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A CYTOGENETIC AND AGRONOMIC STUDY OF INDUCED TRANSLOCATION
LINES OF COMMON WHEAT (TRITICUM AESTIVUM L. EM. Thell)
IMMUNE FROM WHEAT STREAK MOSAIC VIRUS

by

Rama S. Kota

A thesis submitted in partial fulfillment
of the requirements for the degree of Master of Science,
Major in Agronomy, South Dakota State University
1980

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R. S. K.

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the virus has been shown to be highly resistant to tolerance to some strains of the virus has been reported. In several ways it appears that inheritance of this trait is to explain the inheritance of the trait. A good source of resistance to the virus is the *Trifolium pratense* Bean (2n=16) which has been used in crosses with common bean *Trifolium pratense* L. var. *Trifolium*. Transferring the immunity has been difficult because chromosome translocations will not pair and the presence of a gene on a chromosome will suppress the effect of the gene on the other chromosome. Several methods have been used to transfer the trait. Another is by crossing or suppressing a dominant gene on 5B that produces a pair of chromosomes (Wiley et al. 1977). Some of the advantages of the jointed bean are the different characters of the jointed bean (Wiley et al. 1977). The study of characters of jointed bean species can help to our understanding of evolutionary relationships and may improve crop yield (Hansen, 1974). If

INTRODUCTION

Wheat streak mosaic is a serious virus disease that threatens the production of winter wheat in some areas of the United States. It is caused by a virus transmitted by a wheat-curl mite, Aceria tulipae Keifer. Immunity from the virus has not been found in Triticum species but tolerance to some strains of the virus has been reported.

An obvious way to improve this important crop plant is to exploit the variability of its relatives. A good source of immunity found in Agropyron intermedium (host) Beau ($2n = 70$) has been used in crosses with common wheat, Triticum aestivum L. em. Thell. Transferring the immunity has been difficult because homoeologous chromosomes will not pair due to the presence of a gene on 5BL that acts as a suppressant.

Interchanges between chromosomes can be achieved in several ways. One is by irradiation (Sears 1956, 1977). Another is by removing or suppressing a dominant gene on 5B that prevents pairing of homoeologues (Riley et al. 1965, Sears 1975, 1977). A third is by taking advantage of the joining of two telocentrics from different chromosomes originating from misdivision (Morrison, 1954).

The transfer of characters to wheat from alien species contributes to our understanding of evolutionary relationships and may improve common wheat (Larsen, 1974). If

the interchanged segments are homoeologous and compensating, they are transmitted normally through egg and pollen (Dvorak and Knott, 1977).

Once transfers are achieved, it is desirable to evaluate the derived lines cytologically and agronomically. The purposes of this study are two-fold. One is to characterize lines cytologically. Chromosome pairing in F_1 hybrids can indicate the size and nature of translocations. In the Triticinae, chromosome pairing can be reduced as a result of chromosomal structural differentiation. The second purpose is to measure the effects of the Agropyron chromatin on the phenotypes of the lines studied in relation to the recurrent parent, Centurk, and to one another.

A gene 'Ph' allows only pairing of homologues (Wall et al., 1972). It suppresses pairing of homoeologous chromosomes. In tetraploid wheats (AABB, $2n = 28$) and hexaploid wheats (AABBDD, $2n = 42$), only bivalents are formed so disomic inheritance is the rule.

The cytological diploidizing system that limits synapsis to homologous chromosomes in polyploid wheats results from a balanced interaction among pairing promoting and pairing suppressing genes. It was discovered that chromosome 5B of wheat carries a gene that suppresses the pairing of homoeologous chromosomes (Okamoto, 1958; Sears and Okamoto, 1958; Riley and Chapman, 1958). Feldman (1966)

LITERATURE REVIEW

Common wheat Triticum aestivum L. is a hexaploid (AABBDD $2n = 42$) with triplication of genetic material. For this reason it is favorable for use in experiments which involve gross changes in the chromosomes. Sears (1954) and others have shown that the chromosomes of wheat fall into seven homoeologous groups of three pairs of chromosomes, each reflecting the origin of wheat from three related diploids each with seven pairs of chromosomes. Within these seven homoeologous groups of three pairs, chromosomes are so closely related, that an extra dose of any one will compensate for the absence of either of the other two (Sears, 1966).

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pointed out that the activity of chromosome arm 5B is controlled by a single dominant gene. Wall et al. (1971) concluded that common wheat carries a single gene 'Ph', (homoeologous pairing) at the distal end of the long arm of 5B controlling the diploidizing system. In the absence of this gene, the homoeologous chromosomes of A, B and D genomes may synapse with each other and also with at least some homoeologues in related species and genera.

There are number of other genes in wheat that affect pairing. Genes in chromosome arms 3AS and 3DS play a similar but minor suppressing role. There is probably a third minor suppressor on chromosome 4D, which is almost as effective as the gene on 3AS (Driscoll, 1972; Sears, 1977).

There are also some genes that promote pairing. There is a gene on chromosome arm 5BS, which has an opposite but substantially less effect than gene 'Ph'. Moreover genes on chromosome arms 2AS and 3BL also carry genes essential to normal pairing. Absence of these two genes leads to asynapsis. Chromosome arm 3AL also slightly promotes pairing. It is well known that the cytological diploidizing system of wheat is caused by the integrated activity of several genes. Some of these promote, while others suppress synapsis between homoeologous chromosomes but a gene on chromosome arm 5BL plays a major suppressive role. The diploidizing system acts either by amplifying

differences acquired by homoeologous chromosomes during their evolution (Dvorak, 1975) or by preventing the formation of the synaptonemal complex (Dvorak, 1972b).

Some diploid relatives of wheat, particularly T. speltoides (= Aegilops speltoides) and T. tripsacoides (= A. mutica), have genes that promote homoeologous pairing in their hybrids (Riley et al. 1961). The accessory (B-type) chromosomes carried by some strains of Aegilops (Triticum) suppress pairing by acting like the Ph gene (Dover and Riley, 1972). Mochizuki (1962) found that the addition of a particular pair of chromosomes of Agropyron elongatum to durum wheat (a tetraploid) resulted in homoeologous pairing.

The other genera besides Triticum which belong to the subtribe Triticinae of the tribe Triticeae of the family Graminae are Agropyron Gaertn; Secale L; and Haynaldia Shur. Cytogenetic studies in T. umbellulatum-wheat additions (Sears, 1956), Agropyron-wheat additions (Knott, 1958; Weinhues, 1967; Dvorak, 1972) and T. comosum-wheat additions (Riley et al. 1966) have shown that wheat chromosomes do not synapse with their alien homoeologues when the diploidizing system is active. When the diploidizing system is suppressed, however, the wheat chromosomes synapse with their alien homoeologues (Dvorak, 1972b, Dvorak and Knott, 1973, 1974).

The genetic relationships between particular alien and wheat chromosomes are indicated by the degree to which alien chromosomes substitute for wheat chromosomes (Sears, 1975). Convincing evidence for genetic homoeology of chromosomes of Agropyron, Aegilops and Secale with those of wheat comes from a study of the compensation effect in male gametophytes. According to Knott (1968) pollen grains with twenty wheat chromosomes and one Agropyron chromosome function just as well as pollen grains with twenty-one wheat chromosomes. From a study of fifteen substitution lines involving a wheat-Agropyron derivative, Knott (1964) found that the Agropyron chromosome compensated very well for 6A and was homoeologous to it. Johnson (1966) showed that the Agropyron chromosome from PW-327 substituted for members of homoeologous group 6, particularly chromosomes 6A and 6D. Alien substitution lines of Agropyron intermedium developed by Weinhues (1966) were fully fertile and vigorous. The substitutions were probably between homoeologues. The three alien substitution lines developed by Riley et al. (1966) of chromosome 2H of Aegilops comosa are also vigorous and have relatively normal spikes and fertility.

CI 15092, a disomic substitution line developed at South Dakota State University, has a pair of chromosomes from Agropyron intermedium. CI 15092 is vigorous and fertility is as high as 89% (Wong, 1972). The alien pair

probably are homoeologous to the 4th group (Larson, Wells personal communication). If a chromosome of the subtribe *Tricicinae* will only substitute for those of a particular homoeologous group of wheat, then this chromosome may be said to have specific substituting ability (Riley et al. 1966). On the other hand, if an alien chromosome will substitute for the chromosomes of more than one homoeologous group, it may be said to have general substituting ability (Riley et al. 1966).

Among all the related genera, the Agropyrons are noted for their resistance to three types of wheat rusts, to bunt and to wheat streak mosaic. Knott (1961, 1968) transferred stem rust resistance from Agropyron elongatum (Host) Beauv. to common wheat, using the wheat-Agropyron derivative PW-327. Tests of the backcross derivatives of PW-327 and Thatcher showed resistance against stem rust to be dominant. Sears (1968) showed that an Agropyron genome is most closely related to the A genome of wheat. On the cytological side there is not much pairing of Agropyron with wheat chromosomes, when the 5B effect is neutralized. Johnson and Kimber (1966) found 4.8% of pairing of a telocentric of Knott's chromosome in hybrids in which the 5B effect was suppressed.

It is well known that each kind of Agropyron chromosome is able to substitute only for its homoeologous

chromosomes in wheat (Larson and Atkinson, 1970). Agropyron addition and substitution lines appear unlikely to be of direct value in wheat production (Knott, 1968). Addition lines having only one or two alien chromosomes and an intact genetic complement of wheat are less vigorous than normal. They tend to be cytologically unstable giving rise to monosomic additions. Due to gametic selection, only a relatively small number of resistant plants (approximately 20%) are found in the offspring of 43 chromosome plants. About 3-5% of the total offspring will have 44 chromosomes as 22 bivalents. In spite of useful traits such as disease resistance, earliness (Sears, 1956) winter hardiness, higher protein content (Riley and Ewart, 1970) and larger seeds (Weinhues, 1966) which are all transferred to recipient species by alien chromosomes, none of the addition lines have found a place in agriculture (Khush, 1971). The quantitative traits in wheat such as tillering, spike conformation, straw strength and length are adversely affected (Riley and Kimber, 1966). Weinhues (1966) found a delay of germination in addition lines of A. elongatum. Commercial value of addition lines has been limited by cytological instability, reduced fertility and adverse effects on agronomic traits.

The main disadvantage of addition lines as parents in practical breeding is the loss of the added chromosome with the chromosomes of the recipient species and is relatively free of meiotic instability. It must also be able to

to some progeny. For example, from the completely resistant offspring of a 44-chromosome plant, there appear about 10% of plants with $2n = 43$, which are difficult to identify morphologically from plants with 44 chromosomes. If the descendents are harvested for a few generations without elimination of susceptible plants, there would be about 50% of susceptible plants after about seven generations (Weinhues, 1966). The best way to overcome this difficulty is by incorporation of Agropyron gene(s) into the chromosome set of wheat. Incorporation of Agropyron chromatin can be achieved by substituting for a whole chromosome pair of wheat a pair of chromosomes from Agropyrons or by manipulating the exchange of chromosomal segments between wheat and Agropyron (Weinhues, 1966).

In order to develop substitution lines, the resistant plants carrying the right chromosomal combinations must be selected through cytological analysis of pollen mother cells in F_1 and F_2 generations. The cytological techniques used in exploiting aneuploid material in the production of intervarietal and alien substitution lines were developed by Sears (1953) and further expanded by Unrau (1956), Person and Kuspira (1954) and Kuspira and Unrau (1957).

To become a commercial variety, an alien substitution line must demonstrate integration of the alien chromosome with the chromosomes of the recipient species and be relatively free of meiotic instability. It must also be able to

compensate for the missing chromosome. Most rye chromosomes compensate poorly whereas Agropyron chromosomes compensate somewhat better. Few undesirable traits should be present. Most of the substitution lines so far reported have been normal in vigor and fertility (except rye substitution lines) and inferior in yield and quality.

Weique, a substitution line in which rye chromosome V (IR) replaced wheat chromosome 1B, was quite successful as a commercial variety in Germany (Weinhues, 1965; Zeller, 1972). Another substitution line, Agrus, has a pair of 7th homoeologous wheat chromosomes replaced by 7el of Agropyron elongatum (Knott, 1964; Dvorak, 1975).

CI 15092, the source of resistance to wheat streak mosaic virus in the present study, was shown to have a pair of chromosomes from Agropyron intermedium substituted for 4B in wheat (Larson, Wells, personal communication; Wang, et al., 1977a, 1977b). Immunity is completely dominant. Use of CI 15092 as a commercial variety is not feasible because of an inferior phenotype. Genes from Agropyron species are simple to handle and most useful if they are transferred to wheat chromosomes (Knott, 1968).

Even though the alien addition lines are not successful commercially, they have been used in incorporating small segments of alien chromosomes into the chromosomes of wheat by irradiation. Sears (1956) transferred a

segment of chromosome from Aegilops umbellulata (now Triticum) carrying rust-resistance by irradiating a monosomic addition line. The procedure used by Sears was time-consuming and screening for the alien chromosome was not very effective (Driscoll, 1962). Elliott (1957) and Elliot and Larter (1957) used thermal neutrons for the same purpose.

At South Dakota State University, a program was started for incorporating immunity from wheat streak mosaic virus from Agropyron intermedium to Triticum aestivum var. Centurk. CI 15092 was the immediate source. (Sandhu and Wells, personal communication). They selected families segregating 3:1 (resistance to susceptibility), discarding families segregating 1:3 which is a characteristic ratio from monosomic additions.

To appraise the irradiation approach, transfers that have been induced must be evaluated cytogenetically and agronomically. One of the most commonly used methods for identification of the translocation chromosome is the investigation of chromosome pairing at meiosis of their hybrids with common wheat in F_1 . Such studies indicate the degree of homology and structural differentiation of chromosomes. In subtribe Triticinae, chromosome pairing can be reduced as a result of chromosomal structural differentiation (Sears, 1976; Dvorak, 1979).

only T. Immediately following irradiation, assuming a reciprocal translocation is obtained, in the meiosis of X_1 plants, pairing between translocated and unchanged chromosomes would give rise to heteromorphic trivalents. In later generations, the F_1 hybrids would only give rise to heteromorphic bivalents since the changed chromosome without the gene for immunity would not be present because of selection pressure. If an intercalary type of translocation is obtained, 21 ring bivalents are expected to occur in F_1 hybrids. This type of interchange involves two breaks in the same chromosome arm, thus isolating a small segment from the alien chromosome carrying the gene for immunity. The intercalary type of translocation is the most favorable, in which there would be no loss of wheat chromatin but is very rare. The reciprocal type of interchanges would result in loss of wheat germplasm.

Agronomic evaluation of translocation lines beyond cursory observation of qualitative characters involves field trials. Riley-67, a soft-red winter wheat variety developed at Purdue University, is the only induced translocation line that has succeeded as a variety (Knott, 1971). The resistance to leaf rust in Riley-67 was derived from Transfer. Transfer was developed by the pioneering work of Sears (1956) by irradiating a monoisosomic addition line. Sears produced seventeen translocation lines, but

only Transfer was free of deleterious effects. Transfer was a few days earlier in flowering, but was low yielding due to small culms and spikes (Sears, 1956).

Of seven translocations produced by Knott (1961) only one translocation line involving 6A with its homoeologue 6 el, derived from Agropyron elongatum, has normal transmission through pollen. Knott and Dvorak (1976) used this line as a source of stem rust resistance for transfer to Australian cultivars Eagle and Kite. Sharma and Knott (1966) transferred Lr 19 for resistance to leaf rust from Agrus, a substitution line in which 7D was replaced by 7 el from Agropyron (Dvorak and Knott, 1972). They recovered four translocation lines, but only one 'Agatha' was transmitted normally through egg and pollen. A gene for yellow flour in Agatha is linked with a gene for resistance to rust. Dvorak (unpublished) broke that linkage. He crossed a substitution line carrying A. elongatum chromosome 7E, which is homoeologous with group 7 and has white flour, with Agatha to induce crossing over between the gene for resistance and the gene for yellow pigment (Knott and Dvorak, 1976).

The translocation lines developed by Knott (1961, 1968) were low yielding and several days late in flowering but were equal to or better than the checks in protein content. The variety Transec, developed by Driscoll and

Jensen carried two genes for resistance to mildew and stripe rust on 4A/2N translocation (Driscoll, 1965).

Weinhues (1974) produced seven translocation lines, with the genetic background of the wheat variety Heine IV, but none of them outyielded the check.

Cultivars that involved spontaneous translocations between wheat and alien chromosomes have been rather more successful than induced translocation lines. The varieties Kavkaz and Aurora, which have the 1B/1R interchange are being grown commercially in Europe and U.S.S.R. Another variety 'Agent' involving a 3D/Ag spontaneous transfer (Sears, 1974), has been extensively used in wheat breeding programs. Agent is the rust resistant parent of cultivars Gent, Sage and Cloud.

The reason for the absence of deleterious effects in some translocation lines and their presence in other lines appears to depend on the ability of the alien chromatin to compensate for the replaced chromatin of the recipient chromosome. Translocation lines exhibiting normal transmission through the pollen were labelled by Dvorak and Knott (1977) as 'compensating translocations'. Compensating translocations are those in which a segment of a recipient chromosome is replaced by a corresponding segment of a homoeologous chromosome and is able to compensate for the deficiency. The frequency of compensating translocations obtained by irradiation-induced methods is

rather high (Knott, 1968). Knott (1968) pointed out that somatic association of homoeologues would raise the frequency with which radiation induced transfers involve only homoeologues. He suggested that the close association of homoeologous chromosomes may enhance the chances of homoeologous translocations. Feldman et al. (1972) and Feldmann and Avivi (1973) demonstrated that homoeologous chromosomes in wheat are closely associated in somatic cells.

Noronha-Wagner and Mello-Sampayo presented evidence of translocations occurring between homoeologous chromosomes in the backcross progenies of hybrids between Triticum aestivum var. Chinese spring and T. durum var. Ld. 222 (Mello-Sampayo, 1968). In plants, spontaneous somatic cross-overs occur both between homologous and homoeologous chromosomes. This indicates that the heterochromatin of genetically related chromosomes came into contact (Natarajan and Ahnstrom, 1969).

Compensating translocations obtained by ionizing radiation have involved homoeologous chromatin. Dvorak and Knott (1977) indicated that homoeologous chromosome arms might be closely associated with another in somatic cells. The frequency of radiation-induced transfers to homoeologous chromosomes is rather high. Whether this frequency is due to a non-random distribution of

chromosomes within the nucleus or haplontic selection has not been clear. If a translocation is to be free of deleterious effects, compensating segments of homoeologous chromosomes must be interchanged. (Dvorak and Knott, 1977). The transmission rates of compensating translocation lines is quite normal.

Most translocation lines suffer yield loss because of the considerable loss of wheat chromatin (Weinhues, 1966, 1976). However, Knott reported that one of his translocation lines outyielded the recurrent parent Thatcher. Despite the loss of yield, from the plant breeders point of view, excellent parental genes for resistance can be contributed by translocation lines. Selection of favorable back-cross lines might help recover the yield loss (Weinhues, 1974).

For determining cytogenetic affinity, most studies have been limited to the determination of chromosome pairing at MI. Occurrence of chromosome pairs at metaphase I reflects two phenomena: one, chromosome synapsis and two, chiasma formation. When a PMC with complete chromosome pairing is not observed in a reasonably large sample, it is correct to conclude that a specific number of chromosomes have not paired (Dvorak, 1979).

Chromosome or point mutations or temperature could affect the synapsis of chromosomes. Fu and Sears (1973)

reported desynapsis of heteromorphic bivalents before metaphase at high temperature. The desynapsed chromosomes behaved as ordinary univalents. Lin and Ross (1969) observed an increase of univalents as metaphase proceeded in triploid sorghum. Rhodes (1946) suggested that cross-over bivalents could desynapse and the resulting univalents assort to the same pole. Normally, synapsed chromosomes are each transmitted to 1/2 of the gametes. Fu and Sears (1973) observed 51% of 4AB telocentric chromosomes at optimum temperature. Pollen mother cells with reduced pairing would have univalents at meiosis I, particularly in metaphase. Later, these univalents would be subject to misdivision at anaphase I and II and as a result produce inviable gametes. (Soost, 1951; Moens, 1969; Sears, 1974; L. M. S. Sears, 1974).

Sen (1952) observed that genetic changes induced by x-rays and mustard gas produced characteristic morphological changes. He observed that isochromosomes formed ring univalents in the late stages of meiosis. There have been several reports concerning the origin of isochromosomes and telocentrics in Triticum aestivum L. by misdivision in meiosis (Hakansson, 1933; Huskins, 1933; Sears, 1946, 1952a, 1952b; L. M. S. Sears, 1966, 1974; Sanchez-Monge and Mackey, 1948; Makino et al. 1977). Existence of isochromosomes in wheat was first reported by Hakansson, who referred to them

as "co-chromosomes". Huskin referred to them as "chromosomes with two similar halves". From the reports of Koller (1938) and Darlington (1939), it is clear that univalents tend to be subject to misdivision, giving rise to isochromosomes and telocentrics. Sears (1952) observed misdivision of univalents at anaphase I in microsporocytes of wheat. Sanchez-Monge and Mackey reported misdivision only at the second meiotic division in Swedish wheats. They concluded that the origin of isochromosomes in their material could be due to non-disjunction of the two chromatids of a telocentric at meiosis. Sanchez-Monge and Mackey reported 97% of misdivision of univalents in Swedish wheats. Sears (1952a) found misdivision in Chinese spring wheat at a total frequency of 39.7%. Darlington found 98% of misdivision of univalents in Fritillaria karadaghensis. Sears demonstrated that chromosome IX from Chinese spring is more susceptible to misdivision than the corresponding chromosome of any of the other varieties. By misdivision of a centromere, a chromosome can divide into four functional parts at AI (Sears, 1952 in wheat and Upcott, 1937, in Tulips).

Misdivision at T II consists of the pulling apart of the two arms at the centromere. Misdivision of univalents at the second division of meiosis was reported by Nishiyama (1931) in oats, by Darlington (1939) in Fritillaria, and by

Sanchez-Monge and Mackey (1948) in wheat. Many of the second division laggards fail to be included in the telophase nuclei. They form micronuclei which can conveniently be counted at the quartet stage.

Sanchez-Monge and Mackey explained the origin of isochromosomes in their material by nondisjunction of the two chromatids of a telocentric at pollen meiosis.

Darlington in Fritillaria (1940) and Rhoides in maize (1940) found the origin of isochromosomes to be nondisjunction of telocentrics in pollen mitosis. Isochromosomes in wheat are of maternal origin and there is no elimination of deficient gametes, making it possible to determine genetic ratios (Sears, 1944). Isochromosomes are produced at a comparatively low frequency, and frequently escape observation.

It is clear how the isochromosomes and telocentrics originate in wheat according to Sears (1952a) for they are mainly produced at the first division.

Varieties of Triticum aestivum L. differ in their chromosomal constitutions and degree of irregularity. Powers (1938) counted micronuclei at the quartet stage to determine meiotic instability. They concluded that the loss of chromatin was highly correlated with non-orientation and the occurrence of univalents. Love (1949) proposed that the percentage of normal pollen quartets could be called "the meiotic index," and used to indicate the

regularity of chromosome behavior. The meiotic index has been correlated with yield. Love (1951) considered a plant with a meiotic index of 90%-100% to be quite stable. Plants with a meiotic index of less than 90% present difficulties to the plant breeder. In plants having lagging bivalents and a highly disorganized second meiotic division, Mendelian ratios cannot be expected for loci on chromosomes that fail to be included in the gametes. Rupert et al. (1974) cytologically selected for meiotic regularity in successive generations in Triticum. They found a 66.9% increase in seeds per spikelet. They recommended that a casual survey of meiotic division and pollen structure followed by rigid field selection would suffice to eliminate aberrant individual plants and to improve fertility.

Lines believed by Sandhu (1978) to have a translocation for a gene conferring immunity for WSMV were chosen for a cytological and agronomic study. Sandhu used five homozygous translocation lines breeding true for immunity and designated as A, B, C, D and G. He also used six heterozygous lines E, F, H, I, J and L which segregated some susceptible plants even as late as F_3BC_2 and F_3BC_3 generations.

The sources of the lines used in the present study and their genetic ratios for WSMV in the F_3BC_2 generation are presented in Table 1. The pedigree of the lines is

CI 15092/Triticum MATERIALS AND METHODS Centurk

A program to acquire immunity in bread wheat from wheat streak mosaic was started in 1963 in the winter wheat improvement program at South Dakota State University. Lay et al. (1971) developed CI 15092, a 42 chromosome line immune from WSMV from the cross of immune octoploid TA 25 and the susceptible hexaploid wheat. Wong (1972) reported that a pair of wheat chromosomes had been replaced by a pair from Agropyron intermedium in CI 15092.

Monosomic addition seeds (21" + 1A1') tracing back to CI 15092 were irradiated (Wells, personal communication) by fast neutrons. Immune plants grown from those irradiated seeds were used as pollen parents crossed onto a winter wheat variety 'Centurk', the recurrent parent of the population.

Lines believed by Sandhu (1978) to have a translocation for a gene conferring immunity for WSMV were chosen for a cytological and agronomic study. Sandhu used five homozygous translocation lines breeding true for immunity and designated as A, B, C, D and G. He also used six heterozygous lines E, F, H, I, J and L which segregated some susceptible plants even as late as F₆BC₄ and F₈BC₄ generations.

The sources of the lines used in the present study and their genetic ratios for WSMV in the F₈BC₄ generation are presented in Table 1. The pedigree of the lines is

CI15092/Triticum speltoides //Fletcher/3/5* Centurk. Centurk, the recurrent parent of the population, and Sage were used as checks.

Seeds were sown in wooden flats, chilled for five days, allowed to germinate at room temperature, and then vernalized at 35-42°F for 42 days. After vernalization, the seedlings were transplanted to the field or the greenhouse. Two agronomic experiments were conducted in 1978 and 1979 on the east agronomy farm. A third agronomic experiment was conducted in 1979 in the winter and spring in the greenhouse.

Peat moss was used on greenhouse beds as a mulch to avoid loss of moisture and diminish growth of weeds. Thirty days after planting, parathion was sprayed on the plants to control green bugs. Due to an excessive dose of parathion, the first greenhouse experiment suffered from burning of leaves. Sulfur was used to control powdery mildew on the headed plants. Banks of fluorescent lights over F₁ plants were provided for good pollen production in the greenhouse.

To study the cytological behavior of the lines, young spikes were collected from plants grown near the yield test for use in crossing, examination of segregations, and collection of pollen mother cells. To identify the types of translocations involved, the disomic substitution line CI 15092 and Centurk were crossed with the suspected

translocation lines. Immune plants in the lines were used as male parents in crosses with CI 15092 and Centurk, and NI (Table 2).

Seedlings were inoculated using the blast method as described by Gardner et al. (1969). Primary inoculation was kindly supplied by Dr. W. S. Gardner from wheat plants infected with WSMV. Inoculum was increased in the greenhouse by inoculating 10 two-week old seedlings of Centurk grown in each of 10 pots. Fifteen days later, cell sap was extracted from infested plants in a Hobart grinder. The concentrated sap was diluted 1:5 with distilled water. Carborundum (240 mesh/cm) for an abrasive was added to the inoculum at the rate of 22 gms/liter. This mixture was used to inoculate the F₁ seedlings and lines both in the greenhouse and field about 15 days after transplanting. Inoculation was done with a portable sand blaster, at 4.2 to 4.9 kg/cm² air pressure.

To reduce the frequency of escapes from inoculation, each plant was given three blasts of inoculum on three alternate days in a week. Fourteen days after inoculation, plants showing chlorotic, yellow streaks on leaves were considered to be susceptible and were discarded. Centurk was used as a susceptible check.

Young heads were collected from resistant plants and fixed in three parts of absolute alcohol to one part glacial acetic acid by volume and stored in the refrigerator at 34⁰ F.

Raj (1965) suggested that pollen mother cells collected at noon provided more cells in diakinesis and MI stage. PMC's were therefore collected at noon from different plants and on different dates from each line to provide interplant and day to day variation as suggested by Steinitz-Sears (1974).

Several microscopic slide preparations were made from each spike using three anthers per slide. The anthers were squashed in acetocarmine and then observed under the microscope. The slides with meiotic divisions were heated gently over an alcohol flame for a few seconds and the coverslips mounted with wax. Different stages of meiosis were studied.

For an observation of pairing in F_1 s, lines and checks, the diakinesis stage of meiosis was chosen. The occurrence of desynapsis of a bivalent was obtained by studying cells in diakinesis and metaphase I stages. For the occurrence of misdivision of univalents, cells with anaphase I - telophase I and anaphase II - telophase II were studied. Meiotic indices were prepared by observing spore quartets and counting the number of micronuclei. Micronuclei are formed from lagging univalents and fail to be included in the telophase II nucleus.

Pictures of meiotic cells were taken with a Zeiss camera at 90x magnification, using Kodak Plus X Pan black

and white film. Pictures were printed on Kodak Polycontrast paper.

Three yield tests were conducted. In the first test, I used five homozygous lines A, B, C, D and G and six heterozygous lines E, F, H, I, J and L, and two checks, Centurk and Sage. In the second yield test which was conducted in the greenhouse, lines A, B, C, D and G and one check variety, Centurk, were used. A third experiment was conducted in the field using lines A, B, C, D and G and the checks Centurk and Sage. Field and greenhouse tests were of like design but with a modification of plot size appropriate for the space available.

Vernalized seedlings were transplanted in a randomized complete-block experiment with four replications. In the field, each plot consisted of a single row, half of which was a line and half was either Sage or Centurk. Rows were 184 cm long and 30 cm apart. Plants were 8 cm apart in the row. Nine seedlings were transplanted for each line in each replicate. Ellar, an awnless spring wheat variety, was used for border plantings. Three seedlings of Ellar were planted at the end of each row. Three rows were planted on each side of the replicate to reduce border effects and bird damage. Seedlings were watered immediately after transplanting. In the greenhouse test only three seedlings were used in a subplot because of limited space.

In all tests, the phenotypic characters studied were grain yield per plant, tillers per plant, 50-kernel weight, spikelets per primary spike excluding the immature top and bottom spikelets, number of florets per primary spike, number of kernels per primary spike, percent seed set in a primary spike, number of kernels per plant, length of primary spike, and plant height. After the plants were pulled, plant height was measured as the distance from the base of the plant to the tip of the primary spike excluding awns.

All data were analyzed by standard analysis of variance for each character under study, by using complete random block design across the entries.

B. C. Correlation coefficients were obtained between 10 phenotypic characters under study. Multiple regression analysis for dependent variable yield was done on independent characters, which are considered as yield components. Independent variables used for multiple regression analysis were tillers per plant, seed weight, percent seed set and number of kernels per head.

RESULTS

Cytological Studies

Lines A, B, C, D and G (Table 1) are homozygous for reaction to wheat streak mosaic and resemble the recurrent parent, Centurk, in phenotype.

The immunity of the homozygous lines is equal to that of CI 15092, the disomic substitution line used as a source of immunity (Sandhu, 1978).

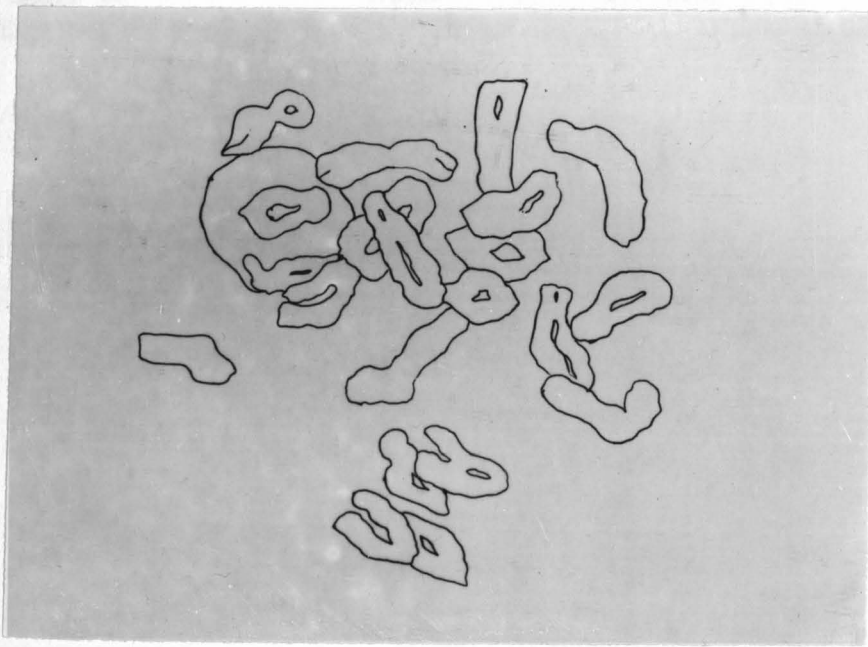
In diakinesis, chromosome spreading was only found in a few cells of different lines. It was not then possible to collect quantitative data at diakinesis. The configurations of chromosomes photographed or drawn for lines A, B, C, D and G in diakinesis of PMC's are described as follows.

- a. The majority of PMC's contained 21" (Figs. 3 and 8).
- b. 20" + i' + i', a double monoisosomic configuration, were observed infrequently (Fig. 6).

Isochromosomes were observed in a ring formation.

Kimber and Sears (1966) suggested that 'i' be used to designate the isochromosome whether or not it is involved in pairing.

In line G, however, no cells with a configuration of 20"+i'+i' were found. In Centurk, no configurations other than 21" were observed. A chromosome configuration of 21"



20:10
20:10
20:10
18:0
18:1
18:3
20:0
15:4
20:10
20:10
19:1
20:10

Fig. 1. Diakinesis in PMC's of Centurk with 21".

Table 1. Sources of seed and segregation ratios for 11 lines backcrossed to Centurk and for two check varieties used in the studies.

Line or check variety	Seed source	Segregation ratios in	
		F6 BC4 I:S	F8 BC4 I:S
1 A	4776-8	16:12	20:0
2 B	976541-0	20:0	20:0
3 C	976567-0	19:1	20:0
4 D	976547-1	50:0	18:0
5 E	977550-0	----	14:1
6 F	47726-0	22:1	17:3
7 G	477557-1	23:0	20:0
8 H	977505-1	11:5	15:4
9 I	977512-1	12:1	20:0
10 J	977516-1	8:0	20:0
11 L	977522-0	14:8	19:1
12 Centurk	-----	----	0:60
13 CI15092	-----	----	40:0

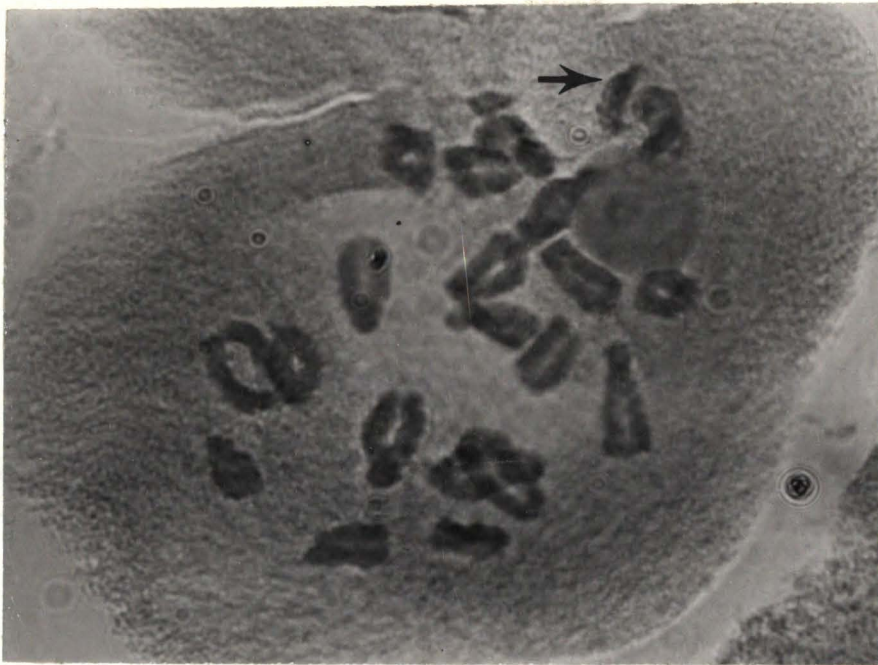


Fig. 2a. Diakinesis in PMC's of the F₁ of Centurk/Line D with 20'' + 1'' (heteromorphic bivalent).

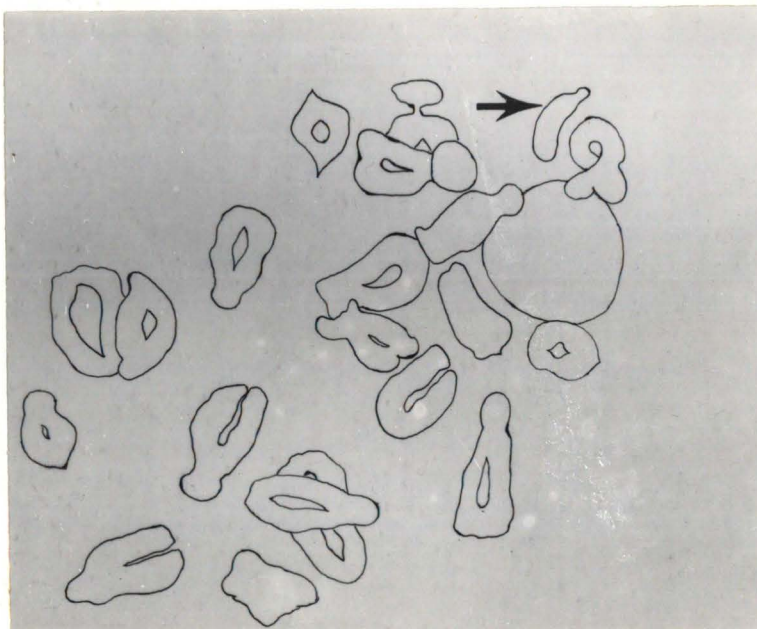


Fig. 2b. Drawing of Fig. 2a showing 20'' + 1'' (heteromorphic bivalent is indicated with an arrow).

Table 2. Pedigrees and sources of F₁s made in the greenhouse, 1979.

Greenhouse culture #	Cross #	Pedigree	Cultures in field used as parents
978268	XR78158	Centurk/A	478201-5 x 478221-21
978262	XR78152	Centurk/B	478201-11 x 478303-8
978263	XR78153	Centurk/C	278729-1 x 478303-61
978264	XR78154	Centurk/D	478201-11 x 478305-16
978265	XR78155	Centurk/G	278729-5 x 478307-4
978270	XR78160	Centurk/F	478201-9 x 478223-8
978269	XR78159	Centurk/J	478201-10 x 478226-5
978259	XR78149	CI15092/F	478234-18 x 478223-8

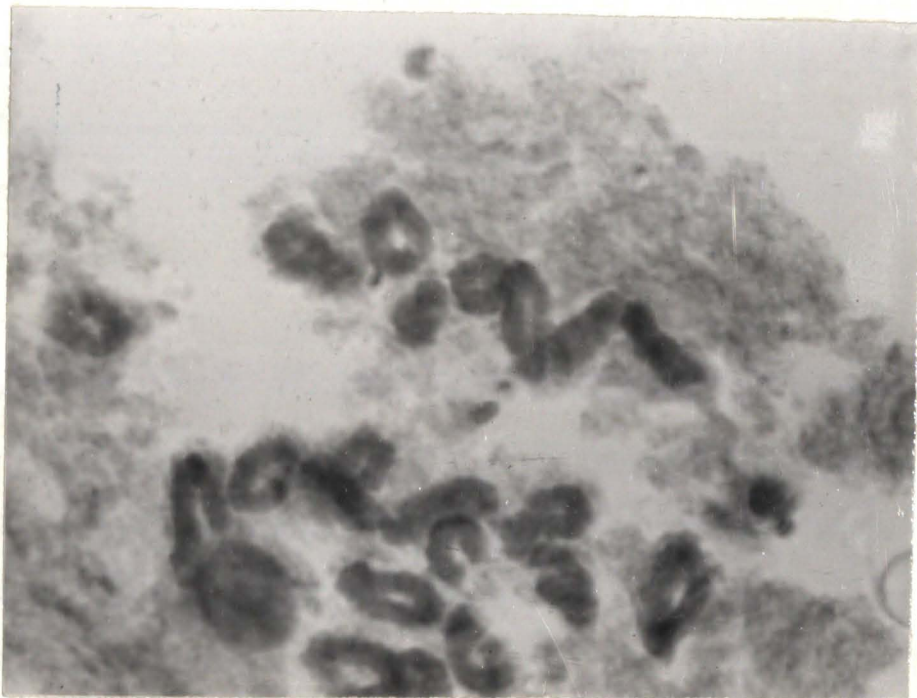


Fig. 3. Diakinesis in PMC's of Line D with 21".

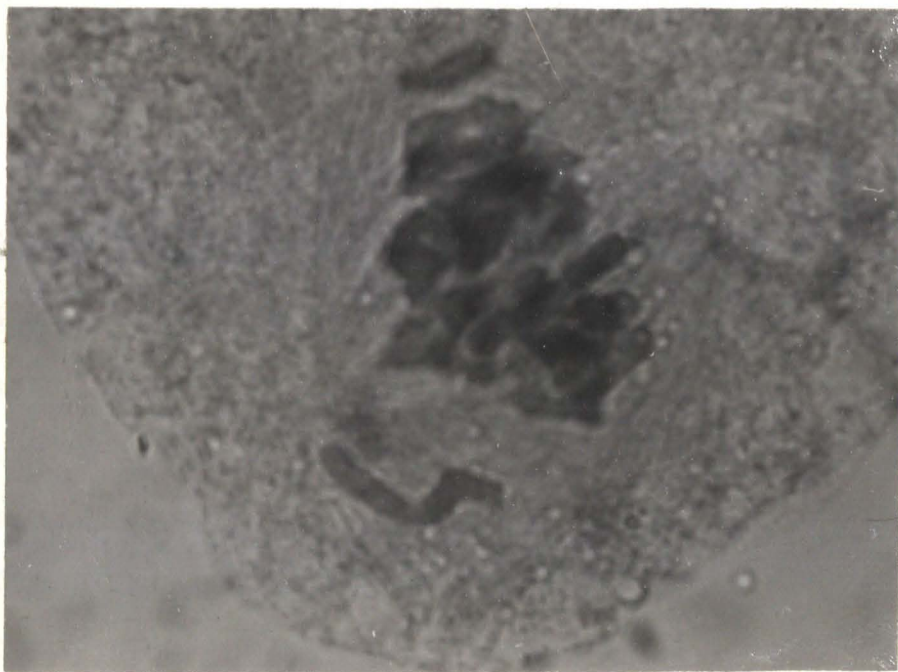


Fig. 4. MI in PMC's of F_1 of Centurk/Line A with 20" + 1"
(heteromorphic rod bivalent isolated from MI plate).

in diakinesis in Centurk is shown in Fig. 1. Cells with a configuration of $20''+i'+i'$ in lines A, B, C and D were few in number. Transmission of spores with isochromosomes is infrequent and occurs only maternally. Isochromosomes and telochromosomes originate from the misdivision of a univalent.

Euploid configurations look alike whether in Centurk or in a translocation homozygote (Figs. 3 and 8, respectively). In the latter, it is not possible to recognize a chromosome pair involved in an interchange. Since all the translocation homozygotes have shown 21 bivalents and are immune from wheat streak mosaic, an interchange between Agropyron and wheat chromosomes must have occurred. That evidence does not distinguish between intercalary and reciprocal translocations.

In the F_1BC_5 hybrids of translocation lines crossed with Centurk, good pairing was observed at diakinesis providing cytological evidence on the nature of interchanges obtained by irradiation. PMC's with chromosomes forming 21 bivalents were most frequently observed. Usually one heteromorphic bivalent and 20 ring bivalents were observed in diakinesis and metaphase I stages. The heteromorphic bivalent was comprised of the unchanged wheat chromosome paired at only one end with the interchanged chromosome. The unchanged wheat chromosome pairing at only one end with the

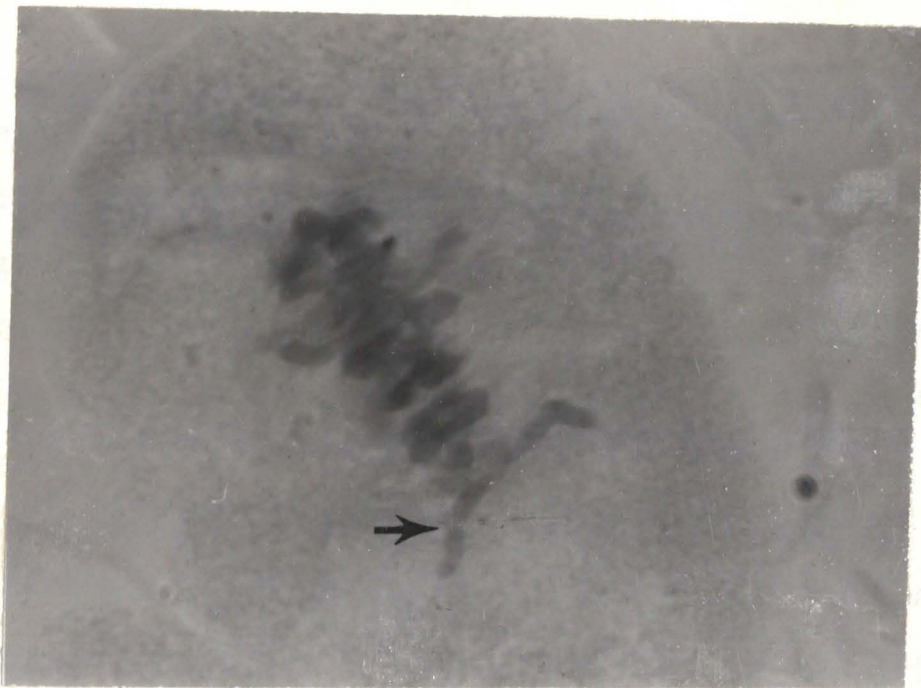


Fig. 5. MI in PMC's of F_1 of Centurk/Line B with $20'' + 1''$ heteromorphic bivalent (pointed with an arrow).

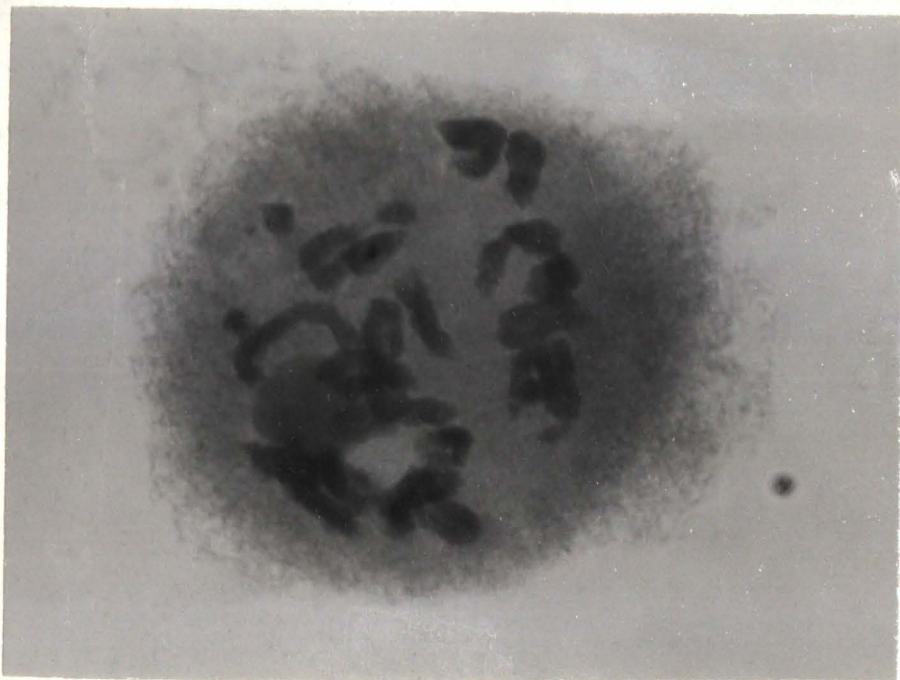


Fig. 6. Diakinesis in PMC's of Line A with $20'' + 1' + 1'$.

interchanged chromosome would have been based on DNA homology and would have involved only one chiasma. Presence of a heteromorphic bivalent in F_1BC_5 hybrids of lines A, B, C, D and G with Centurk indicated that these lines were involved in interchanges which are of reciprocal rather than intercalary type (Figs. 2, 4, 5, 7, and 8).

Different forms of heteromorphic bivalents were found. One had the appearance of a long telochromosome as in Centurk/D (Figs. 2a and 2b). Twenty of 35 translocations obtained by Weinhues produced heteromorphic bivalents in F_1 hybrids resembling a long telocentric chromosome and had the Agropyron centromere. Therefore it is probably reasonable to conclude that line D has the Agropyron centromere translocated with the segment containing a gene for immunity.

The other form of heteromorphic bivalent was rod shaped, and was seen in F_1 hybrids involving lines A and B (Figs. 4 and 5). The heteromorphic rod bivalent in A and B was much longer than the one observed in F_1 cells involving line D (Figs. 2a and 2b). Therefore lines A and B must have involved the whole arm of the Agropyron chromosome without the Agropyron centromere, while less than an entire arm with the Agropyron centromere is represented by line D.

The type of translocation in lines A, B, C and G is reciprocal rather than intercalary since a rod shaped

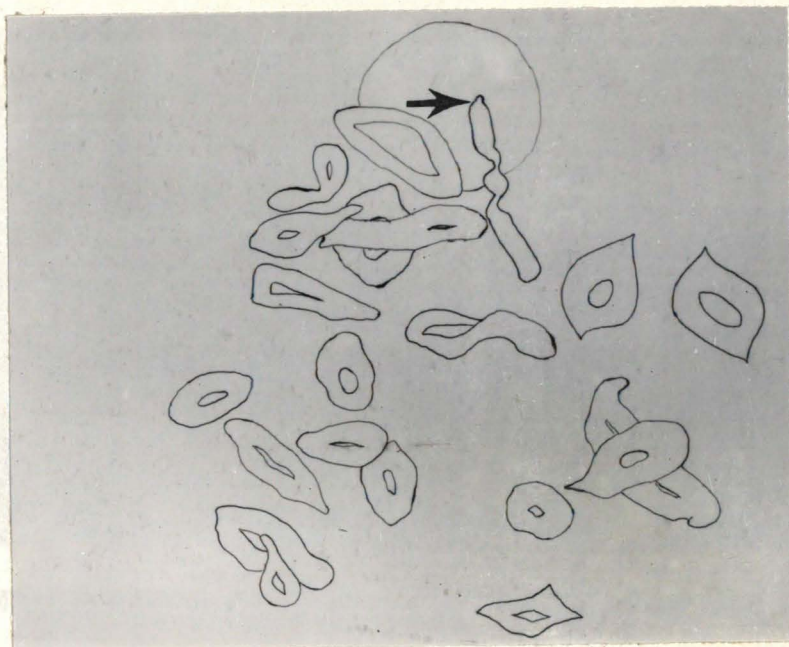


Fig. 7. Drawing of Diakinesis in PMC's of the F1 of Centurk/Line C with 20'' + 1'' heteromorphic bivalent (indicated with an arrow).

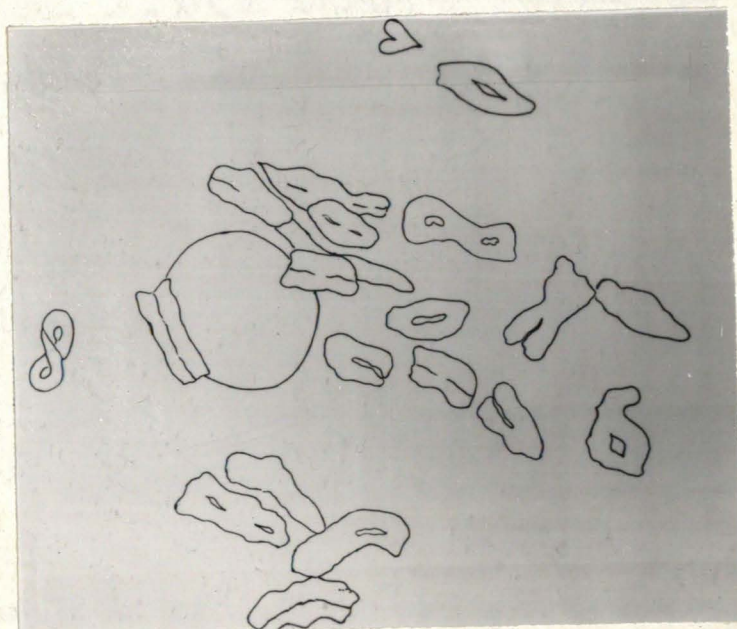


Fig. 8. Drawing of Diakinesis in PMC's of line C with 21''.

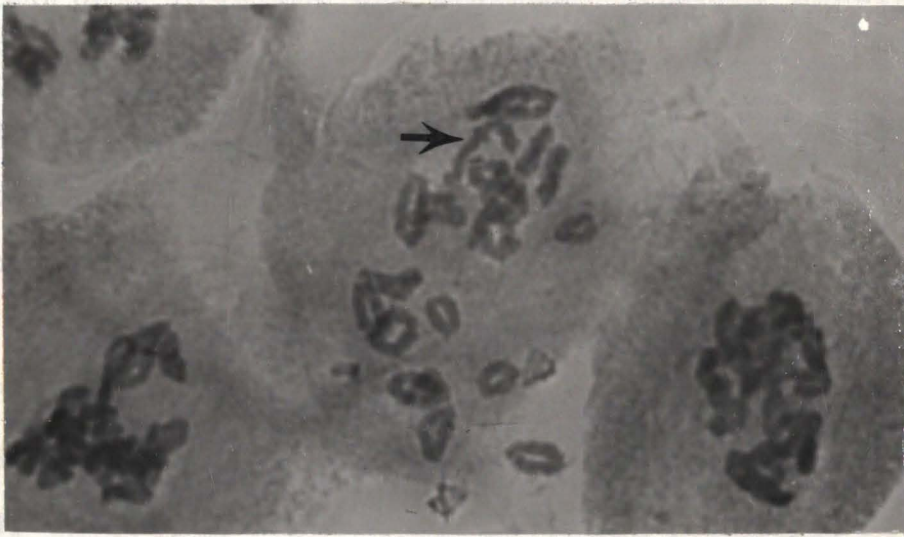


Fig 9a. MI in PMC's of F_1 of Centurk/Line G with $20'' + 1''$ (heteromorph bivalent).

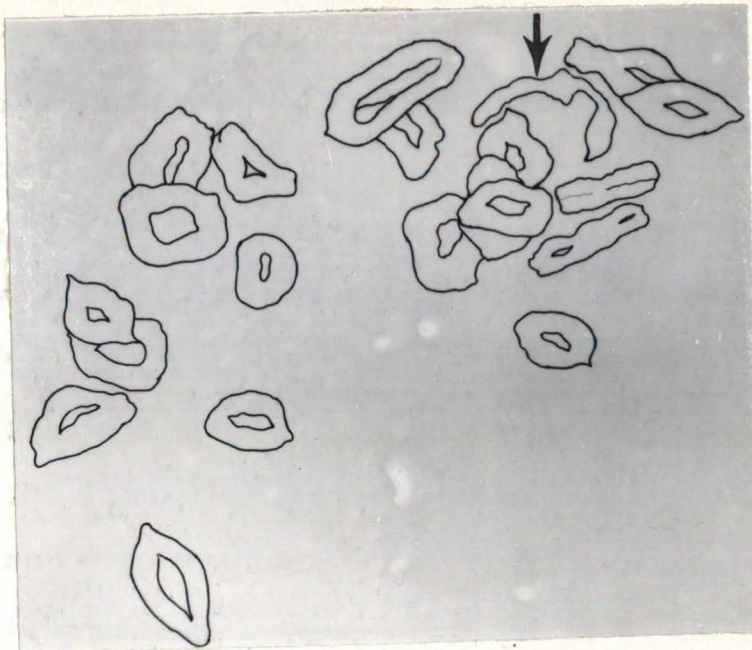


Fig 9b. Drawing of MI in PMC's of F_1 of Centurk/Line G with $20'' + 1''$ (heteromorph bivalent indicated with an arrow).

heteromorphic bivalent was observed in F_1BC_5 hybrids (Figs. 4, 5, 7, and 9). Assuming the gene for immunity is close to the centromere, a break on the Agropyron centromere may have occurred to produce such a translocation to a wheat chromosome (see later).

The heteromorphic rod bivalents observed in the PMC's of F_1BC_5 hybrids involving lines C and G are much longer and morphologically different from those observed in F_1BC_5 hybrids involving lines A and B (Figs. 7 and 8). The type of translocation is still reciprocal in C and G but the whole arm of Agropyron must have been interchanged. However, the differences observed in chromosome morphology of heteromorphic bivalents might also be due to the involvement in interchanges of different chromosomes in the homoeologous group.

The chromosome behaviour in MI stage of the lines and of their F_1BC_5 hybrids with Centurk is summarized in Tables 3 and 4. The different types of PMC's observed were:

- a. 21" and no laggards.
- b. 21" of which one or two were lagging near the metaphase plate.
- c. 20" and two lagging univalents. Infrequently, only one univalent was lagging (Figs. 11 and 14).

Fig. A few cells in the lines A, B, C and D were found having a lagging ring isochromosome (Fig. 20). However, in F_1BC_5 hybrids, no isochromosomes were found in metaphase I stage.

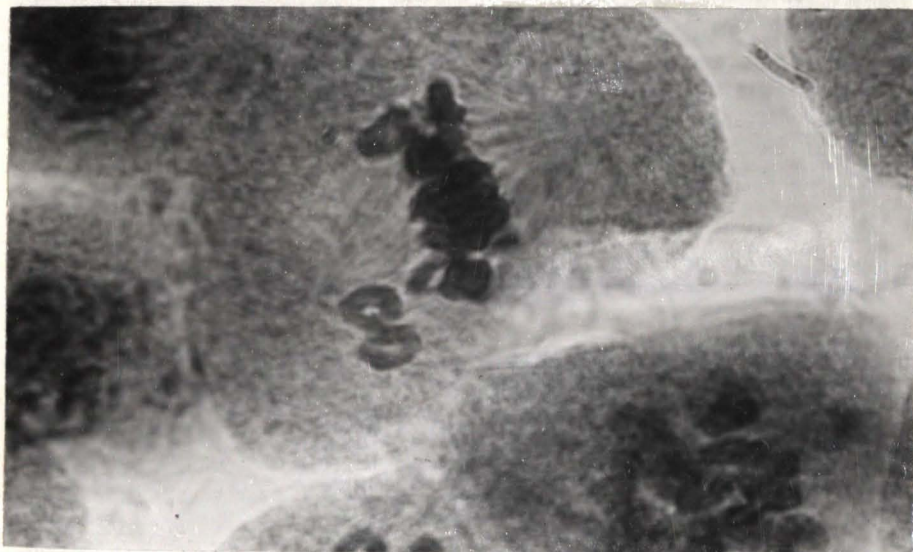


Fig. 10. First meiotic metaphase with two lagging bivalents
in PMC's of line D.

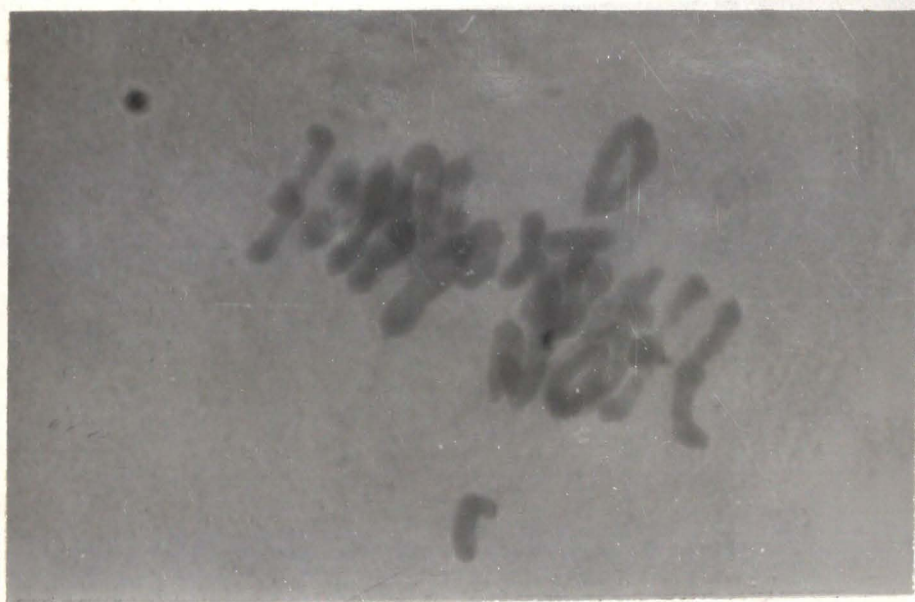


Fig. 11. First meiotic metaphase with one bivalent and one
univalent lagging behind in PMC's of line B.

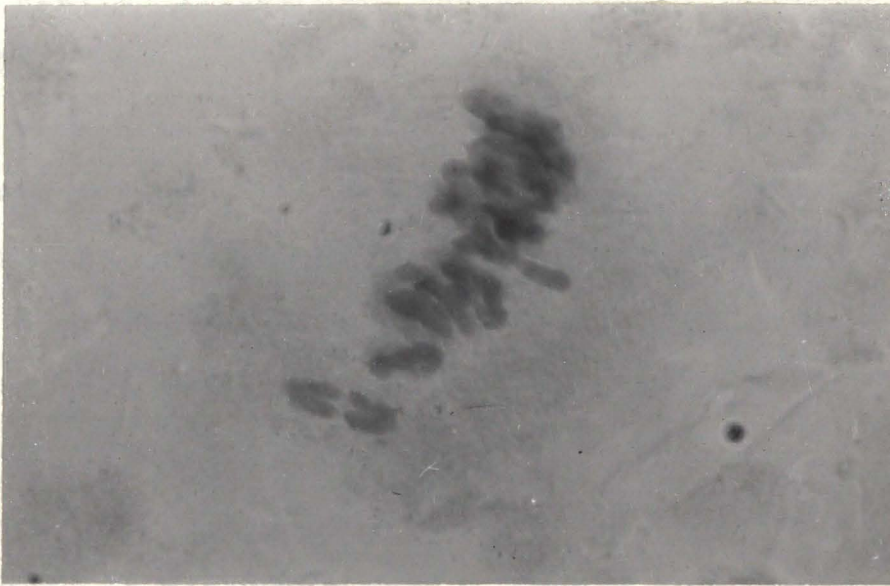


Fig. 12. First meiotic metaphase with one bivalent just desynapsed in PMC's of line B.

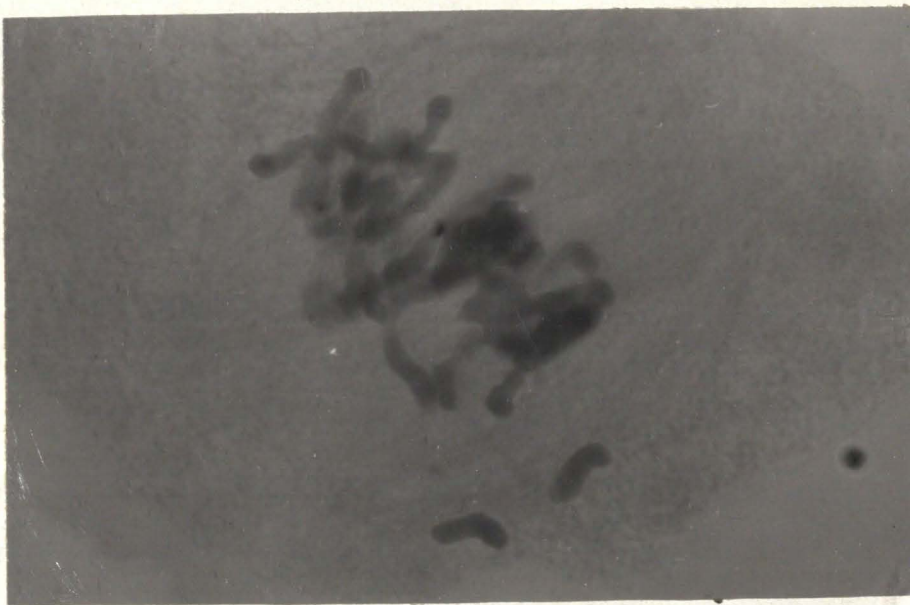


Fig. 13. First meiotic metaphase with 20'' + 2' in PMC's of line B.

Fig. 13 illustrates two univalents isolated from MI plate in line B. They were alike in size and shape.

From Table 3 it is clear that both the check and the lines showed lagging bivalents in MI stage for reasons unknown. In Centurk, 5.5% of PMC's had lagging chromosomes in MI, both bivalents and univalents. All eight lines were more unstable than Centurk, varying from 13% to 32% of total laggards. Line G was most stable of all.

The two univalents in lines and in Centurk must have originated by desynapsis from a lagging bivalent. This assumption is clearly supported in MI, Fig. 12. A pair of chromosomes disjoining before metaphase I could produce univalents, particularly under the stress of high temperature (Fu and Sears, 1973). Temperatures were high in the field at noon when I collected PMC's. In F_1BC_5 hybrids in the greenhouse, the same type of behaviour was observed (Table 4) at moderate air temperature.

The aberration of two univalents in F_1BC_5 hybrids (Table 4) also resulted from desynapsis of a bivalent. The successful transfer of the alien segment means that gametes having the interchanged chromosome compete quite well with gametes having a normal karyotype. A hybrid resulting from a cross of Centurk with a translocation line must have twenty ring bivalents and one heteromorphic bivalent assuming only one chromosome is involved in reciprocal

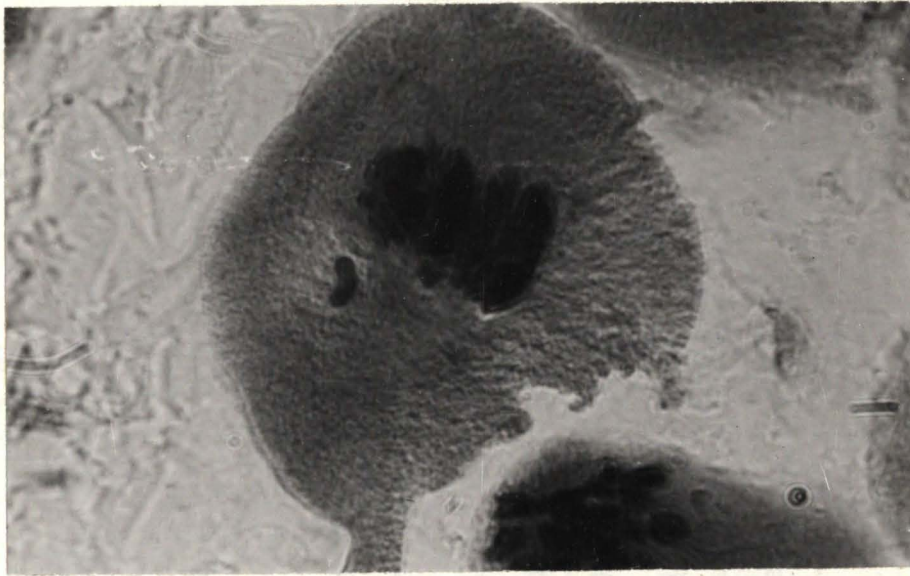


Fig. 14. First meiotic metaphase with one univalent lagging behind the metaphase plate in PMC's of line D.

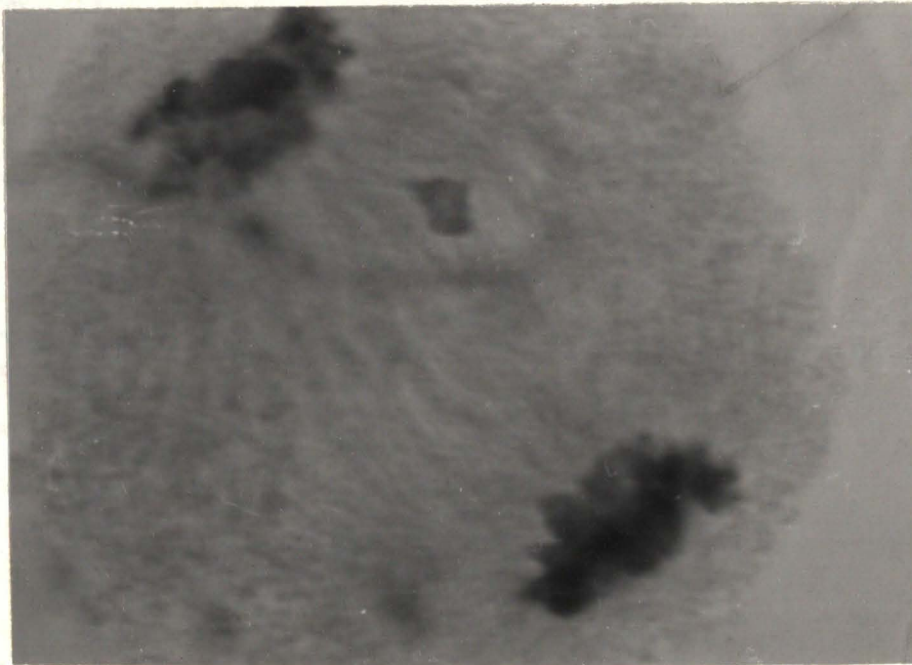


Fig. 15. Nondisjunction of a bivalent, resulting in its movement to one pole in PMC's of Line C.

Table 3. Behaviour of chromosomes of F₇BC₄ lines and Centurk in the MI stage of meiosis in the field, 1978.

Line	Culture #	# of immune plants examined	# of pollen mother cells	% of total laggards	% of lagging bivalents	% of lagging univalents
A	478302	6	1483	24.0	7.1	16.9
B	478303	5	1426	21.7	4.2	17.5
C	478304	4	1505	27.2	7.3	19.9
D	478305	8	1616	21.5	9.4	12.1
G	478307	4	735	13.7	12.2	1.5
F	478223	2	541	32.1	17.0	15.1*
H	478224	3	674	14.9	9.2	5.7
I	478225	2	288	12.9	12.9	0
Centurk --		3	274	5.5	3.3	2.2

*The two univalents in this line differ in size, one may belong to Agropyron.

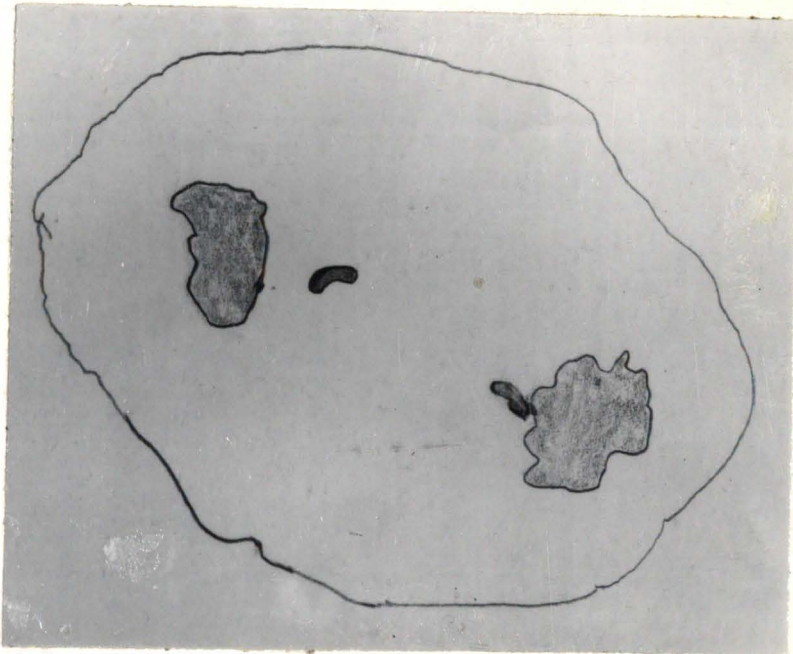


Fig. 16. Drawing of first meiotic telophase with two univalents lagging behind in PMC's of Line D.

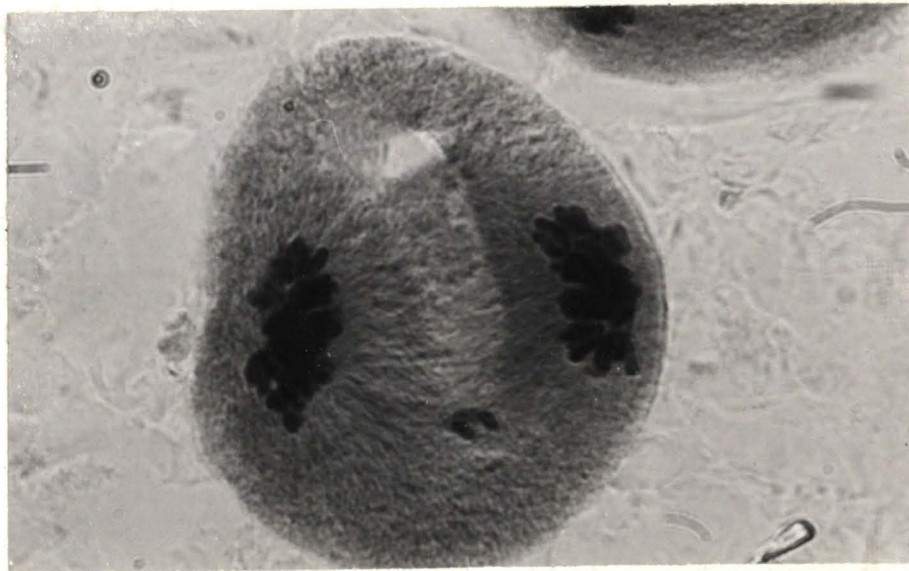


Fig. 17. First meiotic telophase with the sister chromatids of one univalent lagging behind in PMC's of Line D.

Table 4. Behaviour of chromosomes in M_1 of F_1BC_5 hybrids between six lines and Centurk and between CI 15092 and line F in the greenhouse, 1979.

F_1BC_5 hybrids	Culture #	# of immune plants examined	# of pollen mother cells	% of total laggards	% of lagging bivalents	% of lagging univalents
Ctk/A	978268	3	324	8.6	0.6	8.0
Ctk/B	279182	6	509	24.6	4.0	20.6
Ctk/C	279194	4	679	20.2	4.2	16.0
Ctk/D	279181	8	1121	19.4	1.1	18.4
Ctk/G	978265	2	339	4.7	4.7	0
Ctk/J	978269	2	207	19.2	5.3	13.9
CI 15092/F	978259	2	172	4.6	---	4.6



Fig. 18. First meiotic anaphase with two univalents lagging behind the main group of chromosomes in PMC's of Line D.

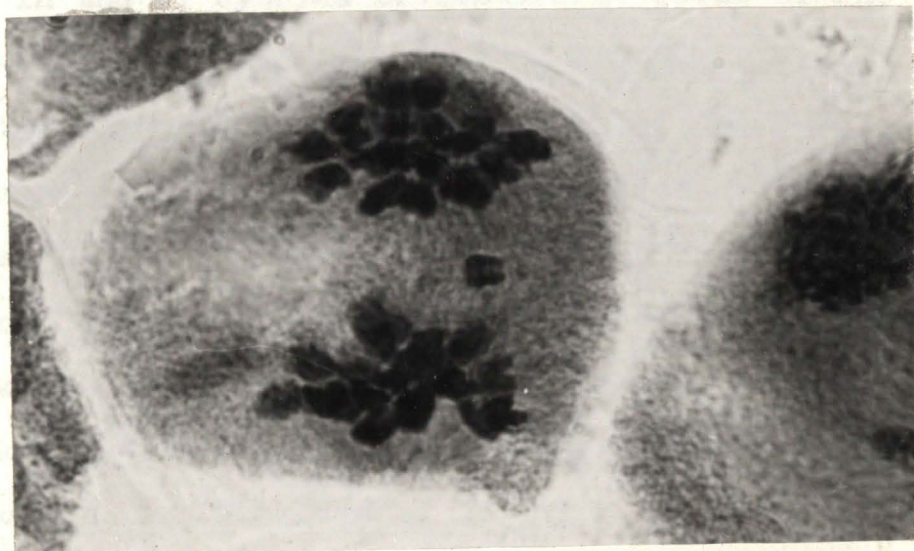


Fig. 19. First meiotic anaphase with an unpaired isochromosome lagging behind in PMC's of Line D.

interchange.

The term desynapsis is preferred to asynapsis because I actually observed pairing in many cells. Terminalization of chiasma normally takes place between diakinesis and metaphase I (Darlington, 1940). Desynapsis then must occur between diakinesis and metaphase I. That no univalents were observed in diakinesis and that two lagging univalents were seen supports the assumption of desynapsis (Fig. 14). Fu and Sears (1973) reported premetaphase disorientation in heteromorphic bivalents of F_1 plants involving 'Transfer' with Chinese spring. The frequency of desynapsis expressed as a percent of univalents was obtained for each line (Tables 3 and 4).

In the F_1 hybrids of Centurk/B, 20.6% of PMC's showed univalents (Table 4). The high occurrence of univalents in this line might be due to the additional desynapsis of heteromorphic bivalents, which were observed in a few cells besides the two univalents already existing. Heteromorphic bivalents never appeared to desynapse in F_1BC_5 hybrids of Centurk with lines A, C, D and G. In F_1BC_5 plants of Centurk/G, no univalents were observed (Table 4), providing evidence of the stability of line G.

The univalents observed in PMC's of line F (Table 3) were unequal in size. Therefore one was probably from Agropyron intermedium. From the study of PMC's of

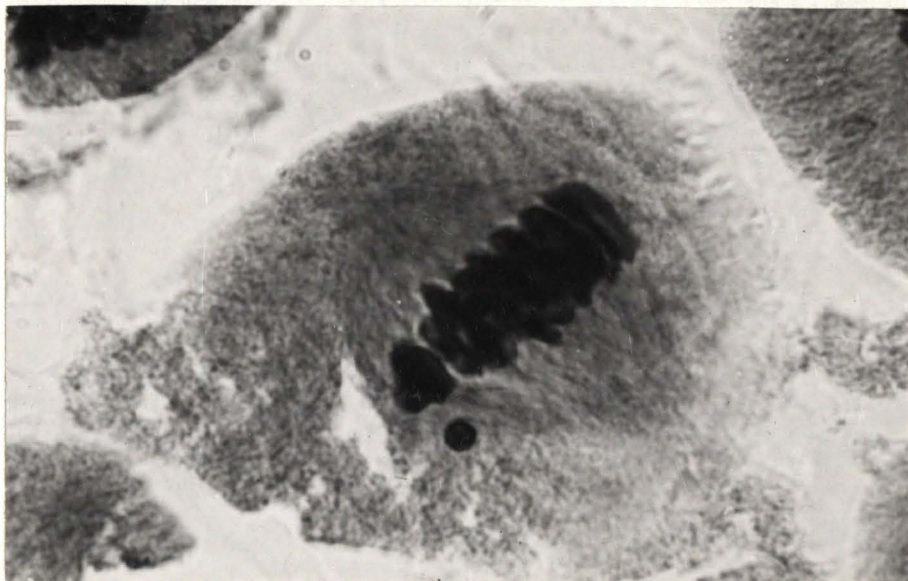


Fig. 20. First meiotic metaphase with a ring isochromosome lagging behind the metaphase plate in PMC's of Line D.

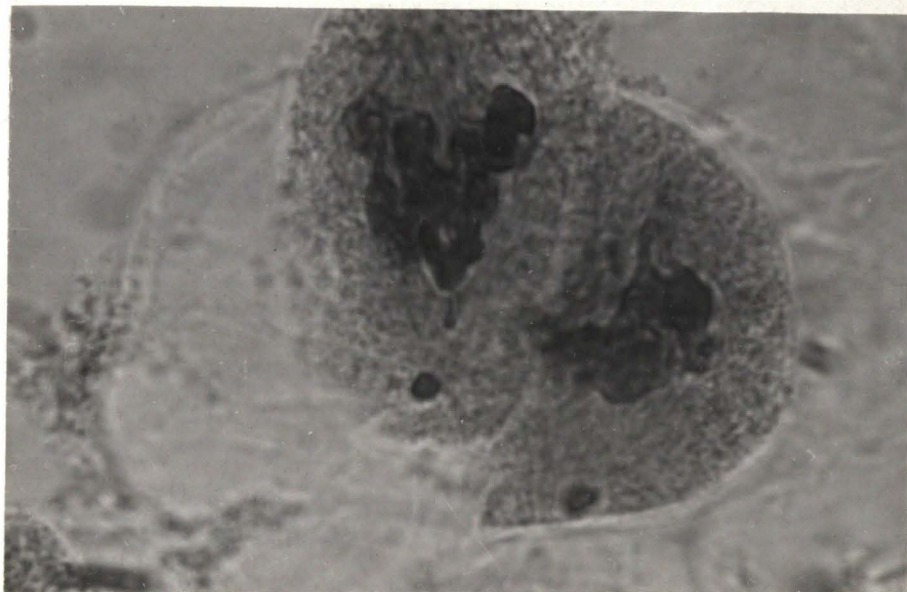


Fig. 21. Two micronuclei formed by lagging chromosomes in interphase in PMC's of Line D.

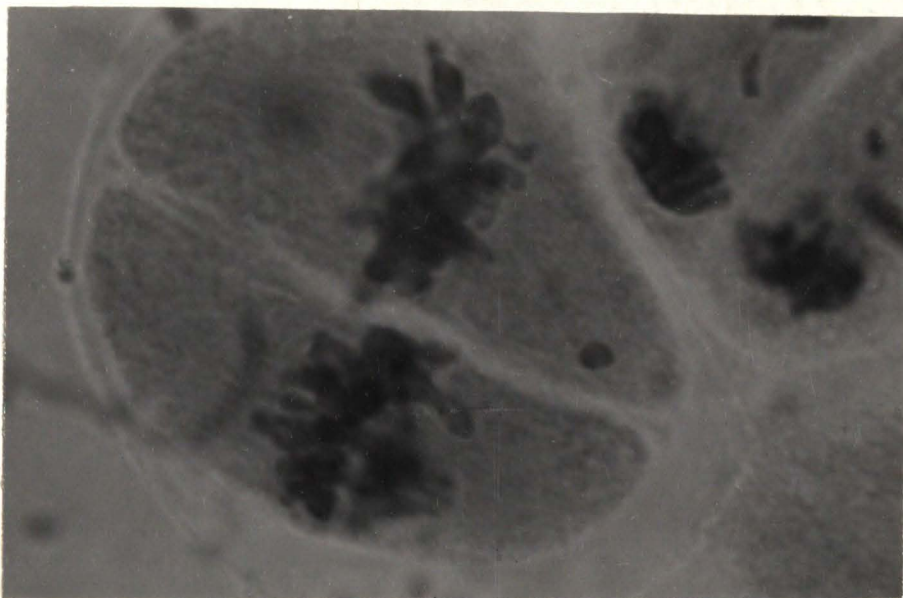


Fig. 22. Ring isochromosome lagging behind at the second metaphase of meiosis in PMC's of Line D.

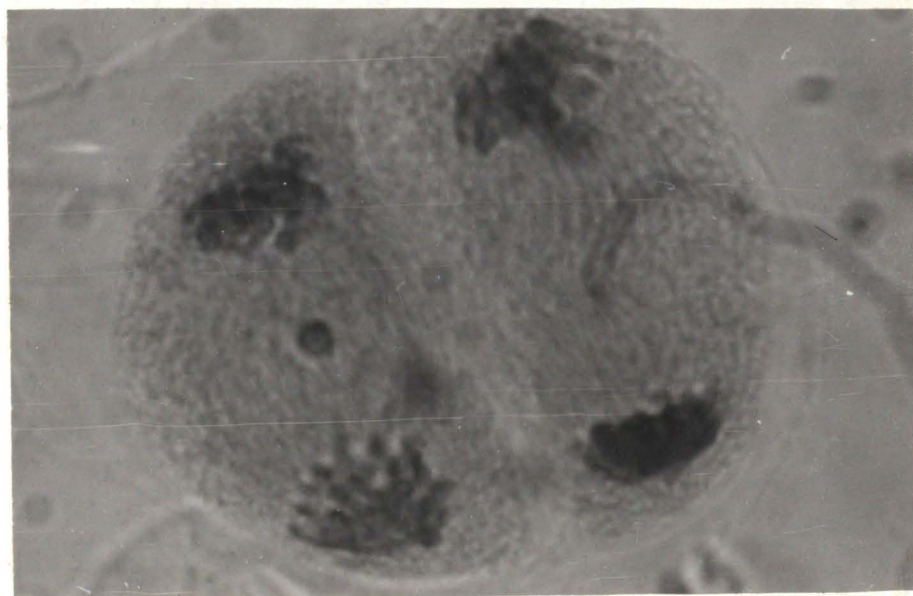


Fig. 23. Ring isochromosome lagging behind in the second telophase in PMC's of Line C.

Table 5. Behaviour of chromosomes in AI-TI stages of meiosis in PMC's of the F₇BC₄ lines studied in the field, 1978.

Line	Culture#	# of immune plants examined	# of cells with normal division	Type and # of univalents								IN + 2T	+ % PMC's showing laggards	% PMC's showing misdivision
				Normal		Isos		Telos						
				1	2	1	2	1	2	3	4			
A	478302	6	307	14	6	6	4	2	4	0	4	0	11.5	5.8
B	478303	5	541	26	10	11	4	36	31	6	2	0	18.9	13.5
C	478304	4	508	58	19	7	4	8	7	5	0	0	17.6	5.1
D	478305	6	791	42	13	9	0	29	19	2	9	12	14.5	8.6
G	478307	4	307	0	0	0	0	0	0	0	0	0	0	0
F	478223	3	316	42	13	5	13	8	10	5	2	8	25.1	12.1
H	478224	2	224	27	7	3	5	0	0	0	0	0	15.8	3.0
I	478225	2	329	15	7	0	0	0	0	0	0	0	0	0
Centurk	---	2	388	8	3	0	0	0	0	0	0	0	0	0

+One normal univalent plus two telosomic chromosomes.

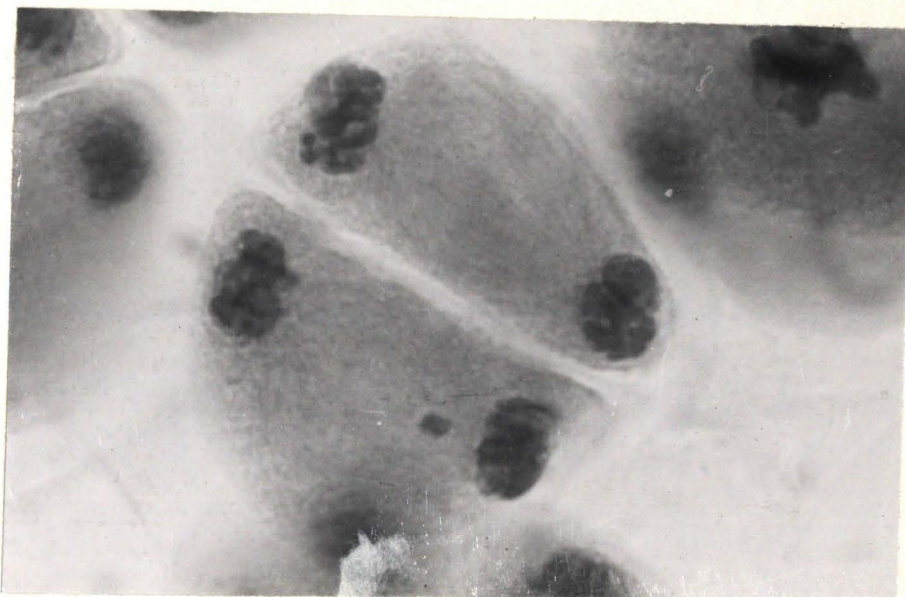


Fig. 24. One lagging telocentric chromosome in the second telophase in PMC's of line B.

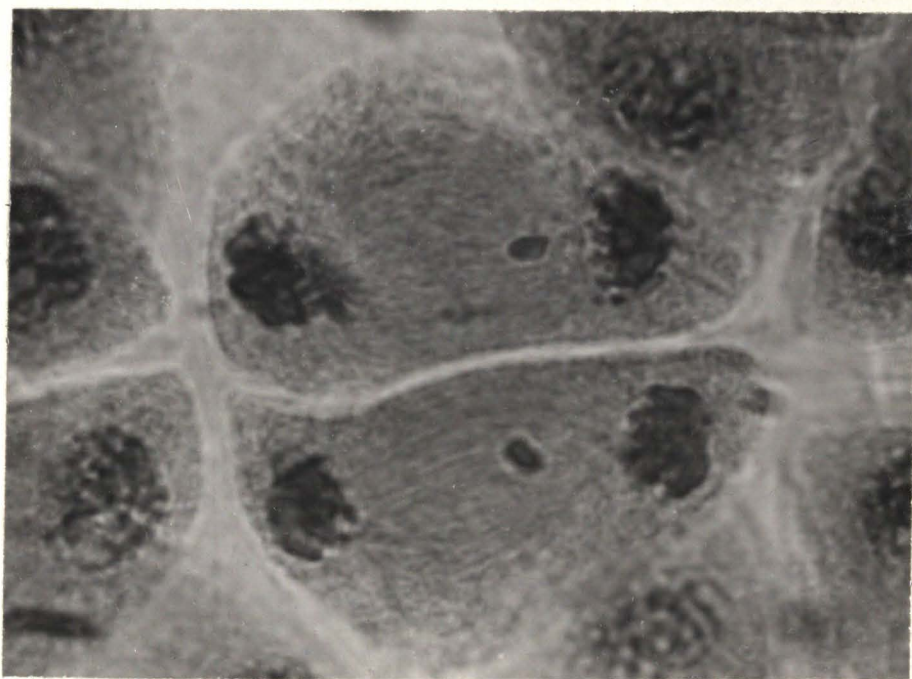


Fig. 25. Two telocentric chromosomes lagging behind in the second telophase in PMC's of line B.

Table 6. Behaviour of chromosomes of seven F₁BC₅ hybrids between seven lines and Centurk in AI-TI stages of meiosis.

F ₁ BC ₅ hybrids	Culture #	# of immune plants examined	# of cells with normal division	Type and # of univalents								IN + 2T [†]	% PMC's showing laggards	% PMC's showing misdivision
				Normal		Isos		Telos						
				1	2	1	2	1	2	3	4			
Ctk/A	978268	3	326	15	5	4	1	0	0	0	0	0	7.67	1.5
Ctk/B	279182	4	646	57	26	16	5	2	0	2	1	0	16.7	4.0
Ctk/C	279194	3	393	23	9	24	8	18	7	1	5	0	24.2	16.0
Ctk/D	279181	4	562	25	12	9	0	29	19	2	9	12	20.8	14.2
Ctk/G	978265	2	241	0	0	0	0	0	0	0	0	0	0	0
Ctk/F	978256	2	313	15	9	0	0	0	0	0	0	0	7.7	0
Ctk/J	978269	2	345	15	11	0	0	0	0	0	0	0	7.5	0

[†]One isochromosome plus two telocentric chromosomes.

CI 15092, Wong et al. (1972) reported two univalents of unequal size, one from Agropyron intermedium. Meiotic irregularity of line F in MI stage was found to be 32.1% (Table 2).

In the F_1 of CI 15092/F, 4.6% of univalents were seen (Table 4). In fact, the F_1 of CI 15092 resembled the Centurk check in regularity of meiosis. The Agropyron univalent in line F would have paired with the Agropyron chromosome in CI 15092 to form a bivalent.

Line F seems not to have a translocation.

Fig. 2 Two univalents per pollen mother cell produce a high percentage of chromosomal aberrations in the offspring. To estimate the rate of misdivision in these lines, anaphase I telophase I and anaphase II - telophase II stages of meiosis were studied. Cells with questionable figures were not included. The different types of aberrations observed in eight lines and Centurk and their F_1BC_5 's were grouped into four classes.

a. Normal division of the two lagging univalents with chromatids passing intact to opposite poles, no misdivision, (Figs. 16 and 18).

b. Isochromosomes either ring or not, which divide and go to different poles. Isochromosomes are formed by a misdivision of a chromosome at the centromere.

Fig. As a result in meiosis isochromosomes tend to pair with themselves to form a ring shaped univalent. In

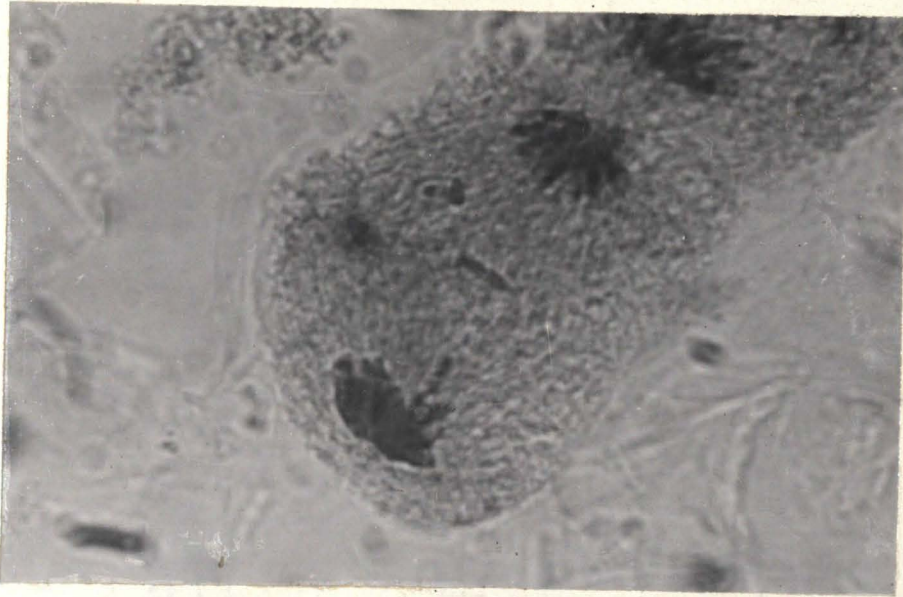


Fig. 26. Misdivision of a univalent forming long and short telocentric chromosomes in the second telophase in PMC's of Line A.

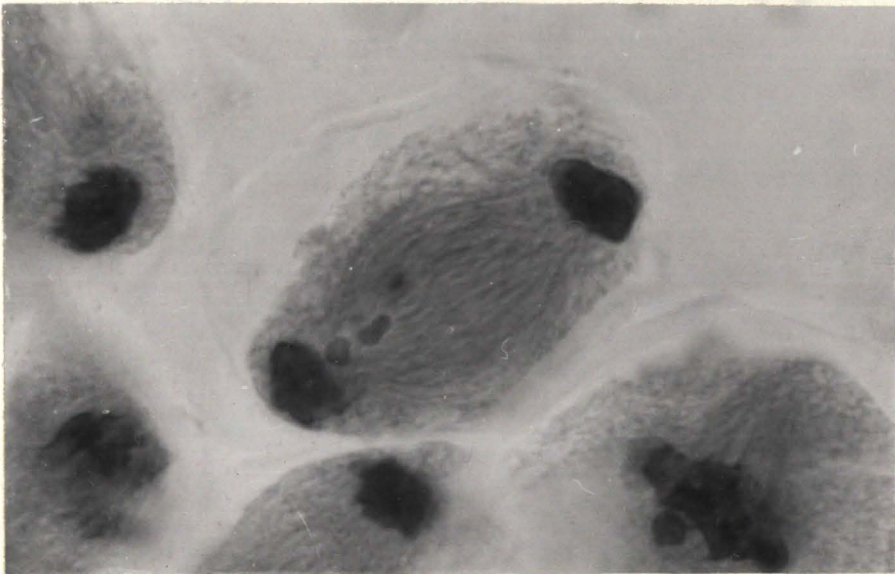


Fig. 27. Three telocentric chromosomes moving to the same pole in the second telophase in PMC's of Line D.

Table 7. Behaviour of chromosomes in AII-TII stages of meiosis in PMC's of F₇BC₄ lines studied in the field, 1978.

Line	Culture #	# of immune plants examined	# of cells with normal division	Type and # of univalents								Ii + 2T ⁺	% PMC's showing laggards	% PMC's showing misdivision
				Normal		Isos		Telos						
				1	2	1	2	1	2	3	4			
A	478302	5	427	13	19	7	10	4	1	4	0	12.5	9.22	
B	478303	5	759	24	5	14	2	64	36	5	6	16	18.5	15.4
C	478304	4	649	47	18	25	13	22	21	17	6	35	23.9	16.3
D	478305	6	614	18	6	11	6	39	25	6	6	15	17.7	14.5
G	478307	3	338	0	0	0	0	0	0	0	0	0	0	0
F	478223	3	273	25	11	11	25	17	18	9	7	9	32.6	23.7
H	478224	2	295	9	1	8	7	19	13	5	13	0	20.3	17.6
I	478225	2	179	10	7	0	0	0	0	0	0	0	0	0
Centurk	---	3	336	3	0	0	0	0	0	0	0	0	0	0

⁺One isochromosome plus two telosomic chromosomes.

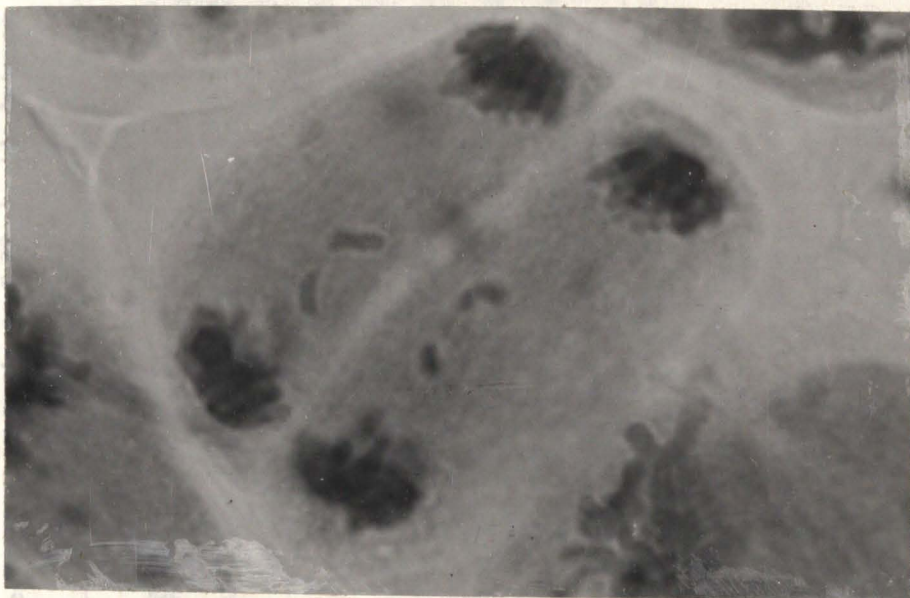


Fig. 28. Two sister chromatids just separated to form telocentric chromosomes in PMC's of Line D.

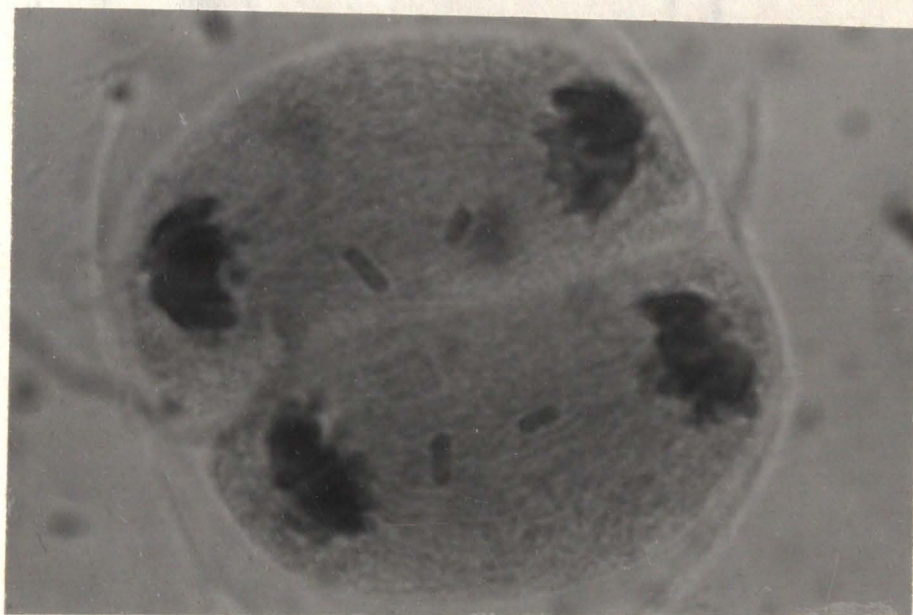


Fig. 29. Four telocentric chromosomes moving to opposite poles in second telophase in PMC's of F_1 of Centurk/line D.

Table 8. Behaviour of chromosomes in AII-TII stages of meiotic division of PMC's in F₁BC₅ hybrids between seven lines and Centurk.

F ₁ BC ₅ hybrids	Culture #	# of immune plants examined	# of cells with normal division	Type and # of univalents								11 + 21 ⁺	% PMC's showing laggards	% PMC's showing misdivision
				Normal		Isos		Telos						
				1	2	1	2	1	2	3	4			
Ctk/A	978268	4	737	25	13	13	2	24	7	9	11	0	14.11	9.0
Ctk/B	279182	7	942	98	45	39	14	42	18	8	7	9	29.7	14.5
Ctk/C	279194	3	540	25	12	13	11	25	12	13	11	0	22.6	15.7
Ctk/D	279181	4	509	44	15	32	3	37	19	2	9	0	31.6	20.0
Ctk/G	978265	5	362	6	3	0	1	0	2	0	1	0	3.6	1.1
Ctk/J	978269	1	204	21	11	6	2	9	5	4	4	3	31.9	16.2
CI 15092/F	978259	2	206	8	5	0	0	0	0	0	0	0	6.3	0

⁺One isochromosome plus two telocentric chromosomes.

this study two different ring chromosomes were observed one smaller than the other in size (Fig. 6).

c. Some cells were found having one normal univalent and two telocentric chromosomes (Fig. 25).

d. One to four telocentrics assort to the same or to opposite poles (Figs. 24, 25, 27, 28 and 29).

These four classes were described by Sears (1952a) in wheat and Sharma et al. (1975) in Agropyron intermedium.

The data in Table 5 show that line B had the highest rate of misdivision at the first meiotic division. All the different types of misdivision reported by Sears (1952a) for chromosome 5A of Chinese spring were observed. In Centurk even though 2.2% of univalents were observed, no misdivision was found in AI stage. Line G is more stable than Centurk cytologically but less fertile for reasons unknown.

The different kinds of univalents observed in seven F_1BC_5 lines, percent of PMC's showing laggards, and rate of misdivision are summarized in Table 6. No misdivision was observed in F_1BC_5 hybrids of G, F, and J with Centurk.

To determine the frequency of misdivision in AII - TII stages, parental lines and F_1BC_5 hybrids, PMC's were counted and grouped as was done at AI - TI stages (Tables 7 and 8). In the second division of meiosis a few cells with a ring isochromosome and two telocentrics were observed. It is clear from observations of late AII, that many of the second

Table 9. Occurrence of micronuclei in the lines and their meiotic indices in the field, 1978.

Line	Culture #	# of immune plants examined	No. of tetrads with indicated no. of micronuclei						Percent of tetrads with micronuclei	Meiotic ⁺ index
			0	1	2	3	4	4		
A	478302	3	460	52	19	5	2	0	14.5	85.5
B	478303	7	1269	178	52	16	4	0	16.5	83.5
C	478304	8	1659	304	182	98	48	43	28.9	71.1
D	478305	12	2035	280	49	21	11	0	15.1	84.9
G	478307	6	967	62	16	0	0	0	7.5	92.5
F	478223	4	985	344	121	41	11	1	34.5	65.5
H	478224	2	628	87	29	11	1	0	16.9	83.1
I	478225	3	730	45	14	0	0	0	8.1	91.9
Centurk	-----	6	1587	37	6	0	0	0	2.7	97.3

+Percent of tetrads without micronuclei.

Table 10. Distribution of micronuclei in tetrads of F₁BC₅ hybrids between seven lines and Centurk.

F ₁ hybrids	Culture #	# of immune plants examined	No. of tetrads with indicated no. of micronuclei						Percent of tetrads with micronuclei	Meiotic index
			0	1	2	3	4	4		
Ctk/A	978268	6	1037	117	27	14	6	0	13.7	82.3
Ctk/B	279182	8	2223	442	142	56	20	5	23.0	77.0
Ctk/C	279194	6	1310	250	68	27	16	0	27.6	72.4
Ctk/D	279181	6	1612	322	103	32	14	0	25.0	75.0
Ctk/G	978265	4	561	62	14	3	0	0	12.3	87.7
Ctk/J	978269	2	211	28	17	12	5	6	32.2	67.8
CI15092/F	978259	4	607	27	7	0	0	0	5.3	94.7

Table 11. Means across four replicates of lines and two check varieties for different characters studied in three seasons.

Character	Site ⁺	Ctk	Sage	A	B	C	D	G	E	F	H	I	J	L
1 Yield per plant (gms)	1	5.23	4.38	3.25	3.08	2.88	4.10	2.75	2.33	1.28	2.84	2.54	1.53	2.58
	2	10.30		2.37	4.75	3.86	6.75	4.46						
	3	3.30	5.81	2.71	3.96	3.21	3.71	2.26						
2 Tillers per plant	1	8	8	6	7	5	8	5	6	5	6	6	4	5
	2	10		4	6	6	10	5						
	3	7	8	5	7	6	7	4						
3 Kernels per primary spike	1	55	48	50	38	51	38	46	35	27	47	46	47	43
	2	46		26	40	36	31	31						
	3	49	44	42	48	47	40	48						
4 50-kernel weight	1	1.17	1.23	1.03	1.08	1.03	1.27	1.06	0.93	1.05	1.09	0.98	.88	1.10
	2	1.47		1.40	1.21	1.27	1.48	1.67						
	3	0.77	1.26	0.91	0.89	0.85	1.10	0.86						
5 Spikelets per primary spike	1	14	15	14	14	13	15	14	12	12	12	13	12	13
	2	15		13	14	14	13	14						
	3	14	15	14	14	15	13	14						
6 Florets per primary spike	1	59	54	60	52	63	51	58	53	45	54	58	55	55
	2	59		49	52	56	49	52						
	3	53	53	52	53	57	47	54						
7 Percent seed set	1	92	89	82	73	79	76	79	66	60	87	78	76	77
	2	80		61	78	65	64	61						
	3	94	84	82	90	75	84	85						
8 Kernels per plant	1	222	190	157	144	142	171	130	121	61	126	128	97	116
	2	317		80	188	155	223	131						
	3	218	213	160	228	184	184	134						
9 Primary spike length (cms)	1	7.7	9.4	8.0	7.6	10.2	7.9	9.5	7.4	6.8	7.6	8.0	7.9	8.4
	2	7.8		7.1	8.3	10.6	8.7	9.4						
	3	7.9	9.7	8.3	8.4	10.5	8.2	9.4						
10 Plant height (cms)	1	83	88	78	80	81	83	80	79	74	78	76	76	78
	2	107		101	106	191	97	98						
	3	74	87	73	81	81	76	76						
11 Days to flowering	1	83	84	78	74	80	71	78	83	79	81	88	79	84
	2													
	3	86	87	82	78	80	76	82						

+1 - 1978 field
 2 - 1979 spring greenhouse
 3 - 1979 field

division laggards were not included in the telophase nuclei and consequently appeared as micronuclei in the spore quartets. Data are presented in Tables 9 and 10 for number of micronuclei in quartets and meiotic indices of parental lines and their F_1BC_5 hybrids. Line G was second to Centurk in meiotic index (Table 9). All lines had lower indices than Centurk (Table 10). Indices varied from 72% to 88% for the five translocation lines. The F_1 of CI 15092/F, a cross between disomic additions, was the most stable with a meiotic index of 95%. Loss of chromosomes by direct observation at the quartet stage can be compared with the self-fertility of the lines (Table 11).

A univalent chromosome may divide equationally at anaphase I or it may misdivide. The products of misdivision may be two telocentrics, four telocentrics, two isochromosomes (one for each arm), or one telocentric and one isochromosome. The logical sources, then, of secondary trisomics are the genotypes with univalent chromosomes. Depending on the frequency of lagging and misdivision of the univalent, n and $n-1$ spores are produced. An appreciable proportion of $n-1$ megaspores abort due to the imbalance caused by the missing chromosome (Khush, 1971).

AGRONOMIC STUDIES

The design used in three experiments on agronomic performance more or less compensated for soil heterogeneity

Table 12. Mean squares for the characters studied in a 1978 test in the field.

Source of Variation	Degrees of Freedom	Mean Squares				
		Grain yield per plant	50-kernel weight	Tillers per plant	Kernels per primary spike	Kernels per plant
Blocks	3	10.75**	0.26**	20.54**	377.08	15464.92
Lines	11	34.0**	0.32*	48.52**	1957.44**	47995.27**
Blocks*Lines	32	3.46	0.05	6.74	155.57	6099.38
Error	309	2.29	0.03	4.47	122.01	4072.79

Table 12 (cont.). Mean squares for the characters studied in a 1979 test in the greenhouse.

Source of Variation	Degrees of Freedom	Florets per primary spike	Percent seed set	Spikelets per primary spike	Height of primary spike	Plant height
Blocks	3	377.57**	1226.84**	6.83*	0.87	259.12**
Lines	11	768.59**	2228.55**	43.81**	31.40**	432.30**
Blocks*Lines	32	55.18	280.88	3.09	0.98	96.48
Error	309	36.54	242.75	1.78	0.36	24.09

*, **Mean squares are significant at the 0.05 and 0.01 probability levels, respectively.

Table 13. Mean squares for the characters studied in a 1979 test in the greenhouse.

Source of Variation	Degrees of Freedom	Mean Squares				
		Grain yield per plant	50-kernel weight	Tillers per plant	Kernels per primary spike	Kernels per plant
Blocks	3	12.56	1.06	4.52	71.05	10062.38
Lines	5	93.04**	4.90**	65.60**	643.48**	77202.16**
Blocks*Lines	15	15.42**	0.21**	32.89*	41.45*	10880.57*
Error	48	5.64	0.08	4.54	38.15	4494.53

Table 13 (cont.). Mean squares for the characters studied in a 1979 test in the greenhouse.

Source of Variation	Degrees of Freedom	Florets per primary spike	Percent seed set	Spikelets per primary spike	Height of primary spike	Plant height
Blocks	3	12.76	212.94	1.72	0.75	353.00
Lines	5	210.22**	1168.98**	10.32**	16.66**	221.26*
Blocks*Lines	15	27.86	48.57	1.63	1.63	201.17**
Error	48	22.18	88.9	1.29	0.23	75.15

*, **Mean squares are significant at 0.05 and .01 probability levels, respectively.

Table 14. Mean squares for the characters studied in a 1979 test in the field.

Source of Variation	Degrees of Freedom	Mean Squares				
		Grain yield per plant	50-kernel weight	Tillers per plant	Kernels per primary spike	Kernels per plant
Blocks	3	14.97**	0.30	20.20	371.07**	43148.45**
Lines	5	14.17**	0.41**	55.63**	408.80**	44639.37**
Blocks*Lines	15	4.75	0.03	6.16	44.06	15375.54
Error	181	3.02	0.02	6.20	76.81	9435.94

Table 14 (cont.). Mean squares for the characters studied in a 1979 test in the field.

Source of Variation	Degrees of Freedom	Florets per primary spike	Percent seed set	Spikelets per primary spike	Height of primary spike	Plant height
Blocks	3	141.34*	270.56	6.87*	5.51**	101.07
Lines	5	370.47**	1139.20**	29.83**	34.28**	379.48**
Blocks*Lines	15	61.91	101.25	4.34	1.28	60.35
Error	181	37.78	110.37	2.02	0.57	50.95

*, **Mean squares are significant at the 0.05 and 0.01 probability levels, respectively.

because of randomization and replication. An analysis of variance was done on plots of Centurk alone. Since the variance between the plots of Centurk was not significant, an analysis of variance was calculated for all the characters studied.

Averaged results of three agronomic tests for the different characters are presented in Table 11. Grain yield and yield components, which are tillers per plant, kernels per primary spike, and weight of 50 kernels were usually lower for the lines than for Centurk except for line D in tillers per plant (8) and line G in 50 kernel weight (1.27). Lines E, F, H, I, J and L are inferior to lines A, B, C, D and G for all the characters studied. This must be due to the effect of the whole Agropyron chromosome present in the former lines.

Mean squares for the characters studied in three experiments are presented in Tables 12, 13 and 14. Mean squares associated with lines were highly significant in all but one instance for all the characters studied in three experiments indicating that the genotypes differed from each other in grain yield and yield components. The block x line interaction was significant in the 1979 experiment in the greenhouse. The only apparent reason may be differential leaf burn caused by an excessive dose of Cygon.

Only lines B and D out yielded Centurk in the 1979 field trial, due to more kernels per plant and larger seeds

Table 15. Simple correlation coefficients for the characters across immune lines studied.

Character	Site	TPP	KPS	SDWT	SPS	FPS	PSS	KPP	PSL	PLHT
Grain yield per plant (yld)	1	0.644**	0.458**	0.533**	0.280**	0.319**	0.442**	0.930**	0.055	0.394**
	2	0.908**	0.643**	0.513**	0.495**	0.544**	0.530**	0.961**	-0.054	0.610**
	3	0.811**	0.355**	0.234**	0.246**	0.283**	0.253**	0.947**	0.180*	0.576**
Tillers per plant (TPP)	1		0.085**	0.255**	-0.033	-0.030	0.146**	0.662**	-0.216**	0.324**
	2		0.515	0.349**	0.345**	0.401**	0.443*	0.929**	-0.309	0.509**
	3		0.213**	0.025	0.168**	0.187**	0.132	0.838**	0.025	0.465**
Kernels per primary spike (KPS)	1			0.152**	0.642**	0.752**	0.902**	0.501**	0.463**	0.145**
	2			0.116	0.669**	0.757**	0.920**	0.707**	0.077	0.577**
	3			-0.102	0.603**	0.732**	0.760**	0.414**	0.359**	0.351**
50-kernel weight (SDWT)	1				0.002	-0.002	0.211**	0.373**	-0.084	0.310**
	2				0.360**	0.301**	-0.035	0.363**	0.060	0.403**
	3				-0.233**	-0.172*	0.012	0.002	-0.008	0.164**
Spikelets per	1					0.907**	0.320**	0.487**	0.718**	0.162**
	2					0.935**	0.382**	0.321**	0.336**	0.509**
	3					0.930**	0.011	0.327**	0.678**	0.480**
Florets per primary spike (FPS)	1						0.412**	0.375**	0.626**	0.147**
	2						0.467**	0.557**	0.296*	0.500**
	3						0.133	0.358**	0.638**	0.480**
Percent seed set (PSS)	1							0.902**	0.243**	0.120*
	2							0.920**	-0.020	0.496**
	3							0.760**	-0.055	0.064
Kernels per plant (KPP)	1								0.106*	0.403**
	2								-0.034	0.638**
	3								0.164*	0.564**
Primary spike length (PSL)	1									-0.015
	2									0.051
	3									0.419**

1 = 1978 field (11 entries)

2 = 1979 spring greenhouse (5 entries)

3 = 1979 field (5 entries)

* and **Significant at 5% and 1% levels of probability, respectively.

respectively (Table 11). These results are in good agreement with those of Sandhu (1978). Centurk is known as a good responsive variety across varied climatic conditions. In the 1979 summer test the soil was often dry, air temperatures were high, and Centurk was shorter than normal.

The fertility of the lines was inferior to Centurk. The fertility of Centurk was high in the field tests which agrees with the high meiotic index (Table 9). Centurk in the greenhouse had a meiotic index of 97% while the seed set was 92% and 94% in 1978 and 1979 field tests respectively. The percent seed set in the greenhouse test in 1979 was rather low, which could have been due to the burning effect of Cygon insecticide or poor pollen development.

Owing to the disturbances observed at different stages of meiosis, the percent seed set of the lines was low. The percent seed set of the lines is in good agreement with their meiotic indices. For line G, even though there was no considerable degree of disturbance at meiosis, seed set of this line was still inferior to Centurk. This may be due to genetic or physiological effects. It is clear that yield loss in translocation lines is not entirely due to meiotic irregularities. From the cytological observations of F_1BC_5 PMC's, it is understood that there is frequently a loss of wheat chromatin. The wheat chromatin replaced by Agropyron chromatin must have contained some genes for yield or yield

Table 16. Coefficients of determination (r^2) for the dependent variable, yield versus the three components of yield.

Character	1978 field	1979 greenhouse	1979 field
Tillers per plant (TPP)	0.415	0.825	0.662
TPP + 50-kernel weight	0.561	0.869	0.713
Other characters	0.699	0.914	0.750

components.

In wheat, grain yield is determined by number of tillers, number of kernels per spike and kernel weight. Only line G equalled Centurk in tillers per plant. Number of kernels per spike of the lines were inferior to Centurk.

Line D equalled Centurk in number of tillers per plant and yielded next to Centurk in 1978 field and the 1979 greenhouse tests. Line D had larger seeds than Centurk. Line D was earlier in flowering than the others. Line A, B, C, D and G were earlier than Centurk and were of course the ones having translocations. In the other lines, the whole alien chromosome probably conferred lateness.

Weight of 50 kernels was significantly different between the lines at 0.01 level of probability. Only the D translocation line had larger kernels than Sage in one test.

Positive and high correlation was found for seed weight and yield (significant at 0.01 level of probability in three experiments, Table 15). Even though line D had good seed weight, its reduced yield compared with Centurk was mainly due to fewer kernels per plant and an inferior seed set. Large seed size alone cannot produce a high yield. Tillers per plant and kernels per spike were positively and highly correlated in three tests. The high positive correlations observed between these characters is encouraged for their simultaneous improvement.

From the multiple regression analysis (table 16) it is known that the number of tillers per plant is the most influential in determining yield and 50 kernel weight second in importance. Seeds per head is least influential of the yield components in affecting yield.

The lower yield of the lines, all of which preponderantly have Centurk germplasm, as caused by loss of important wheat chromatin through irradiation. Desynapsis and misdivision of univalents may have contributed to lower yield by reducing fertility.

Morphological differences were observed between Centurk and the translocation lines. The lines had more erect and fewer leaves than Centurk. Line C lacked auricles on the leaf sheath.

DISCUSSION

Many relatives of wheat and other crop plants carry genes of some potential for crop improvement. Genes from Agropyron are simple to handle and most useful (Driscoll, 1965). If immunity, for instance, conferred by a gene in Agropyron and is located near the end of the chromosome, then an easy transfer can be obtained by simple exchange of distal ends between wheat and Agropyron chromosomes (Fig.30a). However, if the gene concerned lies near the centromere of the alien chromosome, three types of transfers are theoretically possible.

It is possible by irradiation to break the alien chromosome at two points and transfer the segment with the gene for resistance to a position within a wheat chromosome (Fig. 30b). This type of transfer, if the segment is small, limits to a minimum amount of alien chromatin carrying potentially deleterious genes and may reduce the loss of important wheat chromatin. This type of transfer is called "intercalary" and while it is the most favorable one, it is very rare (Sears, 1956).

The second possibility called "reciprocal translocation" results from a break at or within the centromere and the transfer of a whole arm of or part of the arm of the alien chromosome (Fig. 30c). As a result, many possibly deleterious genes along with the gene for resistance will be transferred. The possibility of losing important wheat

genes is high. However, in some cases detrimental effects may be minimal with loss of a wheat segment since the entire arm of certain wheat chromosomes such as 2B can be lost without much affect at least on seed yield.

A third kind of transfer involves a break on the wheat chromosome beyond and not involving the centromere (Fig. 30d). In this type of translocation, also called reciprocal, how much of the alien genetic material is added to the wheat chromosome depends on where the breaks occur.

The lines A, B, C, D and G studied here were found to have reciprocal translocations. None of the lines involved an intercalary translocation. From genetic data obtained by Sandhu (1978), it was clear that a single dominant gene is responsible for immunity to WSMV. From the study of PMC's of the F_1BC_5 of translocation lines, crossed to Centurk, I have learned that the gene responsible for immunity to wheat streak mosaic lies closer to the centromere than it does to the distal end. The heteromorphic bivalent observed (Fig. 2a) in a diakinesis of Ctk/D resembled a long telocentric chromosome. The conclusion that there is a heteromorphic bivalent here as evidenced by its shape is supported by the results of Sears (1956) for translocation 36, and Winhues (1966) for T7. The theoretical origin of the kind of reciprocal translocation found here is shown in Fig. 30d, after Winhues (1966). Most of the translocation lines obtained

by Weinhues had a centromere from Agropyron.

The PMC's of plants in translocation line D were found to have 21 bivalents in diakinesis (Fig. 5). In F_1BC_5 hybrids, the unchanged chromosome of Centurk paired with the interchanged chromosome of line D, to form a heteromorphic rod bivalent with only one chiasma. As shown in Fig. 30d, a break occurred on the alien chromosome through the centromere. A second break may have occurred beyond the gene for immunity but so as to omit a distal portion. A single break on one of the arms of the wheat chromosomes occurred. In the process of rejoining, a new chromosome was formed with an Agropyron centromere and a segment having a gene for immunity. In F_1BC_5 hybrids, the newly formed chromosome paired with the unchanged homologue of Centurk to form a heteromorphic rod bivalent. Other unchanged chromosomes from both parents produced 20 ring bivalents.

If an intercalary translocation had occurred, 21 ring bivalents would be expected both in the heterozygous and homozygous state. On the other hand, if a reciprocal translocation had been produced immediately following radiation in the X_1 plant, a heteromorphic trivalent would appear consisting of these two wheat-Agropyron chromosomes in X_1 pairing with the unchanged homologue to form a heteromorphic trivalent. The immune plants in the present study were at F_7BC_4 . At this point in the propagation of inoculated generations, the wheat-Agropyron chromosome which does

not have a gene for immunity would confer susceptibility and be subject to elimination by selection pressure. In the next backcross generation (F_1BC_5) the wheat-Agropyron chromosome with the gene for immunity would pair with its unchanged homologue to form a heteromorphic bivalent.

It is clear that none of the translocation lines studied here had an intercalary transfer because heteromorphic rod bivalents were observed rather than open bivalents in F_1BC_5 hybrids with Centurk lines A, B, C, D and G.

As explained earlier, only line D has an Agropyron centromere with a gene for immunity. Lines A, B, C and G have the wheat centromere and more or less of the alien arm. (Figs. 3, 4, 7 and 8). The heteromorphic bivalents observed in F_1BC_5 hybrids of lines A, B, C, and G are long and easily distinguishable from other bivalents. The translocations obtained in A, B, C and G would fit the model shown in Fig. 30c, which explains the possible origin of translocations. The heteromorphic bivalents of F_1 hybrids of lines A and B are different from heteromorphic bivalents of lines C and G in their shape, length and morphology due possibly to the involvement of the other members of the homoeologous group, 4A and 4D.

CI 15092 is a disomic substitution line in which a pair of 4B chromosomes were replaced by their homoeologues from Agropyron intermedium (Larson 1973, Wells personal

communication, Wang et al. 1977a. Most of the best translocation lines are interchanges within homoeologous groups of chromosomes (Dvorak and Knott, 1977). Knott (1968) pointed out that due to somatic association of homoeologous chromosomes, the frequency of radiation induced transfers involving homoeologues is high. He further hypothesized that most of the radiation induced transfers devoid of deleterious effects must have involved not only homoeologues but also corresponding segments of homoeologues. The validity of this hypothesis has been proven on a radiation-induced translocation which involved 7el of Agropyron and 7D of wheat. It is rather clear that the homozygous lines used in this study have deleterious effects. Transmission rates of the translocation chromosomes in heterozygotes is also good (Sandhu, 1978). The high frequency of reasonably good phenotypes of translocation lines support Knott's hypothesis that translocations may have involved only chromosomes of the 4th homoeologous group.

The reason for the absence of deleterious effects in some translocation lines and their presence in other lines, depends on the ability of the alien chromatin to compensate for the displaced wheat chromatin. Lines A, B, C, D and G can be considered as compensating translocations even though they are inferior to Centurk. Despite the loss of wheat chromatin, lines B and D fared fairly

well in agronomic tests.

In some translocation lines, reported in the literature, the Agropyron chromatin cannot substitute properly. This may be due to the involvement in the transfer of chromosomes that are not homoeologous between wheat and Agropyron. One effect is poor transfer, through pollen. Such translocations are always reproduced as heterozygotes (Weinhues, 1966).

Immune plants in lines E, H, I, J and L which have the whole alien chromosome always give rise to susceptible plants (Table 2). In these lines the degree of compensation may not be good. Twenty-five translocation lines obtained by Weinhues behaved inconsistently in rust reaction. The susceptible plants might have been due to poor transmission of the translocated segment through pollen or to the segregation of an Agropyron univalent through pollen. Chromosome spreading was not seen in these lines at diakinesis.

In line F in the MI stage, there were 34 PMC's among 547 (6.37%) that had one lagging bivalent and a lagging univalent. The univalent appeared to be from Agropyron because of its smallness. In 15.1% of the cells there were two univalents of unequal size. These results indicate that the whole chromosome of Agropyron intermedium is present in Line F. The cytological data on this line are not in agreement with the genetic data obtained by Sandhu (1978).

Line F seems not to be involved in an interchange.

The deterioration of the Centurk phenotype and cytological aberrations in the translocation lines must be due to the exchange of chromatin. In F_1BC_5 hybrids of Ctk/B, separation of a heteromorphic bivalent was observed in a few cells. Since so few cells were observed with desynapsis of the ring bivalent, no attempt was made to estimate the rate of desynapsis of the heteromorphic bivalent. This explains the higher frequency of univalents observed in PMC's of Ctk/B plants. Fu and Sears (1973), reported separation of heteromorphic bivalents at MI in F_1 hybrids involving the variety "Transfer".

Love (1951) saw two possible sources of meiotic abnormalities leading to the complete disintegration of quartets. One was the failure of pairing due to a lack of complete homology. A second was the genetic disturbance of the meiotic process. Love found that lagging bivalents and the presence of univalents in some cells led to the production of abnormal pollen and a low meiotic index.

The partial sterility observed in the present investigation might be due to lagging of bivalents and univalents. It is difficult to properly interpret the results obtained in the present investigation. The lagging bivalents at MI in Centurk must have been characteristic of the Centurk genotype or due to an environmental factor. Love found that a line 2787C was the source of genes causing

meiotic disturbances in the Brazilian varieties Esteara, Oiten and Rio Negro.

The genes present in the lagging bivalent in Centurk might influence desynapsis in hybrids. Lagging of bivalents in some cells in MI and the presence of two univalents of equal size support the idea that one of the lagging bivalents desynapsed producing two univalents. Unpaired chromosomes lagged behind the bivalents in the MI stage. Usually not more than one bivalent was involved in failure of pairing. Darlington (1940) reported lagging of bivalents in Podophyllum versipelle. He also reported that the non-congression and non-orientation of bivalents was due to failure of repulsion. Dvorak (1972b) attributed the failure of synapsis and crossing-over between already paired chromosomes to the absence of the synaptonemal complex. This results in an enormous variation in chiasmata from nucleus to nucleus. However, there appeared to be no major disturbance of the meiotic process due to lagging univalents. At least two univalents per pollen mother cell may result in a higher percentage of chromosomal aberrations in the offspring.

Soost (1951) found in tomato that cells with reduced pairing have univalents at meiosis I and these cells produced inviable gametes due to misdivision at anaphase I and II. Steinitz-Sears found 14.6% of misdivision in Thatcher (monosomic 3B) and 26.9% in Red Egyptian. The misdivision

rates in the present study ranged from 1.1% to 20.0% at A II. The frequency of misdivision is high in these lines. An alternative explanation cannot easily be put forward. At best, it can be guessed that the more lagging univalents there are, the higher the frequency of misdivision. The relative frequency of isochromosomes and telocentric chromosomes observed in Meiosis II (Tables 7 and 8) agree with what is expected based upon cytological studies, an increase in their prevalence in A II. The relatively low meiotic indices observed in translocation lines are due to the loss of wheat chromatin in meiosis, especially the loss of telocentric chromosomes at the M II division. Deficient pollen rarely functions in competition with normal pollen.

At the first division of meiosis, univalents undergo a variety of types of misdivision, producing both isochromosomes and telocentric chromosomes. At the second division, some of the normal univalents, which escaped misdivision in the MI undergo misdivision and form telocentric chromosomes. Telocentric chromosomes formed at the second division tend to be lost (Sears, 1952a). No isochromosomes or telocentric chromosomes were observed in F_1BC_5 hybrids at the MI stage. Since they appeared at A1-T1 stages, misdivision of the centromere must have taken place at AI stage. Steinitz-Sears observed misdivision in monosomic 3B lines of Thatcher at the MI stage. The ring isochromosomes observed at diakinesis and MI stages in parental lines must have

originated in the previous generation.

Isochromosomes are of maternal origin (Sears 1952b). Small ring chromosomes appeared throughout meiosis. The large ring chromosome must have been subjected to a second misdivision. One ring chromosome and two telocentrics observed at AII - TII support the conclusion that large ring chromosomes are subjected to a second division. The increase of the rate of misdivision from AI to AII results from a second misdivision of univalents which escaped misdivision in meiosis I and of isochromosomes at AII.

Misdivision in meiosis II consists of the pulling apart of the two arms at the centromere (Fig. 28).

Sanchez-Mange (1950) grouped misdivisions in meiosis II into two classes: (1) a - misdivisions (attraction)-(misdivisions) which are due to early separation of the centromere into two halves; (2) p - misdivisions (push-misdivisions) in which the centromere is pulled apart only after the two arms have moved toward opposite poles. Based on this assumption, the misdivision observed at AII may belong to the push-misdivision class.

It is clear that the chromosome pair involved in interchange was not subject to desynapsis and misdivision because the five lines bred true for immunity. Lagging of bivalents and univalents were also observed in the Centurk check at a low frequency (3%). Centurk is the recurrent parent of the translocation lines in this study.

Moens (1969) pointed out that temperature, chemicals and chromosomal and point mutations can interfere with synapsis of chromosomes. Love pointed out that if a bivalent lags at MI, Mendelian ratios may not occur for a particular locus present on the lagging chromosome. Misdivision rates are higher in translocation lines than in F_1 hybrids.

The consequence of translocation and desynapsis was a lower potential grain yield by the translocation lines. Loss of yield in these lines is due to an indirect effect of cytological abnormalities on yield components and Agropyron genes. Yield is quantitatively inherited, literally hundreds of genes being involved (Shebeski and Evans, 1973). Because the number of tillers is influenced by the environment, no firm conclusion can be drawn about effect on number of tillers of translocation lines. Some spikes have shown sterile florets resulting in low percent seed set and few kernels per plant. A study of correlations between the characters showed that many tillers per plant and a high set of seed were positively correlated with many kernels per plant. A second factor which played an important role in determination of yield was the 50-kernel weight which is also positively correlated with yield.

Among the translocation lines used in this study, lines B and D outyielded Centurk in 1979 agronomic tests. These two lines were earlier than Centurk. Line D exceeded Centurk in 50-kernel weight, but fewer seeds per head

probably caused them to be larger than they otherwise would have been. Improvement in number of kernels per spike and percent seed set would make line D a potential variety. Because of immunity from WSMV, earliness, and larger seed, line D may be useful in breeding programs.

Use of the translocation lines in breeding programs, may require many crosses to fit a resistance gene into a congenial genotype. The transmission rate of a translocation through gametes is affected by the genotypes of gametes carrying the translocations. The translocations showed normal rates of transmission to progeny (Sandhu, 1978).

Weinhues was able to incorporate some translocations in varieties such as Rabe. Sharma and Singh (1967) found that the rate of transmission of translocation T4 was considerably lower in Indian wheat varieties than in Canadian varieties. A high rate of transmission of a translocation is advantageous in breeding programs. In order to develop translocation D as a variety, selection for cytological stability and for good plant type needs to be done.

Rupert et al. (1974) increased the seed set in Triticale by selecting plants for cytological stability and good plant type. Improving the fertility of line D would increase its yield. Weinhues suggested selection of favorable backcross lines to recover high yield.

SUMMARY

Cytological study of PMC's showed that lines A, B, C, D and G contained reciprocal translocations. In F_1BC_5 of those lines with Centurk, there were twenty open bivalents and one heteromorphic rod bivalent at diakinesis. The cytological instability of lines varied from less than to more than Centurk. Bivalents and univalents were found lagging at MI stage of meiosis. It was concluded that two univalents resulting from the desynapsis of a bivalent and subjected to misdivision gave rise to isochromosomes and telocentric chromosomes. The meiotic indices of lines were rather low compared to the recurrent parent Centurk. The translocation chromosomes in the five lines were unlike in appearance. The shortest were in A and B. The longest were in C and G. In D a whole arm and the centromere were from Agropyron. Because the five lines bred true for immunity, the cytological irregularities noted must have involved chromosomes other than the translocated member.

The results of this study suggest that all the translocation lines have too large a chromatin segment from Agropyron for them to be of commercial value. Line G, however, had larger seed than Centurk and was more stable cytologically than Centurk. It may then be a promising parent and also the object of efforts to diminish its amount of Agropyron chromatin. Line D had some favorable qualities, too, for use as a parent.

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