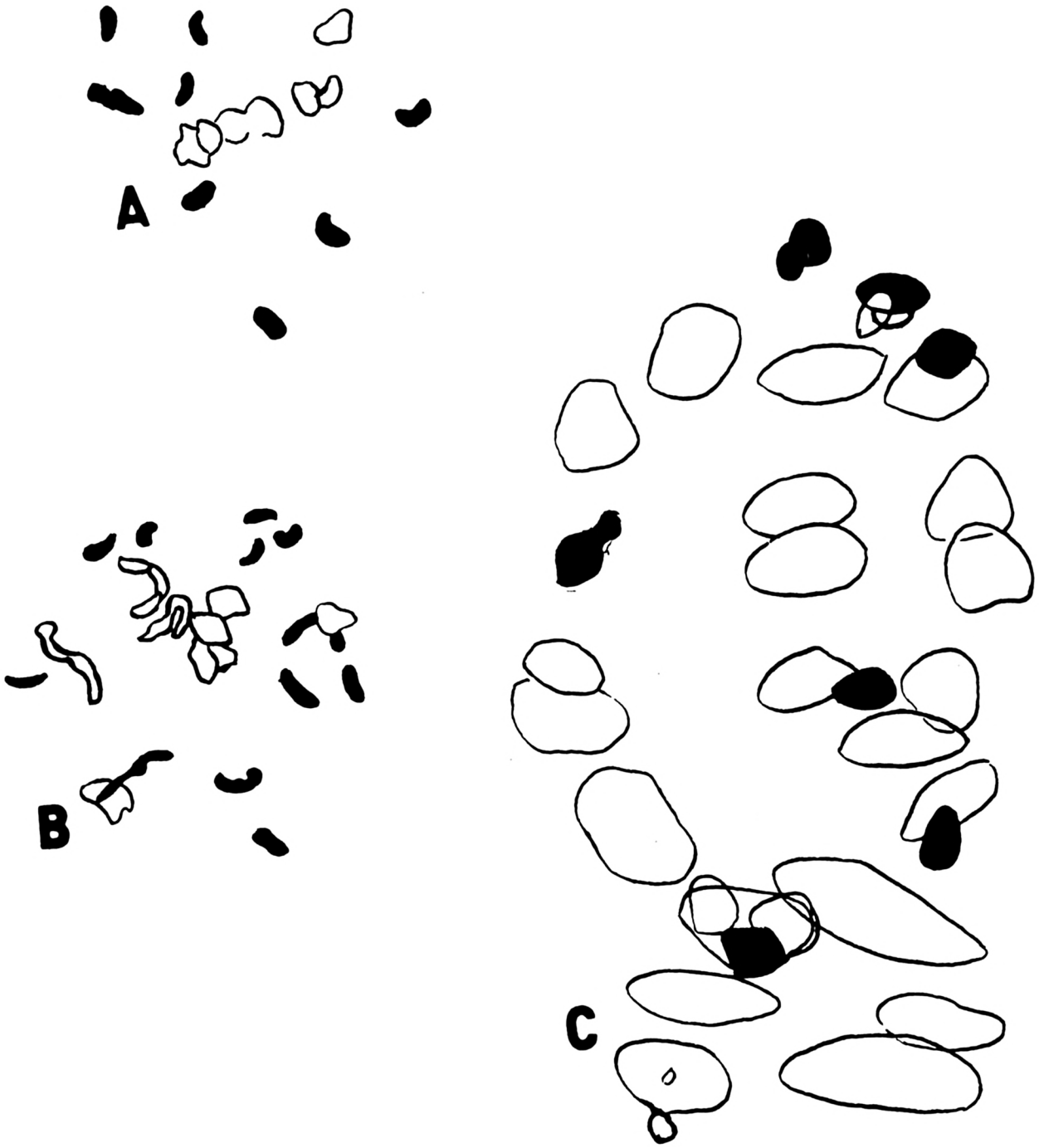
EXPLANATION OF PLATE VIII

A. Line 20, plant 58-99, spike 8-156(a), smear a-8: Metaphase I with $7_{II} + 9_{I}$.

B. Line 20, plant 58-99, spike 8-156(a), smear a-6: Metaphase I with 28 or 29 chromosomes, including 6 ring type bivalents, some end to end bivalents and several univalents.

C. Line 12, plant 58-56, spike 8-166(a), smear a-3: Prometaphase with 21_{II} + several extra chromosomes and fragments.

PLATE VIII



EXPLANATION OF PLATE IX

Line 20, plant 58-96, spike 8-154

A. Anaphase II with 2 intact chromatin bridges in one cell and two ring-like chromosome structures in the other.

B. Late anaphase II with one broken bridge in one cell and an acentric fragment and one lagging chromosome in the other.

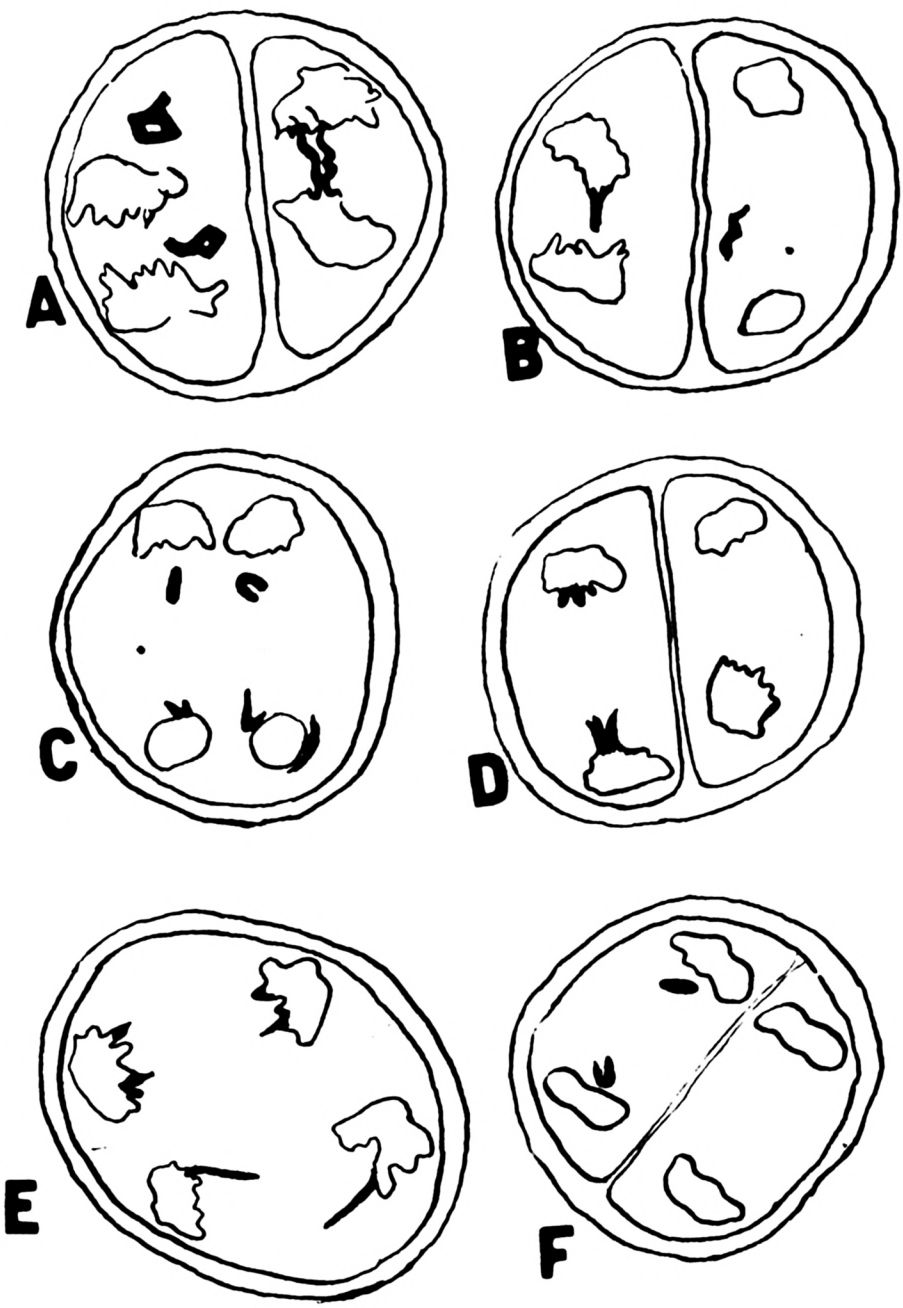
C. Late anaphase II with a broken bridge and lagging chromosomes in the same cell: dyad cell wall formation failed.

D. Late anaphase II with lagging chromosomes included in telophase II nuclei.

E. Late anaphase II with broken chromatin bridge.

F. Telophase II with lagging chromosome left out of the nuclei.

PLATE IX



EXPLANATION OF PLATE X

A. Line 20, plant 58-96, spike 8-154: Tetrad with 5 micronuclei.

B. Line 20, plant 58-96, spike 8-154: Dyad with 3 micronuclei.

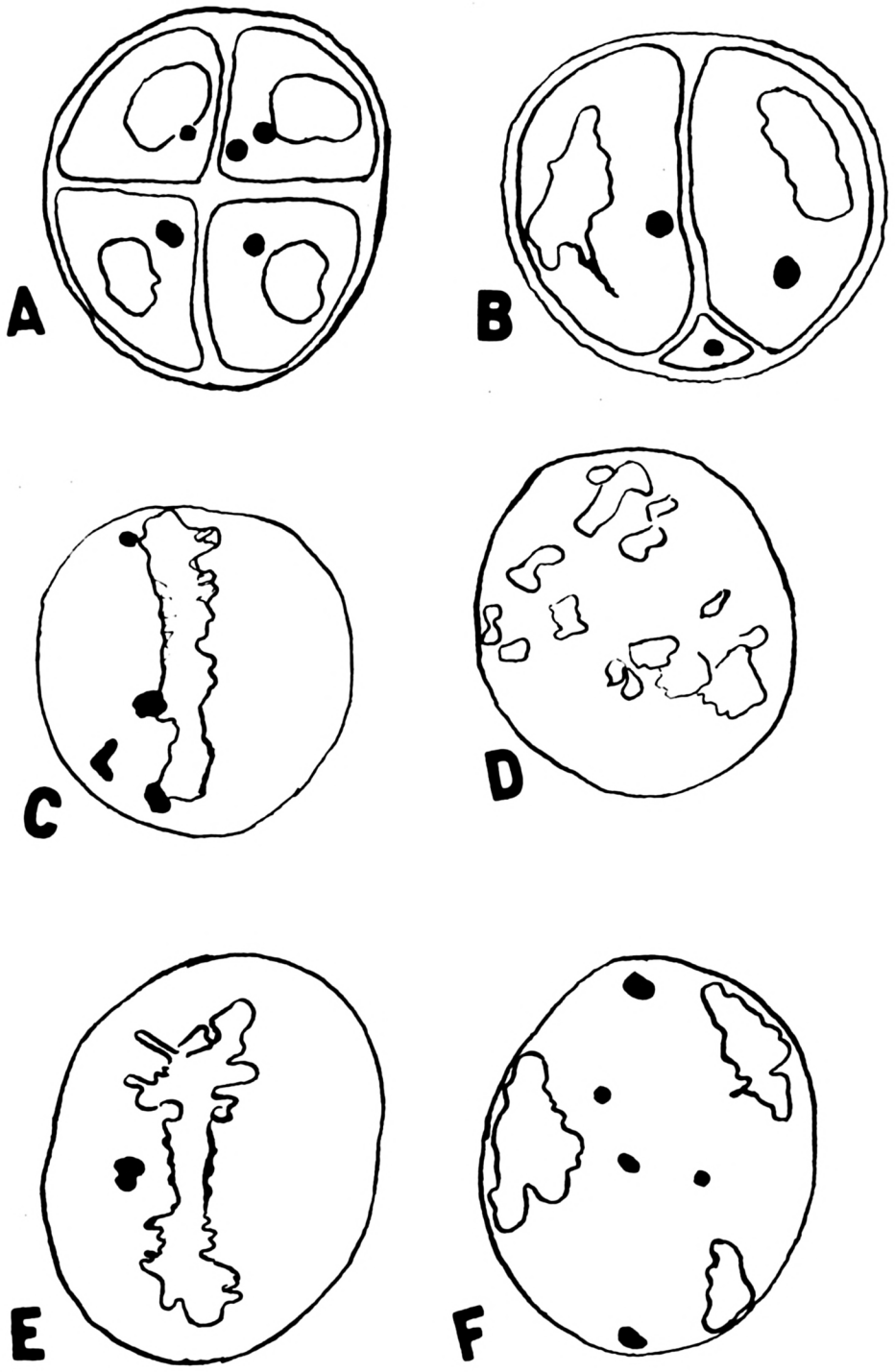
C. Line 20, plant 58-96, spike 8-154: Metaphase II plate with irregular chromosomes in same division figure, following failure of cell wall formation at dyad stage.

D. Line 12, plant 58-59, spike 8-334, smear a-5: Cell at tetrad stage, resulting from metaphase II of the type shown in C.

E. Line 12, plant 58-59, spike 8-334, smear a-5: Metaphase II with irregular chromosomes including 2 off the plate, in same division figure following failure of cell wall formation at dyad stage.

F. Line 12, plant 58-59, spike 8-334, smear a-5: Dyad stage without cell wall, may form a metaphase II with a single division figure, like the one shown in E.

PLATE X



CYTOGENETIC ANALYSIS OF HYBRID STRAINS DERIVED FROM INTERSPECIFIC CROSSES OF TRITICUM AESTIVUM L. AND T. TIMOPHEEVI ZHUK

by

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MASTER OF SCIENCE

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Cytogenetical studies were made of sixteen advanced generation hybrid strains derived from seven different crosses involving Triticum timopheevi and various T. aestivum varieties and strains.

Meiotic stability and chromosome behavior in these hybrid strains were correlated with their chromosome numbers and leaf rust reactions. Meiotic irregularities at metaphase I, anaphase I, dyad, metaphase II, anaphase II and tetrad stages were recorded.

One line, 7, from a cross involving a derived strain from T. timopheevi crosses and Nebred (cross IV;I279-A III-16 x Nebred) was found to be both highly regular in meiosis (meiotic index 95.89 percent normal tetrads) and resistant to all the six races of leaf rust (1, 5, 9, 11, 15, 122) against which it was tested in the immature plant stage. Rust reactions of selfed and backcross progenies of this line indicated that the genes controlling resistance to races 1 and 9 were dominant, those controlling resistance to race 15 incompletely dominant, and those concerned with races 5, 11 and 122 were very slightly dominant. In homozygous condition these genes showed complete resistance, but in heterozygous condition their expression was variable. Presumably, transfer of a chromosome pair or chromosome segment from the T. timopheevi genome to that of T. aestivum is involved.

Of the five strains which were comparable in meiotic regularity to Minturki, the less regular of the controls, one (strain 15) was resistant to race 15, and the other four were resistant to race 9. None was resistant to both these races of leaf rust. There was evidence that mitotic as well as meiotic aberrations were contributing to meiotic instability in these lines and rather wide variations existed.

All the six strains (except strain 11 which had resistance to race 9)

from two different crosses which had a meiotic regularity comparable to that of Cheyenne, the more regular of the controls in meiosis, were susceptible to all the races of rust.

The remaining four strains with irregular meiosis had meiotic indices ranging from 54.70 percent (in strain 12) to 85.50 percent (in strain 20). Variability within the lines was even greater. This tended to obscure differences between the lines, sc that only at tetrad stage were differences between lines 8, 12 and 20 significant. Different plants of the same lines likewise showed no significant differences. On the other hand, different spikes of the same plant taken at different times showed significant differences at most of the meiotic stages, thus indicating the influence of external environment on meiotic irregularity. Different spikes taken from the same plant at the same time did not differ significantly. The effect of internal environment or genetic instability was shown by significant differences found between florets of the same spike. In strains 8 and 20, irregularities at any one stage of meiosis were highly correlated with those at the other five stages. This was also true in line 12, except that anaphase I irregularities had nonsignificant correlations with those at metaphase I, anaphase II and metaphase II.

Various meiotic irregularities were observed in different lines, more frequently in those with low meiotic indices. These include variant chromosome numbers, reduced synapsis, scattering of univalents, bivalents and disjoined chromosomes at anaphase I and chromatin bridges with or without fragments at a anaphase I and anaphase II. Bridges, fragments and reduced synapses indicated that structural alterations involving chromosome segments (translocations and inversions) had taken place. Some of these, presumably,

involved chromosomes of the T. timopheevi genome.