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Harneek S. Sandhu

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THE TRANSFER OF RESISTANCE TO WHEAT STREAK MOSAIC VIRUS (WSMV)  
FROM WHEATGRASS (AGROPYRON INTERMEDIUM (HOST.) BEAUV.) TO COMMON  
WHEAT (TRITICUM AESTIVUM L. EM. THELL.) BY IRRADIATION

BY

HARNEK S. SANDHU

A thesis submitted  
in partial fulfillment of the requirements for the  
degree of Doctor of Philosophy, Major in  
Agronomy (Genetics and Cytogenetics),  
South Dakota State University  
1978

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FROM WHEATGRASS (AGROPYRON INTERMEDIUM (HOST.) BEAUV.) TO COMMON  
WHEAT (TRITICUM AESTIVUM L. EM. THELL.) BY IRRADIATION

This thesis is approved as a creditable and independent investi-  
gation by a candidate for the degree, Doctor of Philosophy, and is  
acceptable for meeting the thesis requirements for this degree.  
Acceptance of this thesis does not imply that the conclusions reached  
by the candidate are necessarily the conclusions of the major department.

Head, Plant Science Department

Date

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H.S.S.



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Abstract

HARNEK S. SANDHU

Under the supervision of Professor Darrell G. Wells

A virus disease, wheat streak mosaic, has been an important, unsolved problem of winter wheat which is a major crop in South Dakota.  $F_1BC_3$  monosomic alien addition seeds having three doses of Centurk were irradiated with fast neutrons to translocate a segment of the alien chromosome accounting for immunity from wheat streak mosaic virus to a Centurk chromosome. Immune plants from the irradiated seeds were used as male parents onto Centurk and about 2,000  $F_1BC_4$  seeds obtained.

Cytological examination of pollen mother cells of 151 resistant  $F_1BC_4$  plants indicated that the majority of the plants continued to have an apparent alien univalent present in addition to the wheat complement.

Fourteen suspected translocations were identified in  $F_2BC_4$  on the basis of genetic segregation. The breeding behavior of nine of these 14 was studied in  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_6BC_4$  and  $F_2$  generations. Most of these lines became more stable with advancing generations. Pollen mother cells of 37 plants in  $F_3BC_4$  and  $F_4BC_4$  were examined cytologically and 21 bivalents counted.

The frequency of transmission of the translocations through male and female gametes of translocation heterozygotes was found to be about 50 percent since in the  $F_2$  generation involving translocation lines

A, B, C, D and G, 81, 75, 75, 78 and 78 percent of the progeny were resistant. In line F, however, immunity was transmitted with a reduced frequency of 68 percent.

A test to evaluate the effects of the suspected translocations on agronomic qualities and yield components of the plants indicated that all the translocation lines except D1 had less tillers per plant than the recurrent parent, Centurk. Fertility in the main tiller was higher in translocation lines C1 and D1 than Centurk. All the resistant lines tested in the field were shorter and headed earlier than Centurk except line E2, which headed three days after Centurk. Seeds were larger in all the lines than Centurk except lines B and C. Number of seeds in the main spike was lower in all the lines except C1. Yield per plant was also lower in all the lines.

Variation in the frequency of transmission of resistance through male and female gametes, plant height, tillers per plant, percent fertility in the main spike, number of seeds in the main tiller, seed size, yield and heading date of the six suspected translocation lines indicate that the substitution of the A. intermedium chromatin for the different segments of a Centurk chromosome had varying effects.

The genetic data show that resistance is controlled by a single dominant gene. Translocation of the gene from A. intermedium to a Centurk chromosome did not affect the expression of resistance.

The study provided at least six translocation lines, some of which may possibly be used as direct releases or certainly as parents to incorporate resistance to wheat streak mosaic virus into commercial varieties.

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## INTRODUCTION

Wheat is an important crop in South Dakota. Spring and winter wheat are seeded on over 3.6 million acres annually producing more than 76 million bushels of grain, an average of 21 bushels per acre.

Many factors have been recognized as responsible for low yields. Next to leaf and stem rust, wheat streak mosaic virus has attracted the most attention as a destructive disease of winter wheat in the Great Plains.

Wheat streak mosaic (WSM) was first collected by G. L. Peltier in 1922 in Nebraska (McKinney, 1953). In Kansas, wheat streak mosaic was collected and identified at Salina as early as 1932; but according to L. E. Melchers, similar viruses were present before 1930. The first report of WSMV in South Dakota came in June, 1949; but there were indications of its being present earlier also (Slykhuis, 1952). McKinney (1953) stated that the disease was present in Western Iowa, Oklahoma, Arizona, California, Washington, Colorado, New Mexico, Montana, North Dakota and Canadian provinces of Southern Alberta, Ontario, Saskatchewan and British Columbia.

Wheat streak mosaic is a disease of winter wheat, but it more or less affects spring wheat, corn, oats, barley and other spring sown crops grown in the vicinity of infected winter wheat. Recently, it has been found that corn lethal necrosis is produced from a synergistic reaction of maize chlorotic mottle virus (MCMV) with either or both

of WSMV and maize dwarf mosaic virus (MDMV) (Niblett and Claflin, 1978).

In wheat, the leaf symptoms consist of characteristic pale green and yellow streaks followed by a more severe blotchy condition. Infected plants are rarely killed, but they can be affected to such an extent as to reduce or prevent seed production. At maturity, the plants are stunted and produce fewer heads than healthy plants. Many times a field is not worth harvesting. Yield reduction by wheat streak mosaic virus (WSMV) in Kansas was estimated at 20, 40, and 30 million bushels in 1949, 1959, and 1974 respectively (Niblett et al., 1974). The average annual loss in yield due to WSMV in South Dakota for the last several years has been estimated at 2 to 5 percent with some isolated areas suffering losses as heavy as 20 to 40 percent (L. S. Wood, personal communication).

Wheat streak mosaic virus is carried and transmitted from plant to plant and spread from field to field by a tiny wind-blown eriophyid mite, Aceria tulipae Keifer (Slykhuis, 1955). Due to their small size (210-250 x 50-60 micron), mites can be carried a long way by strong air currents adding to the difficulty of control. Mite populations can be controlled by a miticide so as to limit wheat streak mosaic but at a prohibitory cost.

The best method of control is to develop varieties resistant, either to WSMV or to its vector mite, Aceria tulipae Keifer. Less successful methods of controlling WSMV are clean cultivation, i.e., destroying volunteer seedlings, and late seeding (Nagel, 1960; Slykhuis, 1957; Staples and Allington, 1956). It is difficult to follow the

cultural practice of late seeding. Farmers do not base their seeding date entirely on the threat of WSMV. They consider soil moisture, amount of fall growth necessary to reduce erosion, number of acres to be seeded in the time available, and additional income from fall grazing. Varieties of winter wheat immune from WSMV are needed badly and will be beneficial to the farmers.

Large numbers of wheat varieties have been tested against WSMV. All reports thus far indicate that there is not a high degree of resistance to WSMV among the cultivated wheat varieties (Andrews and Slykhuis, 1956; Bellingham et al., 1957; Fellows and Schmidt, 1953; McKinney and Sando, 1951; McNeal and Carroll, 1968; Sebesta and Bellingham, 1966; Sill et al., 1964; Schmidt et al., 1956; and Slykhuis, 1955). The most promising sources of immunity are Agropyron elongatum (Host.) Beauv. and A. intermedium (Host.) Beauv. Several attempts have been made to transfer the available immunity from Agropyron to wheat by hybridization. The immune Triticum-Agropyron lines so formed usually have more than 42 chromosomes. The Agropyron chromosome carrying immunity does not pair with wheat chromosomes. Thus, the development of wheat immune from wheat streak mosaic virus is initially a cytogenetic problem.

Sears (1956) developed a method to transfer alien genetic material from substitution or addition lines by irradiation. He successfully transferred leaf rust resistance from Aegilops umbellulata to common wheat. Larter and Elliott (1956) used ionizing radiation to transfer a gene or genes for bunt resistance from an Agrotricum derivative to a hexaploid winter wheat (Triticum compactum). Elliott (1957) and Knott

(1961) successfully transferred stem rust resistance from Agropyron elongatum to common wheat by irradiation. Sharma and Knott (1966) successfully transferred a segment carrying leaf rust resistance from Agropyron elongatum to common wheat. Wienhues (1963) transferred stem rust resistance from Agropyron intermedium to wheat by radiation.

The present investigation deals with the transfer of a portion of an Agropyron intermedium chromosome carrying the gene or genes for wheat streak mosaic virus immunity to a Centurk chromosome.

## REVIEW OF LITERATURE

The use of Agropyron species as a possible source of disease resistance and other desirable characters was suggested by McFadden in 1928 (McFadden and Sears, 1947). The first successful cross of Triticum with Agropyron was made by Tzitzin of Russia in 1930, who crossed Triticum vulgare with Agropyron intermedium (Verushkine and Shechurdine, 1933). According to Vakar (1936), hard and soft common wheats were first crossed with A. elongatum in 1932. The first fertile Triticum by Agropyron hybrids made by North American plant breeders were produced in 1935 (Reitz et al., 1945).

Cross compatibility relationships between species of Triticum and Agropyron were studied by White (1940). He reported that A. elongatum, A. intermedium, and A. trichophorum were successfully hybridized with common wheat. Agropyron elongatum was found more compatible with wheat than A. glaucum. According to Armstrong (1945), A. elongatum and A. glaucum are the species extensively used in crosses with wheat. But the most desirable Agrotricum hybrids have come from crosses with A. elongatum as the wheatgrass parent (Marshall and Schmidt, 1954).

Agrotricum hybrids studied by Lapin (1936) were resistant to drought, salinity, and fungi. Tzitzin (1940) also claimed success in combining several characters like exceptionally high baking quality and resistance to bunt, smut, frost, lodging and shattering in one agrotricum hybrid. Johnston (1940) studied 15 species of Agropyron for their resistance to leaf rust. His investigations indicated that 12 of

the species studied were resistant to all the races of leaf rust while three were moderately susceptible to some races. Reitz et al. (1945) working with Agrotricums in Kansas indicated that a high degree of disease resistance may be transferred from Agropyrons to wheat.

McKinney and Sando (1951) tested 50 selections from hybrids involving Triticum, Agropyron, Aegilops and Secale, and found resistance to wheat streak mosaic virus in 25 of the selections, 16 of which had been derived from A. elongatum. Later, Sando (1953) observed that three hybrid selections, derived from crosses between Triticum vulgare and A. elongatum, were resistant to leaf rust, stem rust and soil-born wheat mosaic virus.

Schmidt et al. (1953) tested Agrotricum hybrids for seedling reaction to eight races of leaf rust and found 40 out of 161 lines to be immune or highly resistant. Strains with spike characteristics intermediate between Agropyron elongatum and Triticum vulgare showed the highest frequency of rust resistance. Three common wheat-like strains were found to be resistant to the eight races of leaf rust. Schmidt et al. also indicated that no one common wheat source contains such a high order of resistance as the Agrotricums.

Schmidt et al. (1956) tested a large number of Agrotricum hybrids from the cross wheat by Agropyron elongatum for their reactions to wheat streak mosaic virus. Reactions varied from immunity equivalent to that of the parent, A. elongatum, through high resistance to systemic ultra-susceptibility including lethality. Additional reactions were local lesions, systemic but symptomless carrier, and systemic but tolerant, suggesting that the immune reaction is controlled by many

genes. Schmidt et al. (1956) anticipated difficulty in transferring a satisfactory level of resistance from A. elongatum to wheat.

Swarup et al. (1956) made cytogenetic studies of  $F_1$ ,  $F_2$ ,  $F_3$  and backcross generations involving Agroticum hybrids (Triticum vulgare x A. elongatum) to determine the location of the gene(s) for the local lesion type of resistance to wheat streak mosaic virus. The  $F_1$  plants between the advanced Agroticum hybrids ( $2n=56$ ) and Pawnee produced local lesions. The  $F_2$  plants showed systemic infections, local lesions, and local lesions turning into a systemic type reaction. The segregation fit no apparent Mendelian genetic ratios.  $F_3$  lines segregated in the same way as did the  $F_2$  populations.

Different types of reactions were found to be associated with not only different numbers, but also with the size of the univalents.  $F_2$  plants having local lesions had a significantly higher average chromosome number (49.5) than did the plants which had a local lesion turning systemic reaction (45.6) or plants with a systemic reaction (43.6). This suggests that the additional chromosomes carried genes for resistance. Plants which gave the local lesion type reactions were grass-like and usually tall with long, narrow spikes, while the plants with other reaction types were more wheat-like. This suggests that the gene or genes for these plant characters were genetically linked with gene(s) for wheat streak mosaic virus resistance. Swarup et al. concluded that the genes for resistance to WSMV were located on more than one chromosome, and transfer of these genes would be difficult or impossible. They suggested that other Agropyron species should be used as sources of resistance.

Ohlendorf (1956) studied  $F_2$ - $F_9$  generations from backcrossing common wheat with the  $F_1$  of T. aestivum x A. intermedium. Backcross progeny were extremely variable in fertility, morphological characters and grain quality. The chromosome number ranged from 41 to 63 in  $F_2$ . By  $F_6$ - $F_7$ , chromosome numbers tended to become stabilized at  $2n=42$  or 56. Lines with other chromosome numbers survived, but they were considerably inferior in vitality to the two main groups. Plants with a high chromosome number possessed many of the characteristics of the Agropyron parent, whereas those with a low chromosome complement closely resembled wheat. One monosomic substitution and one translocation line were produced in this study.

Andrews and Slykhuis (1956) tested 1,124 common wheat varieties against the natural vector, the wheat curl mite, and found that most of the varieties were susceptible. Bellingham et al. (1957) tested 2,477 foreign winter wheat introductions, 1,975 foreign and domestic spring wheats, 99 domestic winter wheats, and many selections from crosses between foreign and domestic varieties. Reaction to WSMV was usually an extreme systemic susceptibility. Some tolerance was present in eleven foreign and a few domestic varieties, but it varied with environment and other factors. About 2,400 plant selections from several tolerant varieties were made in an attempt to improve tolerance, all without success.

Sill et al. (1964) tested 2,000 spring wheat selections and in another study 2,433 entries from the world collection of common wheat and found all to be systemically invaded by the virus. Lesser degrees of resistance were considered of no practical value. McNeal and



Carroll (1968) evaluated 12 varieties of spring wheat from a naturally infected yield test nursery. Reduction in yield ranged from 24.4 to 54.5 percent. Martin et al. (1976) reported that a few of the Scout derivatives like Eagle and Sage have moderate tolerance to WSMV; but in some years, they are severely damaged.

McKinney and Sando (1951), Fellows and Schmidt (1953), Slykhuis (1955), Andrews and Slykhuis (1956), Schmidt et al. (1956), Bellingham et al. (1957), Sill et al. (1964), Sebesta and Bellingham (1966), and McNeal and Carroll (1968) concluded that there did not exist a high degree of tolerance to WSMV among the common wheat varieties.

Sebesta and Bellingham (1966) suggested that a higher type of resistance could be provided by certain related genera. Bellingham et al. (1957) tested several derivatives of wheat by Agropyron and rye by wheat and found that a few of them were resistant to WSMV. But they were doubtful if any of these lines were of agronomic value. Sill et al. (1964) found resistance in the progeny of a few grass-like Agropyron--wheat crosses and in some rye--wheat crosses. Andrews and Slykhuis (1956) tested 41 different Triticum-Agropyron derivatives and found that they differed considerably in their reaction to WSMV and to the mite, Aceria tulipae Keifer. Their work suggested that possible sources of resistance were Agropyron elongatum and A. intermedium. Fellows and Schmidt (1953) tested some Agrotricums and found a wide diversity of reactions to WSMV. The more grass-like selections had the greatest amount of resistance. Shannor and Bridgmon (1962) reported that eight different strains of intermediate wheatgrass were resistant to WSMV.

Caldwell et al. (1956) reported "0" type immunity to leaf rust races in the Triticum vulgare-Agropyron elongatum derivatives from a Purdue cross. Hybrids of T. vulgare with Agropyron have shown considerable chromosome pairing, particularly where Agropyron elongatum was involved. Vakar (1935, 1936, 1937) who reported up to 28 bivalents in T. vulgare x A. elongatum postulated that A. elongatum has three genomes homeologous to the three of T. vulgare plus two other genomes homeologous with each other. However, Peto (1936) found only about 21 pairs and 14 univalents in T. vulgare by A. elongatum and considering the autoploid nature of A. elongatum suggested that only one genome was common to both. However, Stebbins and Pun (1953) suggested that much of this pairing was due to autosyndesis.

Knott (1958), while studying plants of T. vulgare resistant to stem rust and carrying a single A. elongatum chromosome, observed that the univalent of A. elongatum never appeared to pair with a vulgare chromosome. Riley et al. (1958) noted that gene transfer from Agropyron to wheat has not occurred in the many breeding investigations involving hybrids of tetraploid and hexaploid wheats with polyploid Agropyrons. This indicates that there is no genome in Agropyron closely related to a Triticum genome.

Raj (1965) tested 35 advanced generation Agrotricum hybrids against WSMV. Of the 35 hybrids, 5 were wheatgrass-like and resistant, the remainder were wheat-like with various degrees of resistance. Six promising lines of these 35 selections were crossed with commercial wheats. The 35 selections, the six promising lines among the 35 selections, the F<sub>1</sub> hybrids of crosses of these lines with commercial wheats,

and  $F_2$  seedlings were tested for WSMV resistance. Five types of reactions were reported. Cytological studies showed higher chromosome numbers in wheatgrass-like lines and their  $F_1$  hybrids. Cytological abnormalities were more numerous in wheatgrass-like lines and their  $F_1$  hybrids than in the wheat-like lines and their  $F_1$  hybrids. Since the upper limit of chromosome numbers was between 42 and 45 in all wheat-like resistant plants, the genes for resistance were probably present on more than one chromosome. Symptomless carrier plants were wheatgrass-like which suggests that at least one gene for resistance and gene(s) for grass-like nature may be associated. Pairing at metaphase I in all but one of these hybrids was irregular. One hybrid had very good pairing with progeny segregating in a dihybrid ratio for reaction to WSMV. The transfer of resistance in this hybrid was due to a spontaneous translocation.

Sebesta and Bellingham (1966) developed line  $P_3$ -19 from a Sando complex hybrid involving A. elongatum as one of the parents.  $F_1$  plants from  $P_3$ -19 by Wichita gave a mild systemic reaction which was considered intermediate between the resistant and susceptible parents. In  $F_2$  there were 4 resistant, 86 tolerant, 23 intermediate to tolerant, 50 intermediate and 24 susceptible plants. This response was the result of random chromosome segregation. From cytological examination, it was evident that with the loss of the Agropyron chromosome, resistance diminished except for resistant lines 5508 and 5522 which had 42 chromosomes from wheat and two from Agropyron.

Because of the lack of homology between Agropyron and Triticum chromosomes, the possibility of recovering desired crossover

recombinants of simply inherited characters from Triticum-Agropyron hybrids seems remote. Therefore, attempts have been made to develop addition lines or substitution lines having a complete pair of chromosomes from the genus Agropyron.

Knott (1958) observed that some substitution lines of Thatcher having an Agropyron elongatum chromosome pair were normal in vigor and fertility and of the same yield as Thatcher. The addition lines for the same pair of A. elongatum chromosome were late in maturity and somewhat less vigorous than Thatcher. Also, Bakshi and Schlehuber (1959) reported normal vigor and fertility in a substitution line, T.A.P. 67, of Pawnee wheat. But the line was inferior in quality, yield and bushel weight to the parent variety.

Schlehuber and Sebesta (1959) noted that a leaf rust resistant line, C.I. 13523 of the common wheat variety, Triumph, and thought to be a substitution line, was as good as the parent variety in quality of the grain and yield potential. Later, Schlehuber et al. (1962) discovered that C.I. 13523 carried a translocation between an A. elongatum chromosome and chromosome XVI of Triumph.

Konzak and Heiner (1959) selected several bunt resistant lines from derivatives of a cross between T. compactum by A. elongatum. Most of the bunt resistant lines had 44 chromosomes. Certain resistant lines, however, appeared to have 42 normal chromosomes and a pair of isochromosomes. The lines that contained 42 normal chromosomes plus 2 isochromosomes were found to be superior to the 44 chromosome lines in visible agronomic characters. The inferiority of the 44 chromosome lines was

possibly due to the presence of undesirable genes on the arm other than the one having genes for bunt resistance.

Poor vigor and fertility of an addition line derived from A. elongatum x T. durum have been reported by Mochizuki (1960).

Wienhues and Ohlendorf (1960) studied yellow rust (Puccinia striiformis) resistant addition and substitution derivatives of Triticum-Agropyron hybrids. The derivatives varied widely in yield, some of them equaling susceptible wheats of similar origin having 42 wheat chromosomes. The addition lines had retarded growth, reduced germination, fewer tillers, and increased 1,000 seed weight. Wienhues and Ohlendorf further observed that the added Agropyron chromosomes had a more favorable effect on yielding ability when the arm carrying resistance to yellow rust was lacking in the derivatives.

In other efforts to transfer resistance to stem rust from Agropyron to wheat, substitution lines were selected in which one pair of wheat chromosomes was replaced by a pair of Agropyron chromosomes by Anderson and Driscoll (1967), Gupta (1965), Knott (1964), and Wienhues (1967).

Knott (1964), Johnson (1966) and Riley et al. (1966) showed that alien chromosomes could only substitute for their homeologues. However, Jenkins (1966) and Wienhues (1962, 1963) found that alien chromosomes could substitute for wheat chromosomes even when not homeologous.

Knott (1964) found that pollen carrying the added alien chromosome was at a competitive disadvantage. Plants of chromosome constitution 20''+1'+1'A (A is the Agropyron chromosome) were used as female in a cross with hexaploid wheat. About 25 percent of the offspring were resistant to stem rust due to the presence of the Agropyron chromosome.

The occasional misdivision of the Agropyron univalent and loss of the arm carrying the gene(s) for resistance slightly reduced the expected frequency of resistant plants. However, pollen having the Agropyron chromosome substituted for wheat chromosome 6A functioned fully as well as normal pollen. The Agropyron chromosome is homeologous to wheat chromosome 6A.

Johnson (1966) produced a set of 21 lines of wheat, each monosomic for a different wheat chromosome and having an added alien chromosome derived from Agropyron elongatum. The Agropyron chromosome carried resistance to stem rust. In transmission studies, the Agropyron univalent was passed on at random to 20% of the gametes while the wheat univalent was included in 25% of the gametes. In a self-pollinated  $20'+1'+1'A$  plant, the alien substituted male gametes ( $20'+1'A$ ) failed to function except in the case of wheat homeologous group 6. It was suggested that the possibility of producing alien substitution lines in wheat is more restricted than has been suggested by other workers.

El. Sharkawy (1966) selected at random a sample of blue kernels from the  $F_1$  generation of the composite cross involving Agrotricum derivatives. The majority of the blue-kernel plants had 42 chromosomes, but some had 43 and few had 41. Most of the pollen mother cells from blue-kerneled plants showed some irregular chromosome behavior. One or more chromosomes were lagging at metaphase I and at anaphase I. The chromosome carrying the gene for blue-aleurone was transmitted to less than the expected 50% of the gametes due to competition between normal gametes and gametes carrying the alien chromosome.

Larson and Atkinson (1970) reported a line resistant to WSMV with 21 pairs of chromosomes. The line was derived from a cross involving T. aestivum and A. elongatum. This line hybridizes readily with wheat. Through the use of ditelosomic lines of known chromosomes, it was determined that Agropyron chromosomes had replaced wheat chromosomes 4D, 5D, and 6D. Later, Larson and Atkinson (1973) studied the individual substitution of 4D, 5D, and 6D and found that the 4D substitution line was very susceptible while 5D and 6D showed some resistance. The double substitution 5D + 6D was highly resistant but not immune. The disomic 6D substitution had resistance to the mites equivalent to a triple substitution line.

According to Rillo et al. (1970), plants of a Triticum by Agropyron derivative resistant to wheat leaf blotch (Septoria tritici) had chromosome numbers varying from 52-56. These plants crossed with hexaploid wheat produced an  $F_1$  of  $21''+6'$ . This suggests that the Agrotricum line had three complete wheat genomes plus six pairs of Agropyron chromosomes. Segregation in  $F_2$  families fitted a ratio of 7 resistant to 9 susceptible. The backcross  $F_1$  plants fitted a ratio of one resistant to three susceptible. Both these observations suggest that resistance is on a single Agropyron chromosome transmitted 25% of the time through both types of gametes. Resistant addition plants monosomic or disomic for the complete Agropyron chromosome or one of its isochromosomes were later isolated from selected backcross  $F_3$  progenies. The disomic addition plants ( $22''$ ) were cytologically stable, wheat-like, and resistant in the seedling and mature stages. Irradiation was used, but no resistant plant with  $21''$  were recovered.



Many workers have reported alien substitutions from rye to T. aestivum. Common wheat with a particular chromosome added from rye was highly resistant to representative races of the stem rust population. This rye chromosome had no pronounced phenotypic effect in addition or substitution. Acosta (1962) treated monosomic addition  $21''+1'R$  (R is the rye chromosome) plants with X-rays and used the  $X_1$  plants as pollen parents in crosses with normal wheat. Three translocations, two reciprocal and one non-reciprocal, were obtained during this study. Bielig and Driscoll (1970), Gupta (1969), Lee et al. (1970), O'Mara (1940), and Smith (1963) have reported the alien substitutions from rye. Bielig and Driscoll (1970) reported the substitution of chromosome 5R of Secale cereale for chromosomes 5A, 5B, and 5D of hexaploid wheat. The study showed evidence of compensation, in terms of vigor, in all substitution lines. Chromosome 5R rectified the male sterility of nullisomic 5A and 5D. According to Bielig and Driscoll (1970), the long arm of 5R was the more essential arm, and chromosome 5R was homoeologously related to the group 5 chromosomes of wheat.

Smith (1963) studied the transmission rate of a substituted rye chromosome in wheat. The hybrid had a chromosomal constitution of 20 bivalents and two univalents, the univalent chromosome being 5A of wheat and 1R of Secale cereale. Smith (1963) found that the alien addition male gamete  $21'+1'R$  (R is the rye chromosome) was at a competitive disadvantage in the presence of both  $21'$  euploid gametes and  $20'+1R$  alien substitution gametes. According to him, the rye chromosome in the alien substitution gamete was successful because it restored the normal chromosome number and not because of its genetic contribution.



Knott (1964) pointed out that the genetic content could be important, and the alien addition gametes  $21'+1'R$  would be similar to a gamete containing a duplicate chromosome. Sears (1954) demonstrated that similar gametes in wheat trisomics were at a disadvantage when competing with euploid gametes.

Gupta (1969) reported studies of meiosis in a monosomic substitution line,  $20''+1'+1'R$ , and occasionally observed four univalents. The rye univalent divided more often than the wheat univalent at anaphase I, and as a result, lagged more frequently at anaphase II. Telocentric chromosomes and isochromosomes were transmitted more frequently in male gametes than in female gametes. While studying the transmission rate of the rye chromosome in a wheat background, Gupta (1969b) found that nullisomic gametes ( $20'$ ) and substitution gametes ( $20'+1'R$ ) of a cross involving  $21'' \times 20''+1'+1'R$  plants were mostly eliminated and were being transmitted 4.5% and 0.75% of the time, respectively.

Knott et al. (1977) reported the isolation by backcrossing of monosomic and disomic substitutions of an Agropyron chromosome. Plants with  $20''+2'$  and  $21''+1'$  were resistant while  $21''$  or  $20''+1'$  plants were susceptible. This confirmed that resistance is on the added chromosome. Disomic substitution lines were vigorous, fertile and several days earlier than the recurrent parent. In addition to stem rust resistance, the substitution line showed moderate leaf rust resistance in adult plants. Further investigation showed that the Agropyron chromosome had replaced wheat chromosome 7D. The Agropyron chromosome compensates well for 7D in both plants and gametes. Thus, it may be homoeologous with chromosomes of group seven.

Lay et al. (1971) developed a 42 chromosome line of wheat immune from WSMV. The immune line, CI 15092, was selected from a cross between TA 25 (an octoploid Agrotricum developed at the Max Plank Institute in Germany) and Lathrop, spring wheat, in a process of backcrossing and pedigree selection.

CI 15092 at first was thought to be a translocation line, but later, Wong et al. (1974) found it to be a disomic substitution line. F<sub>1</sub> hybrids of CI 15092 and T. aestivum had 20 bivalents and two univalents of unequal sizes at metaphase I of meiosis of pollen mother cells. Immunity from WSMV was completely dominant in hybrids. The chromosome carrying a gene for immunity was transmitted at rates of 27% through male and 21% through female gametes. Self-fertility in CI 15092 was 89% as compared with commercial varieties which were 95-98% fertile in a greenhouse test. In CI 15092, chromosome 4B of wheat has been replaced by a homoeologous chromosome from Agropyron intermedium (Ruby Larson, personal communication).

Sebesta (personal communication) crossed Agrotricum (common wheat x Ae. elongatum) immune from WSMV with wheat and developed two lines, CI 15321 and CI 15322, immune to WSMV. CI 15321 is apparently a disomic substitution line whereas CI 15322 is apparently a translocation line (Martin et al., 1976).

Gerstel (1945), O'Mara (1951), Matsumura (1952), Sears (1956) and Riley (1960) have reported some degree of instability of addition lines obtained in a variety of intergeneric and interspecific crosses. This instability would cause a rapid return of an addition population to the euploid state. Therefore, in general, the use of addition lines as

commercial substitutes for existing varieties seems impossible due to their instability and the possible presence of undesirable genes in addition to the desirable ones on the added chromosomes. Also, the use of substitution lines does not seem feasible either because of the presence of undesirable genes or incomplete compensation for the wheat chromosome pair replaced. However, induced recombinations in euploid derivatives followed by selection for desirable types might lead to success in the transfer of desirable genes only.

The use of irradiation to effect small translocations carrying a particular piece of a chromosome was resorted to in studies of inter-specific hybrids of Vicia by Sveshnikova in 1932 (Burnham, 1956), in Datura by Bergner and Blakslee (1934), in Clarkia by Hakansson (1943), and in T. aegilopoides, T. monococcum by Yamashita (1947).

An X-ray induced translocation of leaf rust resistance from Aegilops umbellulata Zhuk. to Triticum vulgare was reported by Sears (1956). He added the A. umbellulata chromosome carrying a gene or genes for leaf rust resistance to the normal T. vulgare complement. Plants from the addition lines were then irradiated with X-rays before meiosis, and their pollen was used in crosses with the susceptible variety, Chinese Spring. Cytological examination of the resistant  $F_1$  plants was made to detect translocations.

Larter and Elliott (1956) evaluated the efficiency of different types of ionizing radiations in producing translocations in 56 chromosome Triticum-Agropyron derivatives and found thermal neutrons to be the most efficient.

Elliott (1957) successfully used X-rays to transfer Agropyron stem rust resistance to common wheat. Knott (1961) has described three experiments in which radiation was used to transfer stem rust resistance from an A. elongatum chromosome to a Thatcher chromosome. Sharma and Knott (1966) and Wienhues (1962) transferred leaf rust resistance from Agropyron into wheat. Acosta (1962) and Bravo (1963) transferred stem rust resistance and leaf rust resistance from rye into wheat respectively. Sears (1967) translocated gene(s) responsible for the hairy neck characteristic from rye into wheat. All transfers involved essentially the production of a monosomic addition line and then either irradiation of plants (Acosta, 1962; Sears, 1967) or irradiation of seeds (Knott, 1961; Bravo, 1963; Sears, 1967) or irradiation of both seeds and plants (Sharma and Knott, 1966; Wienhues, 1962). When plants were treated, pollen from the irradiated plants was used on normal wheat. When seeds were irradiated, the resulting plants were either selfed or used as pollen parents on normal wheat. Plants were treated with X-rays, and seeds were treated with either cobalt 60 or fast neutrons. In either case, progeny were screened for phenotypic effects sought from the alien chromosome. Cytological observations were made, and those plants with an alien chromosome as an addition were discarded. The remaining group was examined to detect the desired kind of transfer which involved the critical alien segment.

Sears (1956) pioneered a technique where translocations were induced by radiation of monosomic addition lines. Driscoll and Jensen (1963) developed an alternative technique. Their method took advantage of a selection method to reduce the amount of cytological work so that large numbers of plants could be examined in a unit of time. They

irradiated dry seeds of a disomic addition of the alien chromosome carrying the gene for disease resistance. The plants from irradiated seeds were self-pollinated. The progeny of plants not carrying a translocation should not segregate for disease resistance. Plants having a translocation should segregate from the resultant quadrivalent, gametes deficient for the disease resistance locus. The translocations would, therefore, be recognized by the presence of segregating families in the  $F_2$ . This technique eliminates the need for emasculation and hand pollination. On the other hand, it reduces the selection pressure found in the Sears technique that screens the desirable translocations.

Kimber (1971) described a third technique in which the selection pressure that favors the desirable translocation is used to change genetic ratios to aid in the identification of translocations. In Kimber's Method, a selfed monosomic addition line produces approximately 25% of progeny with 43 chromosomes and a very small percentage with 44 chromosomes. The rest were euploids. The dry seeds from these resistant plants are treated with ionizing radiation, germinated, and tested against the disease under consideration in the seedling stage. All the susceptible plants are discarded, and resistant plants are grown to maturity and self-pollinated. The progeny lines from different spikes tested individually for disease reactions should fall into four main classes.

All plants can be susceptible indicating that the parent plant escaped the disease test of the previous generation. The susceptible population is discarded.

All plants in a population can be resistant. Such a line originated from the union of a 22 chromosome pollen grain with a 22 chromosome egg cell creating a 44 chromosome disomic addition line. The entire progeny are discarded.

In the third category, approximately 75 percent of the plants will be susceptible. These progeny result from selfing monosomic addition plants and should constitute about 90-95% of the families in this technique. These progenies should also be discarded.

In the fourth category, about 75 percent of the plants will be resistant, indicating that a translocation has occurred. Variation beyond that due to chance from a 3:1 ratio will indicate the competitiveness of the pollen grain with a translocated segment in relation to euploid pollen. Disease resistant plants in this type of family should show 21 bivalents. So it is advisable to select all progenies which segregate with more resistant plants than susceptible and test their segregation behavior in later generations.

## MATERIALS AND METHODS

The immediate source of immunity from wheat streak mosaic virus (WSMV) used in this study was a disomic substitution line, CI 15092, developed in the wheat improvement project at South Dakota State University. The added chromosome originated in Agropyron intermedium (Host) Beauv ( $2n=70$ ). The original cross (Carsten V/A. intermedium) was made at Max Plank Institute, West Germany, from which a line TA 25 with  $2n=56$  chromosomes was derived. It was found to be immune from wheat streak mosaic (Lay, 1969) at South Dakota State University.

Lay et al. (1971) crossed TA 25 with common wheat and had the  $F_1$  seeds irradiated with fast neutrons. After a process of backcrossing and selection, one 42-chromosome substitution line (CI 15092) immune from wheat streak mosaic virus was isolated.

In the SD wheat improvement program through a process of backcrossing immune monosomic addition plants to Centurk, 322  $F_1BC_3$  seeds were produced which had three doses of Centurk in them. The seeds were treated with fast neutrons through the kindness of Dr. R. Nylan at Washington State University, Pullman. Immune progeny from the irradiated seeds were used as male parents crossed onto emasculated spikes of the euploid ( $2n=6x=42$ ) wheat cultivar 'Centurk'. About 2,000  $F_1BC_4$  seeds were obtained.

In the spring of 1974, the 2,000  $F_1BC_4$  seeds comprising 50 cultures distinguished by the identities of the immune plants from which pollen came were seeded in flats and vernalized for 35 days at  $2^{\circ}$  to  $7^{\circ}C$ . The



vernalized seedlings were transplanted to a greenhouse. Plants were spaced 5 cm x 15 cm. In every tenth row, about 35 seedlings were planted of the susceptible check, Centurk, and five seedlings of the immune check, CI 15092. A mulch of peat moss was used to suppress weeds and reduce loss of moisture. Mulch was so effective that the plants were usually watered only once in a growing season. In the later stage of the crop, sulfur pots were used to control powdery mildew. Progeny testing was done in  $F_1BC_4$ ,  $F_2BC_4$ ,  $F_3BC_4$ , and  $F_4BC_4$ .

#### Inoculation

The blast method described by Gardner et al. (1969) was used to inoculate with WSMV. Primary inoculum consisted of a composite of 42 field collections made by W. S. Gardner from wheat plants infected with WSMV in South Dakota. Inoculum was increased in the greenhouse by inoculating 14-day old seedlings of Hume wheat growing in 15 23 cm pots. Two weeks after inoculation, plants showing WSMV symptoms were used to inoculate two-week old seedlings growing in 120 23 cm pots.

Two weeks later, plants showing WSMV symptoms were collected by cutting above the crown. For every liter of inoculum, 100 gm of freshly cut plant tissue were passed through a Hobart grinder for a dilution of 10:1. The juice and pulp were separated. The pulp was mixed with an equal amount of deionized water and passed through the grinder again. This process was repeated 3-4 times. The extract was filtered through four layers of cheesecloth and made up to one liter by adding deionized water.



Twenty grams of carborundum of 240 mesh/cm were added to each liter of inoculum as an abrasive. The mixture was then placed in a "Port-a-Blast" portable sand blaster and sprayed on each plant with 2-3 intermittent blasts at 4.2 to 4.9 kg./cm<sup>2</sup> air pressure, with the end of the nozzle held about 15 cm from the leaves. The opening of the tube through which the inoculum was drawn was reduced to 2.5 mm and extended to within 3 mm of the bottom of the container. To keep escapes to a minimum, each plant was inoculated on alternate days three times.

Ten to 14 days after the third inoculation, mosaic symptoms typical of WSM developed on susceptible plants which were counted and discarded.

#### Cytology:-

Cytological analyses were made of the pollen mother cells of selected F<sub>1</sub>BC<sub>4</sub>, F<sub>3</sub>BC<sub>4</sub>, and F<sub>4</sub>BC<sub>4</sub> immune plants. Whole heads for cytological examination were collected and fixed for 24 hours in a freshly prepared fixative made of three parts absolute ethyl alcohol to one part glacial acetic acid by volume. The heads were transferred to 70 percent ethyl alcohol and stored in the refrigerator. Generally, the spikes collected at an early boot stage contained anthers that were at the right stage of meiosis for observations.

The aceto-carmine smear technique was used for staining the chromosomes in microsporocytes. The stain was prepared by adding 55 cc. distilled water to 45 cc. glacial acetic acid. The mixture was heated to the boiling point with an excess of carmine (about 0.5 gms). The

solution was boiled for 2-3 minutes or until it began to turn dark. The solution was then cooled in the refrigerator and filtered for use.

Temporary slides were made by macerating the three anthers of a floret in a drop of stain. The debris from the anther walls was removed and a coverslip applied. A paper napkin covering the slide was pressed gently with the thumb to spread the chromosomes and to absorb excessive stain. The paper napkin was removed, and the coverslip was sealed around the edge with a mixture of gum mastic and paraffin. Observations were made on each slide to determine the number of univalents, laggards, and micronuclei at metaphase I, anaphase I, and tetrad stage respectively. Whenever possible, chromosome counts were made in diakinesis.

Photomicrographs were made by using an A0 photomicrographic camera coupled to a B and L research microscope. Kodak Plus-X pan film of ASA 125 was used and developed in D-76 half-strength developer.

The occurrence of a reciprocal translocation involving an alien chromosome and a Centurk chromosome could result in the formation of a trivalent. At meiosis, gametes having 21 and 22 chromosomes would tend to be formed in equal numbers. Assuming that disjunction is almost entirely alternate (Thompson and Thompson, 1937), the first type of gamete will carry 21 normal Centurk chromosomes, and the second will have 20 normal Centurk chromosomes plus the two translocated chromosomes. The resistant  $F_1BC_4$  plants from a cross with Centurk would usually have 20 bivalents plus a trivalent, but occasionally, a resistant plant with 21 bivalents might be obtained if the translocated A. intermedium chromosome is lost. The resistant plants having 20"+1"

would result from the union of a gamete having 21 normal Centurk chromosomes with a gamete having 20 normal Centurk chromosomes plus the two translocated chromosomes. The two translocated chromosomes would tend to pair with the normal homologue and thereby give rise to a trivalent. In the resistant plants having 21 bivalents, one bivalent would consist of a translocated chromosome paired with a normal Centurk chromosome. If the two changed chromosome segments differed in relative size, the pair might be heteromorphic and could then be detected. The pairing between the translocated Centurk chromosome and the normal Centurk chromosome could be affected due to the presence of a sizeable piece of the A. intermedium chromosome, in which case an open bivalent would likely be formed. Meiotic configurations having a chain of four or five or more chromosomes could also result, depending upon the number of chromosomes involved in a translocation complex.

$F_1BC_4$  plants having a non-reciprocal translocation, either terminal or intercalary, would have 21 bivalents plus one univalent at meiosis (assuming the remainder of the A. intermedium chromosome had not been lost). In  $F_1BC_4$  from a cross with Centurk, the resistant plants would have either  $21''$  or  $21''+1'$ . The resistant plants with  $21''$  would be recognized as having a translocation of an A. intermedium chromosome segment carrying a gene or genes for immunity. However, immune plants having  $21''+1'$  would have been presumed to be carrying immunity on the A. intermedium chromosome. Therefore, to detect non-reciprocal translocations in resistant plants from seeds carrying  $21''+1'$ , the following procedure was adopted.

Resistant  $F_1BC_4$  plants having 21''+1' were tested in  $F_2$ . At meiosis, the alien univalent would be lost to half the cells expected to receive it. As a result, 25 percent rather than 50 percent of the gametes would have the A. intermedium chromosome. Both types of gametes are equally functional, since they all contain the full complement of wheat chromosomes and the A. intermedium has no deleterious effect upon functioning of gametophytes. Since 25 percent of both the male and female gametes carry the extra chromosome, 43.75 percent of the progeny should be resistant.

If, however, the resistance gene has been translocated to a Centurk chromosome, in the  $F_2BC_4$ , 50-75 percent of the plants should be immune. A frequency of 50 percent immune plants will result if the translocation is transmitted only through the female gametes. Frequencies ranging from 50 to 75 percent of immune plants could be obtained depending upon the frequency with which the translocated chromosome is transmitted through the pollen. Therefore,  $F_2BC_4$  families having more than 50 percent immune plants were selected for progeny testing.

In the fall greenhouse crop of 1975, 189  $F_1BC_4$  plants were progeny tested along with immune and susceptible checks.

In the spring of 1976, 175 immune  $F_2BC_4$  plants representing nine suspected translocation lines (A, B, C, D, E, F, G, H and N), along with immune and susceptible checks, were progeny tested against WSMV. In the fall of 1976, 152 immune  $F_3BC_4$  and in the fall of 1977, 18  $F_3BC_4$  and 6  $F_5BC_4$  plants were progeny tested against WSMV. A number of immune plants in  $F_3BC_4$  and in  $F_4BC_4$  generations were examined cytologically.

### Transmission of the Translocation Through Male and Female Gametes

Sears (1956), Knott (1961), Sharma and Knott (1966), and Wienhues (1973) have reported differential transmission of the translocated chromosomes through the male and the female gametes. In the present study, the heterozygous immune plants were tested for transmission of immunity through the gametes. In the meantime, while breeding behavior was being checked, each translocation line was crossed with commercial varieties and with advanced lines in the winter wheat breeding project. 1,190  $F_1$  plants were inoculated, and the immune selections were selfed. Segregation in  $F_2$  was used to establish the frequency of transmission of immunity through gametes.

### Effects of the Suspected Translocation Lines on Agronomic Characters

The tentatively identified translocation lines having 21 bivalents might differ from each other and from Centurk in morphology, yield, and quality. The variability between the translocation lines would largely depend on the size of the added piece of A. intermedium chromosome, the size of the piece of wheat chromosome which was lost, and the particular chromosome involved. A preliminary evaluation of the effects caused by the interactions of these factors was made under field conditions by comparing immune plants with the recurrent parent, Centurk. The characters studied were: days to heading, plant height, number of tillers per plant, number of florets in the main spike, number of seeds in the main spike, percent fertility of the main tiller, 100 seed weight, and yield per plant.

In the first test, homozygous immune lines in  $F_5BC_4$  from seedlings vernalized for 35 days were studied in a randomized complete block design of split plots in three replicates under field conditions. The test included six different suspected translocation lines, each represented by two sister lines designated  $A1^*$ ,  $A2^*$ ,  $B1$ ,  $B2$ , etc. Centurk was included as a standard check. The rows were 30 centimeters apart and three meters long. Each row consisted of five spring wheat border plants at either end and ten plants of each of two sub plots of a sib or a check. Plants were 10 cm apart. Four sub plots of Centurk check and 12 sub plots of two sibs of each six suspected translocation lines were randomly arranged in each of three replications. Spring wheat at ends of rows and in three rows both at the beginning and at the end of the replicates reduced border effect and damage by birds and rodents. The seedlings were watered immediately after planting. Watering was repeated several times as needed. Panogen 15 was sprayed on the plants on five alternate days during anthesis to control scab.

The heading date recorded for each entry was the day when half the heads were out of the boot. The number of tillers per plant was recorded. Plant height was measured at two places and the average recorded. The number of florets, the number of seeds, and percent fertility were recorded for the primary spike of each plant. The percent fertility was based on the number of seeds in the first and second florets of all the spikelets excluding the top and bottom ones

\*The number 1 and 2 such as  $A1$  and  $A2$  identify two different progeny lines within a suspected translocation source.

on each spike. Hundred seed weight and yield per plant were observed for all entries.

The lines tested in the field were not inoculated but were progeny tested later in the greenhouse against WSMV. Four to nine  $F_6BC_4$  seeds from each plant, along with susceptible and immune check, were sown in flats. Fourteen days later, the seedlings were inoculated three times on alternate days. Two weeks later, the reactions to WSMV were recorded.

An observation planting to compare apparently homozygous immune  $F_5BC_4$  lines with the recurrent parent, Centurk, was also made in the field from seedlings vernalized 35 days. We used 32 three-meter long rows of three or more sibs from six different suspected translocation lines along with three rows of Centurk. The space between rows was 30 centimeters and between plants within a row was 6.35 centimeters. Observations on the general morphology of the plants were made. Irrigation and scab control were practiced.



## RESULTS

The 1,684  $F_1BC_4$  plants comprising 50 cultures based upon identity of the pollen source were tested against wheat streak mosaic virus in the greenhouse. Forty-six cultures segregated. Four were completely susceptible, most probably originating from male plants that were escapes or represented chance deviations from expected segregation ratios. All 10 plants of the immune check (CI 15092) were immune, and all 150 plants of the Centurk check were susceptible (Table 1).

Pooling the  $F_1$  backcross data from 50 cultures gave 310 immune and 1,374 susceptible plants (Table 1). Transmission of the gene for immunity through the male parent when calculated from this ratio is 18.4%.

#### Cytological Examination of the Immune $F_1BC_4$ Plants

One hundred and fifty-one immune  $F_1BC_4$  plants from 30 cultures were examined cytologically for 21 bivalents and the possible presence of the Agropyron univalent. The majority of the resistant plants in 28 cultures had a univalent present in addition to the wheat complement (Figure 1). Plants in 15 cultures out of 30 examined had two univalents (Figure 2), and in seven cultures had three univalents (Table 2).

Plants in 23 cultures had laggards. Almost all of the cultures had micronuclei (Table 2). Not even a single plant of 151 examined had only 21 bivalents. Cytological examination at this point did not rule out the possibility of the occurrence of translocations of Agropyron

Table 1. Reaction to wheat streak mosaic virus of  $F_1BC_4$  plants. The immune pollen parents came from irradiated  $2n+1$  seed.

Immune male N1 parental source	$F_1BC_4$ culture no.	Pedigree	WSMV reactions	
			*Imm.	**Susc.
	274270	CI 15092 Imm. (Check)	10	0
	274271	Centurk (Susc. Check)	0	150
973331-1	274272	CI 15092/T. speltoids/Fletcher/3/5* Ctk	3	49
973331-2	274273	" " " "	9	16
973331-3	274274	" " " "	2	14
973331-4	274275	" " " "	25	54
973331-5	274276	" " " "	1	7
973331-6	274277	" " " "	2	13
973331-7	274278	" " " "	0	4
973331-8	274279	" " " "	18	51
973331-9	274289	" " " "	9	24
973331-10	274281	" " " "	12	49
973331-11	274282	" " " "	6	30
973331-12	274283	" " " "	3	17
973331-13	274284	" " " "	3	23
973331-14	274285	" " " "	2	16
973331-15	274286	" " " "	9	72
973331-16	274287	" " " "	5	25
973331-17	274288	" " " "	3	58
973331-18	274289	" " " "	1	5
973331-19	274290	" " " "	0	2
973331-20	274291	" " " "	1	4
973331-21	274292	" " " "	4	13
973331-22	274293	" " " "	6	40
973331-24	274294	" " " "	3	13
973331-26	274295	" " " "	20	48
973331-27	274296	" " " "	6	34
973331-28	274297	" " " "	6	28
973331-29	274298	" " " "	7	64
973331-30	274299	" " " "	5	53
973331-31	274300	" " " "	1	16
973331-32	274301	" " " "	6	28
973331-34	274302	" " " "	21	55
973331-35	274303	" " " "	5	14
973331-36	274304	" " " "	0	3
973331-38	274305	" " " "	7	94
973331-39	274306	" " " "	2	3
973331-41	274308	" " " "	5	23
973331-41	274309	" " " "	1	35
973331-45	274310	" " " "	5	52
973331-46	274311	" " " "	1	73
973331-47	274312	" " " "	4	5

Table 1. (continued)

Immune male NI parental source	F <sub>1</sub> BC <sub>4</sub> culture no.		WSMV reactions	
			*Imm.	**Susc.
973331-45	274313	CI 15092/T. speltoids/Fletcher/3/5*		
973331-23	274314	" " " "	14	16
973331-25	274315	" " " "	7	10
973331-33	274316	" " " "	4	17
973331-37	274317	" " " "	5	35
973331-43	274318	" " " "	5	7
973331-48	274319	" " " "	10	19
973331-51	274322	" " " "	20	21
973331-52	274323	" " " "	0	4
973331-53	274324	" " " "	9	26
			<u>1</u>	<u>5</u>
		TOTAL	310	1,374

\*Imm. = Immune

\*\*Susc. = Susceptible

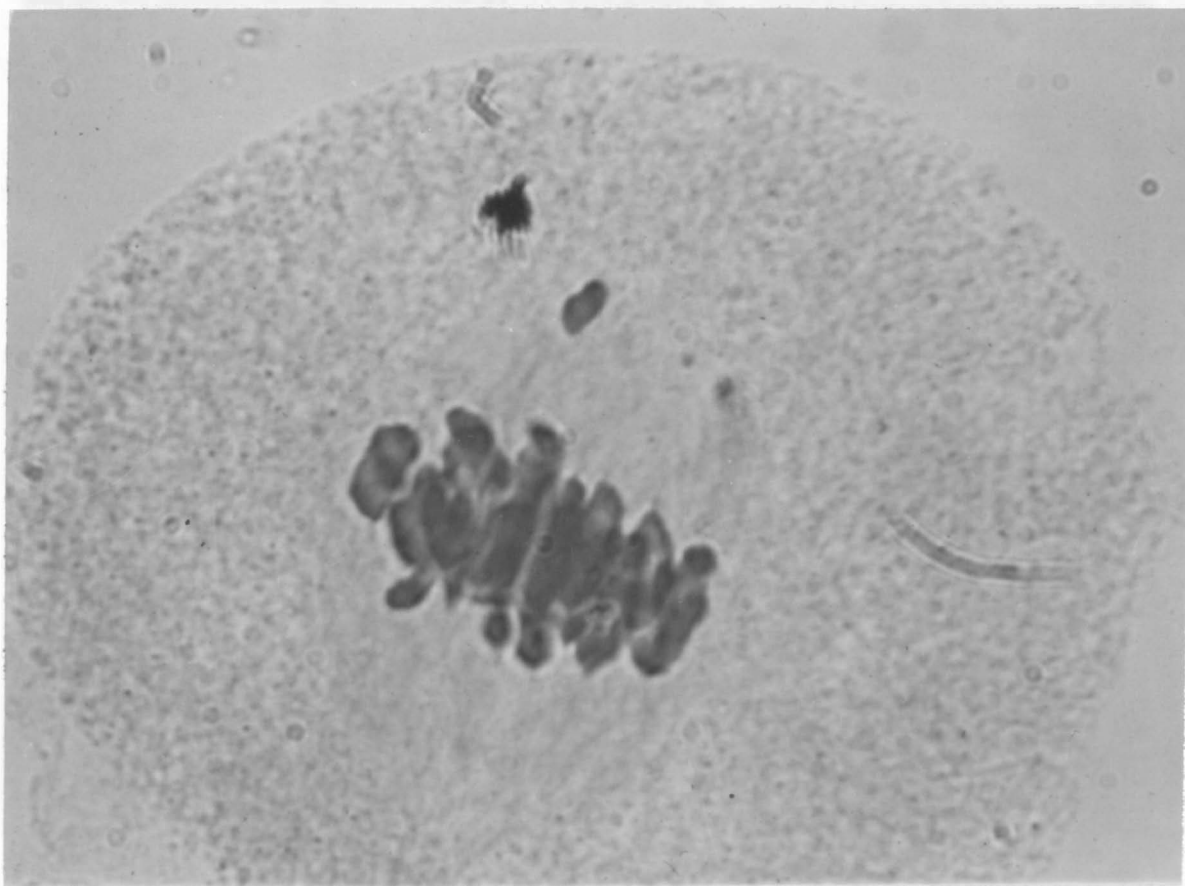


Figure 1. Pollen mother cell from an  $F_1BC_4$  immune plant.  
Metaphase I showing one univalent which may be the alien  
chromosome isolated from the metaphase plate.

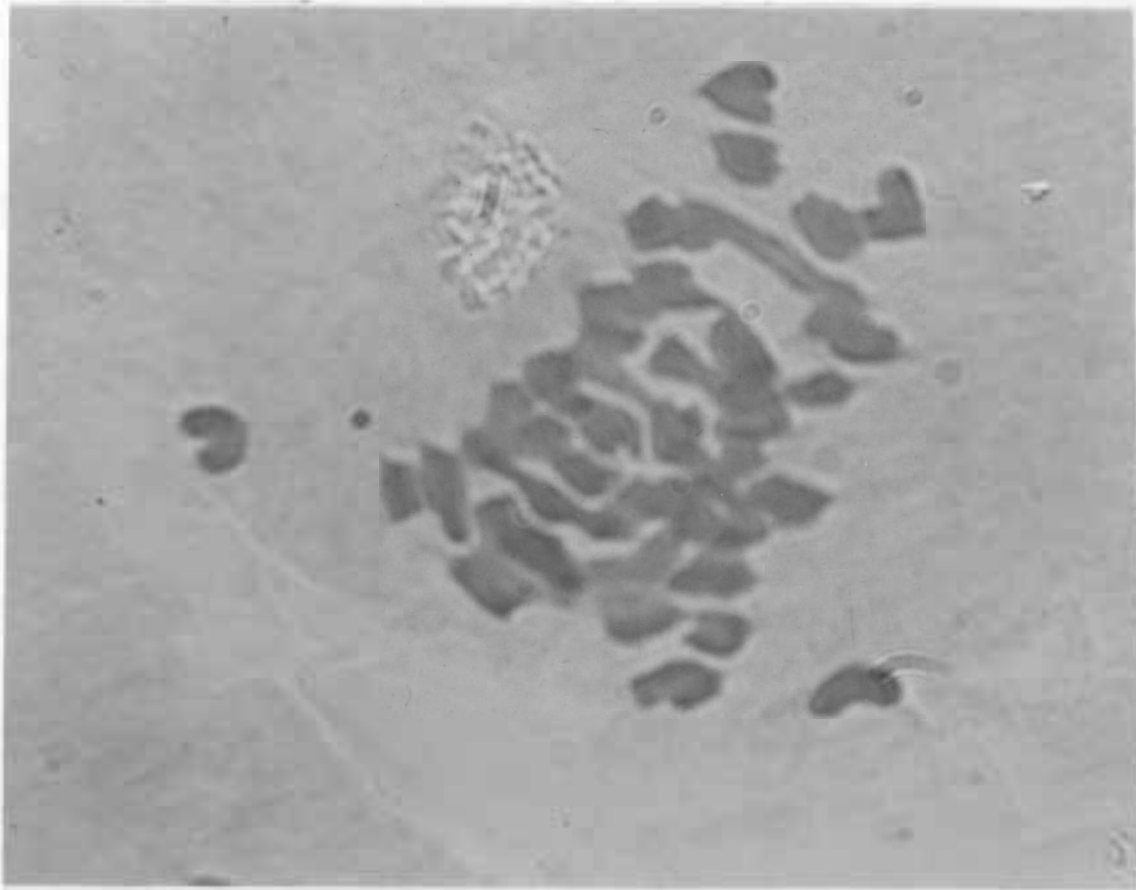


Figure 2. Pollen mother cell from an  $F_1BC_4$  plant. Metaphase I showing two univalents isolated from the metaphase plate.

Table 2. Cytological examination of PMC from  $F_1BC_4$  plants grown in the greenhouse. Pollen parents of the  $F_1BC_4$  plants were grown from irradiated  $2n+1$  seed.

Culture	No. of immune plants examined	$F_1BC_4$ WSMV reaction		Number of PMC with:				Micro-nuclei	Ring of two/four
		Imm.	Susc.	One univalent	Two univalents	Three univalents	Laggards		
274272	3	3	49	16	1	1	3	26	4
274273	6	9	16	31	5	0	12	19	3/2
274274	2	2	14	22	0	0	6	5	2
274275	15	25	54	116	9	1	26	89	3
274277	2	2	13	7	0	0	1	5	0
274279	12	18	51	32	3	0	5	16	11
274280	4	9	24	24	3	0	5	37	0
274281	6	12	49	38	2	1	16	19	1
274282	1	6	30	3	0	0	0	1	0
274283	1	3	17	3	0	0	0	1	0
274284	3	3	23	38	0	0	9	24	0
274286	7	9	72	43	2	0	14	41	0
274287	3	5	25	17	0	0	0	22	0
274288	2	3	58	17	0	0	1	11	0
274289	1	1	5	7	0	0	3	18	0
274292	2	4	13	15	0	0	2	16	0
274293	3	6	40	17	2	0	0	12	0
274294	2	3	13	6	0	0	0	3	0
274295	3	20	48	23	1	1	8	13	3
274311	1	1	73	4	0	0	0	2	2
274312	4	4	5	18	3	2	7	22	0
274313	14	14	16	92	24	1	33	50	17
274314	7	7	10	29	11	1	10	11	5
274315	4	4	17	14	4	0	8	22	0
274316	2	5	35	0	0	0	3	10	2
274317	4	5	7	9	0	0	2	9	1
274318	10	10	19	46	10	0	15	27	2
274319	19	20	21	88	5	0	19	61	3
274323	7	9	26	24	0	0	6	35	0
274324	1	1	5	0	0	0	0	9	0

Only those cells in which the chromosome configuration was clear are reported, and consequently, the numbers are small.

intermedium chromatin to a Centurk chromosome. A univalent could be the remnant with centromere of the Agropyron intermedium chromosome after loss of the segment carrying the gene or genes for immunity from WSMV. Therefore, to detect translocations, in the fall of 1975, 189 resistant  $F_1BC_4$  plants were progeny tested along with immune (CI 15092) and susceptible (Centurk) checks. Susceptible plants which showed characteristic symptoms (Figure 3) two weeks after inoculation were counted and discarded. All the 400 plants of Centurk were susceptible. Of three cultures of the immune check (CI 15092), two bred true for immunity while the third, for unknown reasons, segregated into 15 immune to 5 susceptible plants.

One hundred and twenty-one  $F_1BC_4$  plants which had 21 bivalents plus an alien chromosome (in cytological examination) were excluded from the progeny test. Fourteen different suspected translocations from 189  $F_2BC_4$  families were identified from genetic ratios (Table 3).

In the spring of 1976, 175 immune  $F_2BC_4$  plants representing 14 suspected translocation lines were progeny tested. Genetic data on 9 of them were encouraging (A, B, C, D, E, F, G, H and N) among the ratios in 95  $F_3BC_4$  lines. One hundred and sixty plants of Centurk and 34 plants of CI 15092 were also inoculated. All the 160 plants of Centurk were susceptible, and all the 34 plants of CI 15092 were immune (Table 4,  $F_3BC_4$ ).

In the fall of 1976 and spring of 1977, 169 immune  $F_3BC_4$  plants representing nine suspected translocation lines identified in the spring of 1976 were further progeny tested (Table 4). Two hundred and forty-eight plants of Centurk and 39 plants of CI 15092 were also inoculated.





Figure 3, Leaves of plants from a segregating  $F_2BC_4$  line:  
A from a resistant, B and C from susceptible plants.

Table 3. Genetic ratios in which immune plants predominated in  $F_2BC_4$  suggesting that translocations were present.

Designation of suspected translocations	Culture no.	Source	$F_2$ ratios imm:susc.	Percent immune	P from $X^2$ for goodness-of-fit to 3:1 ratios
A	975111	274275-11	20:8	71	> .05
B	975114	274275-20	28:9	76	> .05
C	975121	274279-10	21:14	60	< .05*
D	975137	274283-5	22:7	76	> .05
E	975234	274302-23	23:11	68	> .05
F	975269	274323-7	10:2	84	> .05
G	975301	274279-16	19:10	65	> .05
H	975110	274275-9	16:8	67	> .05
I	975119	274279-1	21:12	64	> .05
J	975120	274279-9	15:9	63	> .05
K	975122	274279-17	32:14	70	> .05
L	975124	274279-18	15:4	79	> .05
M	975138	274283-6	23:18	56	< .01**
N	975205	274273-5	16:4	80	> .05

\*Significant at 5% level

\*\*Significant at 1% level

All the 248 plants of Centurk were susceptible. Both the immune checks from disomic substitution lines segregated into 8 immune to 11 susceptible and 10 immune to 10 susceptible.

#### Line A

Ten  $F_3BC_4$  progeny lines from 20  $F_2BC_4$  immune plants were tested for their breeding behavior against WSMV (Table 4). Three of the 10  $F_3BC_4$  lines were homozygous immune which is close to the expected number of 25%. Seven  $F_3BC_4$  lines segregated. None of the lines bred true for susceptibility.

Line A was further tested for breeding behavior in  $F_4BC_4$  in the 1976 fall greenhouse crop. Twenty-two  $F_4BC_4$  progeny lines from two homozygous immune cultures in  $F_3BC_4$  were inoculated. Out of 137  $F_4BC_4$  plants from homozygous immune culture 276411, 121 were immune and 16 were susceptible, not an expected Mendelian ratio. Culture 276413 segregated 155 immune to 15 susceptible, also not an expected Mendelian ratio (Table 4,  $F_4BC_4$ ).

Line A was crossed with commercial varieties and advanced lines in the winter wheat breeding program, and 166  $F_1$  seeds were obtained. The  $F_1$  plants from these seeds when tested against WSMV produced 154 immune and 12 susceptible plants (Table 5). The susceptible  $F_1$  plants either were selfs or an expression of cytological instability.

From three different crosses involving Line A (Table 5),  $F_2$  progeny were studied. Ten of the 12  $F_2$  ratios were clearly Mendelian but two deviated significantly from 3:1 ratios. In two of the three crosses in the totals of  $F_2$  progeny, there were more immune plants (82.4% and

Table 4. Reactions to wheat streak mosaic virus in various generations of line A and of the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 1975	I:S		Spring 76	I:S		Fall 76	I:S
274275-11	975111	20:8	975111-1	276411	12:0	276411-6	976501	18:1
			111-2	412	6:3	411-7	502	18:2
Centurk Susc. Check		0:400	111-3	413	11:0	411-8	503	20:1
CI 15092 Imm. Check		24:0	111-4	414	7:2	411-10	504	12:2
" " "		15:5	111-5	415	7:6	411-5	505	14:3
			111-6	416	4:3	411-3	506	14:2
			111-7	417	6:1	411-4	507	5:1
			111-8	418	8:0	411-1	508	6:1
			111-9	419	9:4	411-9	509	4:1
			111-10	420	7:6	411-12	510	5:0
						411-2	511	1:2
			Centurk Susc. Check		0:160	411-11	512	2:0
			CI 15092 Imm. Check		34:0			121:16
						276413-11	976513	13:1
						413-7	514	16:0
						413-8	515	14:3
						413-5	516	15:1
						413-2	517	19:1
						413-4	518	11:0
						413-3	519	10:2
						413-10	520	20:0
						413-9	521	20:3
						413-10	522	17:4
								155:15
						Centurk Susc. Check		0:248
						CI 15092 Imm. Check		8:11
						" " "		10:10

Table 5. Reactions to wheat streak mosaic virus of the F<sub>1</sub> and F<sub>2</sub> involving line A and of resistant and susceptible checks grown in the greenhouse.

Cross	Male parents	F <sub>1</sub>		Source	F <sub>2</sub>		P from X <sup>2</sup> for goodness-of-fit to 3:1 ratios
		Culture	I:S		Culture	I:S	
CTK*2/CIMMYT// line A.	276411-8	976629	4:0	976629-1	177913	17:5	>.05
				629-2	914	6:2	>.05
				629-3	915	14:4	>.05
				629-4	916	1:2	>.05
Lancota/line A.	976520-2	177826	7:1				
" "	976520-3	177827	6:0				
" "	976520-5	177828	15:0				
Sage/line A.	976518-2	177860	3:4				
" "	976520-8	177861	8:0				
SD75475/line A.	976520-4	177872	11:0				
" "	976520-5	177873	11:0				
Ctk/line A.	976518-2	177890	10:3				
" "	976520-5	177891	8:0				
SD75375/line A.	4774-6	977202	9:0				
Sage/line A.	4773	977214	2:0				
Roughrider/line A.	4772	977219	8:1				
SD76142/line A.	4773	977210	4:0				
SD75375/line A.	4775-2	977241	9:0	977241-1	178131	22:12	>.05
				241-2	132	31:2	<.05
				241-3	133	24:4	>.05
				241-4	134	28:4	>.05
				241-5	135	21:5	>.05
						126:27	<.05
		(82.4%) (17.6%)					
Ctk/line A.	4774-14	977242	7:1	977242-1	178127	59:8	<.05
				242-2	128	68:17	>.05
				242-3	129	67:17	>.05
						194:42	<.05
		(82.2%) (17.8)					
NE 69291/line A.	4775-19	977270	8:0				
NE 75424/line A.	4774-7	977272	8:0				
SD 75375/line A.	4775-2	977311	8:0				
Centurk/line A.	4774-14	977312	8:2				
			154:12				

82.2%) than expected on the basis of dominant monogenic inheritance. In the literature, there is little evidence that a translocation is transmitted in excess through either eggs or pollen. The one exception is in the case of Sharma and Knott (1966) where their translocation 4 had an 80.9% transmission rate upon selfing.

The exact parents of the  $F_2$  crosses were not examined cytologically, but  $F_4BC_4$  plants of line A in homozygous immune culture 976514 (Table 4) were examined cytologically. Difficulty was experienced in obtaining adequate separation of metaphase chromosomes. Counts were made only on those cells in which chromosome configurations were clear. Twenty-one bivalents were counted in six cells. In cytological examination, no laggards, no micronuclei, and no open bivalents were observed in the six cells (Table 13).

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_2$  segregation ratios and cytology of immune  $F_4BC_4$  plants give some evidence of a translocation in line A.

Some  $F_4BC_4$  plant progeny within line A derived from homozygous immune  $F_3BC_4$  lines segregated suggesting cytological instability (Table 4,  $F_4BC_4$ ). The reason for the instability is not known. Wienhues (1973) also reported instability in translocation lines in different generations. Sebesta and Bellingham (1966) concluded that in translocation homozygotes, chromosome containing a gene or genes for resistance sometimes lagged behind and were lost during gamete formation. Some of our susceptible plants were sterile and dwarfed, which may indicate loss of a whole chromosome pair. High temperature in the greenhouse has been known to break down resistance to WSMV. Niblett

(1977) reported that the resistance of CI 15092 broke down at about 35°C.

#### Line B

Ten of 28  $F_2BC_4$  immune plants were progeny tested for their breeding behavior against WSMV (Table 6). Five (50%) out of ten  $F_3BC_4$  lines were homozygous immune and the remaining five segregated. None of the  $F_3BC_4$  lines were completely susceptible, although in one case, culture 276422, 14 out of 16 plants were susceptible.

Forty-four plants from five  $F_3BC_4$  homozygous immune lines were progeny tested in  $F_4BC_4$  in the 1976 fall greenhouse crop. Four  $F_3BC_4$  homozygous immune cultures--276426, 276427, 276429, and 276430--produced 122, 91, 223, and 187 immune plants and 9, 5, 15, and 6 susceptible plants respectively, not expected Mendelian ratios (Table 6,  $F_4BC_4$ ). The fifth  $F_3BC_4$  homozygous immune line from 276423 when progeny tested produced 114 (71.7%) immune and 45 (28.3%) susceptible plants, a good fit to a 3:1 ratio. But when an immune plant from this population was crossed with Lancota (Table 7) and the  $F_2$  examined, a ratio of 82:110 was obtained which does not support the presence of a translocation. A ratio of 82:110 is typical of segregation from a monosomic addition plant.

Line B was crossed with commercial varieties and advanced lines in the winter wheat breeding program, and 312  $F_1$  seeds were obtained.  $F_1$  plants tested against WSMV segregated 300 (96.2%) immune to 12 (3.8%) susceptible (Table 7). Susceptible plants could have been selfs or the chromosome involved in immunity had been lost during gamete formation.



Table 6. Reactions to wheat streak mosaic virus in various generations of line B and of the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 76	I:S
274275-20	975114	28:9	975114-1	276421	6:2	276423-3	976523	16:4
			114-2	422	2:14	423-2	524	10:9
Centurk Susc. Check		0:400	114-3	423	8:0	423-1	525	11:10
CI 15092 Imm. Check		24:0	114-4	424	7:3	423-4	526	18:0
" " "		15:5	114-5	425	6:1	423-7	527	17:4
			114-6	426	7:0	423-6	528	18:2
			114-7	427	7:0	423-5	529	11:9
			114-8	428	3:4	423-8	530	13:7
			114-9	429	13:0			<u>114:45</u>
			114-10	430	9:0	276426-1	531	20:0
						426-2	532	19:0
			Centurk Susc. Check		0:160	426-3	533	15:3
			CI 15092 Imm. Check		34:0	426-5	534	20:0
						426-4	535	17:0
						426-7	536	16:3
						426-6	537	15:3
								<u>122:9</u>
						276427-4	538	18:1
						427-3	539	9:4
						427-6	540	23:0
						427-7	541	20:0
						427-2	542	10:0
						427-5	543	5:0
						427-1	544	6:0
								<u>91:5</u>

Table 6. (continued)

Source	$F_4BC_4$	
	Fall 76	I:S
276429-11	976545	26:5
429-12	546	16:3
429-10	547	20:0
429-9	548	15:2
429-8	549	18:0
429-2	550	18:0
429-7	551	19:1
429-13	552	19:0
429-6	553	17:3
429-1	554	16:0
429-5	555	18:1
429-3	556	14:0
429-4	557	7:0
		<u>223:15</u>
276430-4	976558	17:1
430-1	559	20:0
430-2	560	22:0
430-3	561	20:0
430-9	562	23:0
430-8	563	19:2
430-7	564	20:3
430-6	565	23:0
430-5	566	23:0
		<u>187:6</u>
Centurk Susc. Check		0:248
CI 15092 Imm. Check		8:11
" " "		10:10

Table 7. Reactions to wheat streak mosaic virus of the F<sub>1</sub> and F<sub>2</sub> involving line B and of resistant and susceptible checks grown in the greenhouse.

Cross	Male parent	F <sub>1</sub>		Source	F <sub>2</sub>		P from X <sup>2</sup> for goodness-of-fit to 3:1 ratio
		Culture	I:S		Culture	I:S	
Lancota/Line B	976526-2	177829	17:0	177829-2	977256	42:40	<.05
				829-3	257	-	-
				829-4	258	24:39	<.05
				829-5	259	16:32	<.05
Lancota/Line B	976526-4	177830	7:0			82:110	
" "	976526-6	177831	10:0			(42.7%) (57.3%)	
" "	976526-11	177832	11:0				
" "	976564-1	177833	11:0				
Vona/Line B	976526-2	177845	2:0				
" "	976529-9	177846	5:0				
" "	976549-16	177847	2:0				
Sage/Line B	976534-5	177862	2:1				
" "	976536-2	177863	16:0				
" "	976547-16	177864	4:0	177864-0	977567	188:58	>.05
SD 75475/Line B	976523-3	177874	11:2				
" "	976526-2	177875	7:3				
" "	976538-3	177876	4:0				
" "	-7	177877	16:0				
" "	976547-1	177878	10:0				
" "	-8	177879	9:1				
" "	-14	177880	8:1				
" "	-16	177881	9:1				
" "	976564-1	177882	9:0				
Ctk/Line B	976523-3	177892	4:0				
" "	976526-2	177893	20:2				
" "	-4	177894	8:0				
" "	-11	177895	12:0				

Table 7. (continued)

Cross	Male parent	F <sub>1</sub>		Source	F <sub>2</sub>		P from X <sup>2</sup> for goodness-of-fit to 3:1 ratio
		Culture	I:S		Culture	I:S	
Ctk/Line B	976536-1	177896	12:0				
" "	-7	177897	9:0				
Centurk/Line B	976538-3	177898	12:1				
" "	976547-1	177899	8:0				
				177899-2	977568	24:11	>.05
				899-3	569	22:13	>.05
				899-4	570	24:10	>.05
				899-5	571	31:7	>.05
				899-6	572	23:9	>.05
						124:50	>.05
Centurk/Line B	976547-7	177900	7:0				
				177900-2	977573	26:8	>.05
				900-3	574	26:7	>.05
				900-4	575	30:6	>.05
				900-5	576	27:11	>.05
				900-6	577	28:12	>.05
						137:44	>.05
Centurk/Line B	976559-7	177901	19:0				
" "	561-3	902	4:0				
" "	561-8	903	15:0				
TOTAL			300:12			@ 449:152	.05
						(74.7%) (25.3%)	

@ Excluding the ratio of 82:110 from the progeny test of 177829.

Four  $F_1$  families were progeny tested in  $F_2$ . In three  $F_2$  families, the ratios were Mendelian. There were 449 (74.7%) immune and 152 (25.3%) susceptible plants.

The exact parents of the cross were not examined cytologically. But seven  $F_4BC_4$  plants from three different homozygous immune cultures--976526, 976534, and 976561--were studied cytologically and 21 bivalents counted in 30 different cells. There were no open bivalents, only one cell had a laggard, and no micronuclei were observed in the plants examined (Table 13).

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_2$  segregation data and cytological evidence showed that both a translocation and alien chromosome additions occur in line B. The translocation is transmitted normally through the eggs and pollen.

#### Line C

Ten of 21  $F_2BC_4$  plants were progeny tested. Two (20%) of the 10  $F_3BC_4$  lines were homozygous immune, which is close to the expected number of 25%, and 8 (80%) lines segregated. None of the  $F_3BC_4$  lines were homozygous susceptible, but three cultures--276455, 276457, and 276460--were nearly so (Table 8,  $F_3BC_4$ ). All the 160 plants of the Centurk check were susceptible. All the 34 plants of CI 15092 were immune.

From one  $F_3BC_4$  homozygous immune line, 12 out of 13  $F_3BC_4$  plants were progeny tested in the 1976 fall greenhouse crop. Of 255  $F_4BC_4$  plants, 234 (91.8%) were immune and 21 (8.2%) were susceptible (Table 8,  $F_4BC_4$ ), not an expected Mendelian ratio.

Table 8. Reaction to wheat streak mosaic virus of lines in various generations in line C and of the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 76	I:S
274279-10	975121	21:14	975121-1	276451	9:3	276458-10	976567	19:1
			121-2	452	4:9	458-8	568	21:1
Centurk	Susc. Check	0:400	121-3	453	4:7	458-1	569	21:2
CI 15092	Imm. Check	24:0	121-4	454	5:8	458-3	570	19:0
"	"	"	121-5	455	1:8	458-7	571	20:1
		15:5	121-6	456	7:0	458-13	572	29:4
			121-7	457	1:11	458-12	573	20:2
			121-8	458	13:0	458-4	574	20:2
			121-9	459	3:3	458-9	575	18:1
			121-10	460	1:12	458-6	576	15:2
						458-5	577	18:2
			Centurk	Susc. Check	0:160	458-2	578	14:3
			CI 15092	Imm. Check	34:0		TOTAL	234:21
						Centurk	Susc. Check	0:248
						CI 15092	Imm. Check	8:11
						"	"	"
								10:10

Six  $F_3BC_4$  and 8  $F_4BC_4$  plants from the progeny tests (276458, 976568, and 976577) were examined cytologically and 21 bivalents counted in 46 PMCs for evidence of a translocation. Four cells had an open bivalent. Four cells had a lagging chromosome which may be the cause of instability in  $F_4BC_4$ . In five cells, one micronucleus was present (Table 13).

Line C was crossed with commercial varieties and advanced lines and 227  $F_1$  plants obtained, of which 210 (92.5%) were immune and 17 (7.5%) were susceptible (Table 9). These 17 susceptible plants could be selfs or an expression of cytological instability.

From 25 different crosses involving line C (Table 9),  $F_2$  progeny of 7 were studied. Twenty-eight of the 34  $F_2$  ratios are Mendelian and six deviate significantly from a 3:1 ratio. In all the seven crosses, totals of  $F_2$  ratios of families of individual crosses fit a 3:1 ratio, evidence of a translocation. Immunity in translocation line C is transmitted normally through the eggs and pollen. Of 753  $F_2$  plants tested, 562 (74.6%) were immune and 191 (25.4%) were susceptible.

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ , and  $F_2$  data and cytological examinations of immune  $F_3BC_4$  and  $F_4BC_4$  plants gave evidence of a translocation in line C.

#### Line D

Ten of 22  $F_2BC_4$  immune plants were progeny tested (Table 10). Two were homozygous immune while 7 segregated. One  $F_3BC_4$  line had a single susceptible plant.  $F_3BC_4$  lines exhibited a wide range of segregation ratios showing all gradations from almost all immune plants to almost all susceptible plants.



Table 9. Reactions to wheat streak mosaic virus of the F<sub>1</sub> and F<sub>2</sub> involving line C and of resistant and susceptible checks grown in the greenhouse.

Cross	Male parent	F <sub>1</sub>		Source	F <sub>2</sub>		P from X <sup>2</sup> for goodness-of-fit to 3:1 ratios
		Culture	I:S		Culture	I:S	
SD 713-2/Line C	276456-2	976632	8:0	976632-1	177917	4:4	>.05
				-2	918	17:0	<.05
				-3	919	15:3	>.05
				-4	920	14:1	>.05
				-5	921	14:3	>.05
				-6	922	25:5	>.05
				-7	923	29:5	>.05
				-8	924	21:15	<.05
							139:36
SD 713-13/Line 'C'	276456-2	976633	3:0	976633-1	177925	5:16	<.05
				-2	926	14:5	>.05
				-3	927	25:2	<.05
						44:23	>.05
SD 7149-3/Line 'C'	276456-2	976634	2:0	976634-1	177928	20:11	>.05
				-2	929	24:7	>.05
						44:18	>.05
						26:9	>.05
Ctk *3/CIMMYT, sib 2//Line 'C' (27611-4)	276456-4	976635	4:0	976635-1	177930	26:9	>.05
				-2	931	5:6	<.05
				-3	932	25:6	>.05
				-4	933	15:4	>.05
						71:25	>.05
Ctk *3/CIMMYT, sib 3//Line 'C' (27615-6)	276458-4	976636	3:0	976636-1	177934	10:6	>.05
				-2	935	18:6	>.05
				-3	936	17:9	>.05
						45:21	>.05
Ctk *2/CIMMYT//Line 'C' (27618-3)	276458-4	976637	6:0	976637-1	177937	2:2	>.05
				-2	938	0:1	>.05
				-3	939	4:1	>.05

Table 9. (continued)

Cross	Male parent	F <sub>1</sub>		Source	F <sub>2</sub>		P from X <sup>2</sup> for goodness-of-fit to 3:1 ratios
		Culture	I:S		Culture	I:S	
				976637-4	177940	8:3	>.05
				-5	941	6:0	>.05
				-6	942	4:0	>.05
						24:7	
Ctk <sup>*</sup> 3/CIMMYT, sib 1//Line 'C' (2769-1)	276458-5	976638	8:1	976638-1	177943	25:11	>.05
				-2	944	14:11	<.05
				-3	945	28:7	>.05
				-4	946	24:8	>.05
				-5	947	29:5	>.05
				-6	948	12:6	>.05
				-7	949	35:5	>.05
				-8	950	28:8	>.05
						195:61	>.05
Lancota/Line C	976571-7	177834	9:0		TOTAL	562:191	>.05
" "	976571-14	177835	3:0			(74.6%) (25.4%)	
" "	976572-8	177836	5:0	CI 15092	177993	51:0	
" "	976577-10	177837	4:7	Centurk	177985	26:104	
Vona/Line C	976571-14	177848	28:2				
Lancota/Line C	976572-8	177849	9:0				
" "	976572-9	177850	4:0				
Sage/Line C	976572-8	177865	7:0				
" "	976577-10	177866	8:0				
Ctk/Line C	976569-1	177904	20:0				
" "	976571-7	177905	2:0				
" "	976577-3	177906	25:2				
" "	976577-7	177907	4:0				
" "	976577-10	177908	6:3				
NE 75586/Line C	4778-35	977274	8:1				
CO 725061/Line C	4778-35	977279	8:0				
CO 533147/Line C	4778-35	977281	13:0				
Ctk/Line C	4778-1	977543	13:1				
		TOTAL	210:17				

Fourteen  $F_3BC_4$  plants were progeny tested from two homozygous immune  $F_3$  lines. Out of 152  $F_4BC_4$  plants from homozygous immune culture 276482, 146 were immune and 6 were susceptible, not an expected Mendelian ratio.  $F_3BC_4$  immune plants from culture 276485 when inoculated produced 88 immune and 12 susceptible plants, also not an expected Mendelian ratio (Table 10). Five  $F_5BC_4$  plants from culture 47710 (not inoculated) were progeny tested against WSMV. All the 101  $F_6BC_4$  plants were immune.

Line D in crosses with commercial varieties and advanced lines yielded 236  $F_1$  plants of which 200 were immune and 36 were susceptible (Table 11). The susceptible  $F_1$  plants either were selfs or an expression of cytological instability.

One  $F_2$  population which came from bulk seed of three immune  $F_1$  plants produced 103 plants of which 80 were immune and 23 susceptible, a good fit to a 3:1 ratio. In the cross, Vona/Line D, four  $F_2$  plants from an uninoculated  $F_2$  of 53 plants were progeny tested. Three of the four  $F_3$  families segregated according to dominant monogenic inheritance. The fourth family (178138) produced a ratio of 57:39 which deviated significantly from a 3:1 ratio (Table 11).

Thirteen  $F_4BC_4$  plants from 976582 and 976590 were examined cytologically (Table 13), and 21 bivalents were counted in 28 cells. In three cells, one chromosome was lagging. In one cell, a micronucleus was observed. No cell showed open bivalents.

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_2$ , and  $F_3$  segregation ratios and the cytology of homozygous immune  $F_4BC_4$  plants were evidence of a translocation in line D.

Table 10. Reactions to wheat streak mosaic virus in various generations of Line D and of susceptible and resistant checks grown in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>		Source	F <sub>6</sub> BC <sub>4</sub>		
	Fall 75	I:S		Spring 76	I:S		Fall 76	I:S		Fall 77	I:S	
274283-5	975137	22:7	975137-1	276481	3:2	276482-4	976579	16:0	47710-1	977524	24:0	
			-2	482	9:0	-2	580	28:2	-3	525	20:0	
Centurk Susc. Check	0:400		-3	483	3:2	-5	581	10:0	-4	526	18:0	
CI 15092 Imm. Check	24:0		-4	484	6:6	-8	582	19:0	-5	527	19:0	
"	"	"	15:5	-5	485	5:0	-1	583	19:0	-6	528	20:0
				-6	486	2:1	-6	584			101:0	
				-7	487	5:0	-3	585	18:1	177986	977500	1:226
				-8	488	2:7	-9	586	18:1	177993	Imm. Ck.	0:19
				-9	489	0:1	-7	587	18:2			
				-10	490	7:1			146:6			
			Centurk Sus. Check	0:160		276485-1	976588	16:3				
			CI 15092 Imm. Check	34:0		-2	589	17:2				
						-4	590	19:1				
						-5	591	19:3				
						-3	592	17:3				
								88:12				
						Centurk sus. check		0:248				
						CI 15092 imm. check		8:11				
						"	"	"				10:10

\*47710 was derived from 976579-9.

Table 11. Reactions to wheat streak mosaic virus of  $F_1$  and  $F_2$  involving line D and of resistant and susceptible checks grown in the greenhouse.

Cross	Male Parent	$F_1$		Source	$F_2$		P from $X^2$ for goodness-of-fit to a 3:1 ratio
		Culture	I:S		Spring 78	I:S	
Centurk/Line D	976581-7	177909	9:0				
" "	976585-1	177910	5:1				
Lancota/Line D	976581-5	177836	5:0				
" "	976581-6	177839	16:0				
" "	976585-14	177840	2:0				
" "	976588-8	177841	10:0				
Vona/Line D	976590-15	177852	8:0				
Sage/Line D	976581-4	177867	17:0				
SD 74221/Line D	47719	977179	6:4				
SD 75375/Line D	47719	977203	9:2				
SD 73160/Line D	4779	977209	10:0				
Sage/Line D	4779	977215	11:0				
Roughrider/Line D	4779	977220	9:1				
Line D//Ctk*4/CIMMYT	g 47721-1	977247	3:5	977247-0	178130	80:23	>.05
47731-b/Line D		977261	8:3				
47731-b/Line D		977262	9:0				
" "		977263	4:5				
47731-c/Line D		977264	8:1				
TX 59 A569-1/Line D		977288	8:1				
TX 73A2694/Line D		977291	1:0				
TX 71A937/Line D		977292	1:2				
SD 7113-16/Line D		977298	6:4	977251-1	178136	61:17	>.05
Trans. D/Roughrider		977308	4:0	977251-2	178137	46:21	>.05
SD 75375/Line D		977314	5:1	977251-3	178138	57:39	<.05
Line D//Ctk*4/CIMMYT		977317	6:3	977251-4	178139	17:7	>.05
NE 75424/Line D		977318	9:3				
TOTAL				200:36			

\*Four  $F_3$  plants of 53 plants in  $F_2$  (977251 not inoculated) were progeny tested in Spring 78.

977251-plants 1- 4 have the pedigree, Vona/Line D.

Line E

Ten of 23 immune  $F_2BC_4$  plants were progeny tested and all segregated in  $F_3$ . None of the lines was homozygous either for immunity or for susceptibility (Table 12,  $F_3BC_4$ ).

Ten  $F_3BC_4$  plants were progeny tested from an  $F_3$  10:1 ratio. Six  $F_4BC_4$  families segregated in 3:1 ratios. One  $F_5BC_4$  plant from culture 47724 (grown in the field and not inoculated) which traces to 976597 (22:0) when progeny tested bred true for immunity.

Line E was crossed with two commercial varieties and two advanced lines (Table 14). The  $F_1$  ratio across crosses was 20:1. The susceptible plant may have been due to cytological instability. No additional data was obtained on line E because of the relatively poor phenotype. These data do not conclusively establish either that line E has the alien chromosome or a translocation involving it.

Line F

Ten  $F_2BC_4$  immune plants were progeny tested (Table 15) exhibiting a wide range of segregating ratios. Three  $F_3BC_4$  lines bred true for immunity, four segregated, and the remaining three were homozygous susceptible. The ratio of 3:4:3 is close to the expected ratio of 2.5:5:2.5 (Table 15). From 276503, an  $F_3BC_4$  homozygous immune line, nine of 11 plants were progeny tested. Of 203  $F_4BC_4$  plants, 197 were immune and 6 were susceptible, not an expected Mendelian ratio. The reason for instability is not known.

Line F was crossed with commercial varieties and advanced lines and 98  $F_1$  seeds obtained. Ninety-one  $F_1$  plants were immune and 7 were

Table 12. Reaction to wheat streak mosaic virus in various generations of line E and the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>		Source	F <sub>6</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 76	I:S		Fall 77	I:S
274302-23	975234	23:11	975234-1	276491	2:7	276497-9	976593	19:3	47724-4*	977550	19:0
			234-2	492	4:3	497-10	594	20:2			
Centurk Sus. Check		0:400	234-3	493	8:1	497-7	595	24:0			
CI 15092 Imm. Check		24:0	234-4	494	1:4	497-6	596	18:3			
"	"	"	234-5	495	3:2	497-8	597	22:0			
		15:5	234-6	496	1:1	497-3	598	22:4			
			234-7	497	10:1	497-2	599	18:1			
			234-8	498	4:2	497-1	600	20:1			
			234-9	499	9:2	497-4	601	16:4			
			234-10	500	6:8	497-5	602	15:6			
			Centurk susc. check	0:160		Centurk susc. check	0:248				
			CI 15092 imm. check	34:0		CI 15092 imm. check	8:11				

\*47724 was derived from 976597-8.

Table 13. Cytological examination of PMC from immune  $F_3BC_4$  and  $F_4BC_4$  plants grown in the greenhouse.

Trans.	Generation	Source	Culture	WSNV I:S	Number of cells with			Number of cells counted with $2n=42$
					One open bivalent	One chro. lagging	Micro- nuclei	
A	$F_4BC_4$	276413-7	976514-2	16:0	0	0	0	6
B	$F_4BC_4$	423-4	526-6	18:0	0	0	0	—*
B	$F_4BC_4$	423-5	526-7	18:0	0	0	0	4
B	$F_4BC_4$	426-5	534-1	20:0	0	0	0	6
B	$F_4BC_4$	426-5	534-5	20:0	0	0	0	5
B	$F_4BC_4$	430-3	561-6	20:0	0	1	0	7
B	$F_4BC_4$	430-3	561-7	20:0	0	0	0	5
B	$F_4BC_4$	430-3	561-15	20:0	0	0	0	3
C	$F_3BC_4$	975121-8	276458-1	13:0	0	2	3	3
C	"	121-8	458-4	13:0	0	0	0	5
C	"	121-8	458-7	13:0	0	0	2	3
C	"	121-8	458-8	13:0	0	2	0	4
C	"	121-8	458-9	13:0	2	0	0	3
C	"	121-8	458-13	13:0	0	0	0	4
C	$F_4BC_4$	276458-8	976568-1	21:0	0	0	0	3
C	"	458-8	568-16	21:0	0	0	0	5
C	"	458-8	568-20	21:0	2	0	0	6
C	"	458-5	577-2	18:2	0	0	0	4
C	"	458-5	577-3	18:2	0	0	0	2
C	"	458-5	577-9	18:2	0	0	0	—*
C	"	458-5	577-10	18:2	0	0	0	2
C	"	458-5	577-17	18:2	0	0	0	2
D	"	276482-3	976582-2	18:1	0	0	0	5
D	"	482-3	582-8	18:1	0	0	0	5
D	"	482-3	582-12	18:1	0	0	0	—*
D	"	482-3	582-14	18:1	0	0	0	—*
D	"	276485-4	976590-1	19:1	0	0	0	3
D	"	485-4	590-3	19:1	0	0	0	—*
D	"	485-4	590-4	19:1	0	2	1	2
D	"	485-4	590-8	19:1	0	0	0	—*
D	"	485-4	590-9	19:1	0	0	0	5
D	"	485-4	590-13	19:1	0	1	0	1
D	"	485-4	590-14	19:1	0	0	0	—*
D	"	485-4	590-15	19:1	0	0	0	5
D	"	485-4	590-19	19:1	0	0	0	2
E	$F_3BC_4$	975110-3	276403-3	4:0	0	0	2	4
H	"	110-5	405-4	4:0	2	2	0	3

\*No cell was found in the diakinesis stage.

Only those cells in which the chromosome configuration was clear are reported; and consequently, the numbers are small.



Table 14. Reactions to wheat streak mosaic virus of the  $F_1$  involving line E and of the immune and susceptible checks grown in the greenhouse.

Male parent	Cross	Culture	$F_1$ I:S
177868	Sage/Line E	976595-6	3:0
977264	47731b/Line E	47723-7	8:0
977289	Tx69A569-1/Line E	2235	4:0
977309	♀ Line E/Roughrider	22-5	5:1
			TOTAL 20:1

Table 15. Reactions to wheat streak mosaic virus in various generations of line F and of the susceptible and immune checks grown in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 76	I:S
274323-7	975269	10:2	975269-1	276501	2:4	276503-1	976603	22:1
			269-2	502	1:1	503-2	604	22:1
Centurk Susc. Check		0:400	269-3	503	11:0	503-3	605	22:1
CI 15092 Imm. Check		24:0	269-4	504	1:0	503-4	606	23:2
" " "		15:5	269-5	505	2:3	503-5	607	24:0
			269-6	506	0:13	503-6	608	20:0
			269-7	507	0:1	503-7	609	22:1
			269-8	508	16:0	503-11	610	20:0
			269-9	509	0:9	503-8	611	22:0
						Centurk Susc. Check		0:248
			Centurk Susc. Check		0:160	CI 15092 Imm. Check		8:11
			CI 15092 Imm. Check		34:0	" " "		10:10

Table 16. Reaction to wheat streak mosaic virus of the  $F_1$  and  $F_2$  involving line F and of the susceptible and immune checks grown in the greenhouse.

Cross	Male parent	$F_1$		Source	$F_2$		P from $X^2$ for goodness-of-fit to 3:1 ratios
		Culture	I:S		Culture	I:S	
Ctk* 2/CIMMYT//Line F (27612-1)	276503-2	976639	2:0	976639-1	177951	10:6	>.05
				-2	177952	2:1	>.05
Ctk* 3/CIMMYT, sib 2//Line F (2769-2)	276508-7	976640	8:0	976640-1	177953	1:0	>.05
				-2	177954	4:11	<.05
				-3	177955	10:6	>.05
				-4	177956	2:3	>.05
				-5	177957	2:8	<.05
				-6	177958	3:3	>.05
				-7	177959	1:3	<.05
				-8	177960	11:19	<.05
					<u>34:53</u>	<.05	
Ctk* 3/CIMMYT, sib 1//Line F	276508-7	976641	2:0	976641-1	177961	5:2	>.05
				-2	177962	23:10	>.05
						<u>28:12</u>	>.05
Lancota/Line F	976603-11	177801	12:4				
" "	976605-1	802	9:0				
" "	976605-3	803	10:0				
" "	976605-8	804	1:0	Centurk Susc. Check		1:226	
				CI 15092 Imm. Check		0:19	
Sage/Line F	976641-3	817	5:1				
" "	976605-1	853	2:2				
" "	976605-3	854	12:0				
Ctk/Line F	976605-8	177884	10:0				
Ctk/Line F	976605-1	977265	9:0				
Ctk/Line F	47721-1	977265	9:0				
			<u>91:7</u>				

susceptible (Table 16). These 7 susceptible could have been selfs or an expression of cytological instability. Three of the crosses were progeny tested in  $F_2$  (Table 16). In two crosses, the ratios were Mendelian. But in the third (976640) Ctk 3/CIMMYT, sib 2//Line F, a ratio of 34:53 was obtained which does not support the presence of a translocation. A ratio of 34:53 is typical of segregation from a monosomic addition plant.

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_2$  data were evidence of both a translocation and alien chromosome addition in line F (Table 16).

#### Line G

Eleven  $F_2BC_4$  plants were progeny tested. One  $F_3BC_4$  line was homozygous immune, 9  $F_3BC_4$  lines segregated, and one bred true for susceptibility. The observed ratio of  $F_3$  lines of 1:9:1 corresponds closely to the expected Mendelian ratio (Table 17) of 2.75:5.5:2.75.

Three  $F_3$  lines--276584, 276587 and 276588--were progeny tested. The four  $F_4BC_4$  families from 276584 (10:0) bred true for immunity which is evidence of stability. Four families from 276587 (8:2) segregated a preponderance of susceptible plants indicating that the gene controlling immunity was still on the alien chromosome. Four families from line 276588 (8:2) segregated but not in a pattern clearly supporting the occurrence of a translocation (Table 17).

Line G was crossed with commercial varieties and advanced lines and 31  $F_1$  plants obtained of which 28 were immune and 3 were susceptible. The 3 susceptible plants were either selfs or an expression of cytological instability. From five different crosses,  $F_2$  involving Line G

Table 17. Reactions to wheat streak mosaic virus in various generations of line G and of the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 77	I:S
274279-16	975301	19:10	975301-2	276582	5:4	276584-3	977555	24:0
			301-4	583	7:3	584-5	556	24:0
Centurk Susc. Check		0:400	301-8	584	10:0	584-6	557	23:0
CI 15092 Imm. Check		24:0	301-10	585	5:4	584-7	558	24:0
" " "		15:0	301-11	586	2:7			95:0
			301-12	587	8:2	276587-1	559	9:15
			301-15	588	8:2	587-2	560	15:10
			301-16	589	5:5	587-3	561	6:12
			301-17	590	0:8	587-4	562	14:10
			301-18	591	5:5			
			301-19	592	4:16	276588-1	563	3:6
						588-2	564	2:0
			Centurk Susc. Check		0:160	588-3	565	16:3
			CI 15092 Imm. Check		34:0	588-4	566	19:0
						Centurk Susc. Check		0:248
						CI 15092 Imm. Check		8:11
						" " "		10:10

(Table 18) were studied. Twenty-one of the 22  $F_2$  ratios were Mendelian, and one deviated significantly from a 3:1 ratio. In four of the five crosses, totals of  $F_2$  ratios for individual crosses also fit 3:1 ratios, evidence of a translocation. In the fifth cross, one  $F_2$  ratio is Mendelian and one deviates significantly. This may be a chance variation from expected. One homozygous immune  $F_3BC_4$  plant, 276584-5, was crossed with SD 713-2. In  $F_2$ , there were 214 immune and 56 susceptible plants, a good fit to 3:1 ratio (Table 18). Plant 276584-5, when progeny tested, bred true (24:0) for immunity, an evidence that plant 276585-5 has a translocation.

$F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ , and  $F_2$  data are evidence that line 276584 has a translocation.

#### Line H

In line H, 10 of 16  $F_2BC_4$  plants were progeny tested (Table 20). In two  $F_3BC_4$  lines, all the seedlings died due to root rot. Of the remaining eight, two were homozygous immune and 6 segregated.

Six immune plants from one segregating  $F_3BC_4$  line were progeny tested. Two were homozygous immune. Three segregated in conformance with 3:1 ratios. One  $F_4$  line had three immune and 18 susceptible, not a Mendelian ratio (Table 20).

Two  $F_3BC_4$  plants from two homozygous immune lines, 276403 (4:0) and 276405 (4:0), were examined cytologically; and 21 bivalents were counted in 7 cells, some evidence of a translocation. One open bivalent, one laggard and one micronucleus were observed in two cells (Table 13).

Table 18. Reactions to wheat streak mosaic virus of the  $F_1$  and  $F_2$  involving line G and of the resistant and susceptible checks grown in the greenhouse.

Cross	Male parent	$F_1$		Source	$F_2$		goodness-of-fit to 3:1 ratios
		Culture	I:S		Spring 77	I:S	
Ctk* 3/CIMMYT, sib 1//Line G (27615-6)	276584-2	976642	7:2	976642-1	177963	22:14	>.05
				642-2	964	10:8	>.05
				642-3	965	19:10	>.05
				642-4	966	29:5	>.05
				642-5	967	35:7	>.05
Ctk* 3/CIMMYT, sib 2//Line G (27616-1)	276584-2	976643	3:0	976643-1	968	115:44	>.05
				643-2	969	2:0	>.05
				643		11:6	>.05
Ctk* 2/CIMMYT, sib 1//Line G (27620-2)	276584-2	976644	8:0	643		13:6	>.05
				644-1	970	1:1	>.05
				644-2	971	5:1	>.05
				644-3	972	5:2	>.05
				644-4	973	5:1	>.05
				644-5	974	7:3	>.05
SD 713-2/Line G	276584-5	976645	8:0			23:8	>.05
				976645-1	177975	25:10	>.05
				645-2	976	25:7	>.05
				645-3	977	30:6	>.05
				645-4	978	21:7	>.05
				645-5	979	31:10	>.05
				645-6	980	25:9	>.05
				645-7	981	27:3	>.05
				645-8	982	30:4	>.05
Ctk* 2/CIMMYT, sib 2//Line G (27618)	276584-7	976646	2:1			214:56	>.05
				976646-1	177983	34:3	<.05
				976646-2	177984	21:4	>.05
TOTALS			28:3		421:121	>.05	

Table 19. Percentage of immune and susceptible plants in different  $F_2$  crosses grown in the greenhouse.

Parental lines	Total no. of $F_2$ plants	Number of immune plants (%)	Number of susceptible plants (%)	P from $X^2$ for goodness-of-fit to 3:1 ratios
A	438	356 (81.3)	82 (18.7)	<.05
B	601	449 (74.7)	152 (25.3)	>.05
C	753	562 (74.6)	191 (25.4)	>.05
D	103	80 (78.0)	23 (22.0)	>.05
F	59	40 (67.8)	19 (32.2)	>.05
G	541	420 (77.6)	121 (22.4)	>.05



Table 20. Reactions to wheat streak mosaic virus in various generations of line H and of the susceptible and immune checks in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Fall 75	I:S		Spring 76	I:S		Fall 77	I:S
274275-9	975110	16:8	975110-1	276401	---	276410-1	977502	21:0
			110-2	402	2:4	410-2	503	12:7
Centurk Susc. Check		0:400	110-3	403	4:0	410-3	504	21:0
CI 15092 Imm. Check		24:0	110-4	404	---	410-4	505	17:3
" " "		15:5	110-5	405	4:0	410-6	506	3:18
			110-6	406	4:6	410-7	507	14:6
			110-7	407	5:3			
			110-8	408	4:2	Centurk Susc. Check		0:248
			110-9	409	5:5	CI 15092 Imm. Check		8:11
			110-10	410	6:2	" " "		10:10
			Centurk Susc. Check		0:160			
			CI 15092 Imm. Check		34:0			

The data does not conclusively establish that line H has either the alien chromosome or a translocation involving it.

#### Line N

Fifteen of the 16 immune  $F_2$  plants were progeny tested (Table 21). None of the  $F_3$  lines was homozygous for immunity. Five were completely susceptible and 10 segregated. Line N was further tested for breeding behavior in  $F_4BC_4$  in the 1976 fall greenhouse crop. Most  $F_4$  lines segregated an excess of susceptible plants over immune, an indication of the presence of an alien chromosome.

#### Test of Agronomic Qualities

The objective of this study was to determine the agronomic qualities of lines having five doses of Centurk in them and immunity to WSMV from Agropyron intermedium. Six lines, each represented by two sibs, were compared under field conditions with Centurk for days to half headed, plant height, tillers per plant, percent fertility of the main spike, number of seeds in the main spike, weight of 100 seeds and yield per plant. Averaged results are reported in Table 22. The complete results are reported in appendix tables 1-6.

Heading dates ranged from 78-88 days, while Centurk headed in 85 days. Most of the lines were earlier than Centurk or of the same maturity. The F lines headed earlier than Centurk or the other lines (Table 22 and Figure 5). All the lines were shorter than Centurk. Plant height ranged from 83 to 99% of Centurk (Table 22 and Figure 4).

One or more lines equaled or exceeded Centurk in one or more of these qualities: tillers per plant, fertility of the main tiller,

Table 21. Reactions to wheat streak mosaic virus in various generations of line N and of the susceptible and immune checks grown in the greenhouse.

Source	F <sub>2</sub> BC <sub>4</sub>		Source	F <sub>3</sub> BC <sub>4</sub>		Source	F <sub>4</sub> BC <sub>4</sub>	
	Spring 75	I:S		Fall 75	I:S		Spring 76	I:S
274273-5	275205	16:4	275205-1	975272	9:3	975277-1	276511	0:10
			205-2	273	0:25	277-2	512	5:10
Centurk Susc. Check		Frozen due	205-3	274	9:16	277-3	513	0:11
CI 15092 Imm. Check		to blizzard	205-4	275	0:15	277-4	514	8:6
"	"	"	205-5	276	0:20	277-5	515	4:7
			205-6	277	20:10	277-6	516	2:12
			205-7	278	0:27	277-7	517	4:8
			205-8	279	16:8	277-8	518	5:10
			205-9	280	12:17	277-9	519	8:6
			205-10	281	9:9	277-10	520	4:7
			205-11	282	18:10	975279-1	521	6:11
			205-12	283	21:15	279-2	522	5:6
			205-13	284	8:14	279-3	523	4:8
			205-14	285	0:14	279-4	524	2:8
			205-15	286	4:11	279-5	525	9:7
						279-6	526	7:6
			Centurk Susc. Check		0:400	279-7	527	7:3
			CI 15092 Imm. Check		24:0	279-8	528	0:11
			"	"	15:5	279-9	529	0:6
						279-10	530	9:0
						975282-1	531	7:11
						282-2	532	2:11
						282-3	533	8:3
						282-4	534	2:13
						282-5	535	3:10
						282-6	536	6:9
						282-7	537	1:10

Table 21. (continued)

Source	F <sub>4</sub> BC <sub>4</sub>	
	Spring 76	I:S
975282-8	276538	6:6
282-9	539	3:9
282-10	540	7:5
975283-1	541	4:8
283-2	542	5:7
283-3	543	5:7
283-4	544	6:6
283-5	545	6:6
283-6	546	6:6
283-7	547	5:7
283-8	548	7:6
283-9	549	5:6
283-10	550	9:4
		192:303
Centurk Susc. Check		0:248
CI 15092 Imm. Check		8:11
" " "		10:10

number of seeds in the main tiller, 100 seed weight. In number of tillers per plant, line D2 is highest of all (Table 22 and Figure 6). Lines C1 and D1 were essentially the same as Centurk but greater than the rest of the lines in percent fertility of the main spike (Table 22 and Figure 7). Seeds per main spike are lower in the lines than for Centurk except for Centurk in C1 (Table 22 and Figure 8). Hundred seed weights of lines A1, A2, D1 and E1 were higher than for Centurk (Table 22 and Figure 10). In yield per plant, Centurk out-yielded all the translocation lines. Line D1 was second to Centurk with a yield of 94% of Centurk (Table 22 and Figure 9).

There is a significant difference between the lines at the 1% level of probability for tillers per plant (Table 23), fertility in the main spike, number of seeds in the main spike, hundred seed weight and yield per plant (Tables 24, 25, 26 and 27). Sister lines, however, did not differ for these agronomic characters at either the 1 or at 5 percent levels (Tables 23-27). From the results of this field experiment (Table 22), it is apparent that line D was superior in seed yield and in spikes per plant. But line C was superior in seeds per spike. Line A had larger seeds than the check or the other lines. Line F was earlier in maturity than the rest.

The translocation lines tested for agronomic characters in the field were considered to be immune but could not be inoculated with WSMV. To verify their presumed immunity, all were progeny tested and found to have been immune (Table 28). The proportions of immune progeny ranged from 90 to 100 percent. Some of the progeny lines were completely immune. All the 61 Centurk check plants were susceptible while

Table 22. Comparisons between agronomic characters of six lines grown from vernalized seedlings with those of the recurrent parent, Centurk, in the field in 1977.

Check or line**	Days to head*	Centurk check as 100%					
		Height	Tillers per plant	% fertility of main spike	No. of seeds in main spike	100 seed weight	Yield per plant
Centurk	85	100	100	100	100	100	100.0
A1	85	90	73	90	68	117	49
A2	86	93	60	81	64	102	43
B1	83	96	77	94	65	99	47
B2	82	92	83	94	66	90	49
C1	84	94	69	101	112	90	56
C2	85	95	66	95	88	93	70
D1	81	94	96	101	90	107	94
D2	80	99	101	98	88	97	82
E1	85	85	89	90	67	102	46
E2	88	94	92	92	75	92	52
F1	78	90	86	95	69	100	58
F2	79	83	77	81	56	96	45

\*Days to head were counted from the transplanting date, 4/23/77, to the date when 50% of heads were out of the boot leaf.

\*\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a line.

Table 23. Analysis of variance of tillers per plant of six different lines and the Centurk check under field conditions.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	F at the	
					0.05	0.01
Lines	6	755.05	125.84	21.85**	3.00	4.82
Sister Lines	1	0.35	0.35	7.11	18.51	98.50
Replications (Blocks)	2	2.67	1.34			
Line x Sister	6	77.54	12.92	1.34	3.00	4.82
Line x Replications	12	69.10	5.76			
Sister x Replications	2	9.84	4.92			
Line x Sisters x Replications	12	116.16	9.68			
Error	378	2,882.00	7.62			
TOTAL	419					

\*\*Significant at 1 percent level.

Table 24. Analysis of variance of the fertility of the main spike of six lines and the Centurk check under field conditions.

Source of Variation	Degrees of freedom	Sum of squares	Mean square	F value	F at the	
					0.05	0.01
Lines	6	10,256.99	1,709.49	9.34**	3.00	4.82
Sister lines	1	1,160.32	1,160.32	1.41	18.51	98.50
Replications (Block)	2	60.52	30.26			
Line x Sisters	6	3,623.15	603.86	2.79	3.00	4.82
Line x Replications	12	2,196.52	183.04			
Sisters x Replications	2	1,640.92	820.45			
Line x Sisters x Replications	12	2,601.96	216.83			
Error	378	58,440.21	154.60			
TOTAL	419					

\*\*Significant at 1 percent level.



Table 25. Analysis of variance of the number of seeds in the main spike of six lines and the Centurk check under field conditions.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	F at the	
					0.05	0.01
Lines	6	18,904.98	3,150.83	98.71**	3.00	4.82
Sister lines	1	534.80	534.80	4.38	18.51	98.50
Replications (Block)	2	148.49	74.15			
Line x Sisters	6	1,712.99	285.50	4.02*	3.00	4.82
Line x Replications	12	383.10	31.92			
Sisters x Replications	2	244.42	122.21			
Line x Sisters x Replications	12	850.64	70.89			
Error	378	20,378.24	53.90			
TOTAL	419					

\*\*Significant at 1 percent level.

\*Significant at 5 percent level.

Table 26. Analysis of variance of 100 seed weight per plant of six lines and the Centurk check under field conditions.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	F at the	
					0.05	0.01
Lines	6	5.68	0.95	5.59**	3.00	4.82
Sister lines	1	0.78	0.78	1.18	18.51	98.50
Replications (Block)	2	0.08	0.04			
Line x Sisters	6	1.62	0.27	1.35	3.00	4.82
Line x Replications	12	1.99	0.17			
Sisters x Replications	2	1.32	0.66			
Line x Sisters x Replications	12	2.43	0.22			
Error	378	12.53	0.03			
TOTAL	419					

\*\*Significant at 1 percent level.

Table 27. Analysis of variance of yield per plant of six lines and the Centurk check under field conditions.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	F at the	
					0.05	0.01
Lines	6	1,981.91	330.32	148.13**	3.00	4.82
Sisters	1	4.87	4.87	0.26	18.51	98.50
Replications (Block)	2	3.55	1.77			
Line x Sisters	6	57.22	9.54	0.79	3.00	4.82
Line x Replications	12	26.75	2.23			
Sister x Replications	2	36.86	18.43			
Line x Sisters x Replications	12	144.81	12.07			
Error	378	2,134.27	5.65			
TOTAL	419					

\*\*Significant at 1 percent level.

Table 28. Progeny test in the greenhouse to wheat streak mosaic virus of  $F_6BC_4$  lines from the field experiment.

Entries*	No. of Plants	No. of seedlings tested	No. of Immune Seedlings (%)	No. of susceptible Seedlings (%)	No. of progeny lines completely susceptible
A1	25	138	136 (98.6)	2 (1.4)	0
A2	20	109	109 (100.0)	0 (0.0)	0
B1	29	187	185 (98.9)	2 (1.1)	0
B2	30	178	175 (98.3)	3 (1.7)	0
C1	30	189	182 (96.3)	7 (3.7)	0
C2	30	186	179 (96.2)	7 (3.8)	0
D1	30	208	208 (100.0)	0 (0.0)	0
D2	30	209	188 (90.0)	21 (10.0)	0
E1	29	196	184 (93.9)	12 (6.1)	0
E2	29	202	194 (96.0)	8 (4.0)	0
F1	30	216	216 (100.0)	0 (0.0)	0
F2	30	203	201 (99.0)	2 (1.0)	0
Centurk		61	0 (0.0)	61 (100.0)	0
CI 15092		58	56 (96.6)	2 (3.4)	0

\*Numbers 1 and 2, as in A1 and A2, identify different progeny lines within a translocation source.

56 (96.6%) of 58 seedlings of the immune check (CI 15092) were resistant (Table 28).

In an unreplicated field experiment (Table 29), six lines were compared morphologically among themselves and with the Centurk check for leaf attitude, leaf width, height, heading date and seed size. Leaf streaking caused apparently by Xanthomonas translucens appeared in this experiment (J. D. Otta, personal communication). Reactions of different lines to streaking are reported in Table 29. Seeds were larger than Centurk in most of the experimental lines which had been deliberately selected for their larger seed which accounts for uneven numbers of sibs of lines in the planting. All the lines were earlier than Centurk in heading except two cultures of E, 47722 and 47723. Fifteen of the lines were shorter than the 64 cm height of the shortest of the Centurk checks.

Leaf attitude was strikingly different between lines. Line E (Figures 13, 14) had the same spreading habit of leaf growth as that of Centurk (Figures 15, 16). (Line C, Figures 11, 12), line D (Figures 12, 13) and line F (Figures 14, 15) had erect medium-erect leaves. Line A and B had medium erect leaves (Figures 11 and 16). Translocation lines C and D had the broadest leaves, whereas line F had narrower leaves than Centurk (Figures 13, 14). Line E was also immune from streaking while line D was most susceptible of the entries. None of these lines was as severely affected by streaking as some winter wheat selections growing in the same field. Phenotypic appearances of heads from different lines are compared with Centurk in Figure 17. Heads of lines C, D and E had more erect awns than Centurk, whereas lines A, B and F had medium

spreading awns (Figure 17). Shown also is a head of A. intermedium and of TA25 (Octoploid), the source of immunity in this study.



Table 29. Agronomic comparisons between vernalized lines transplanted to the field.

Culture	Suspected translocation/Ck	Seed Size	Leaf width	Date of half heading	Mean height in cm	Leaf attitude	Leaf streaking**
47731	Centurk	Centurk ck	Centurk ck	6/13	70	Spreading	1
4772	A	Centurk--	Like Centurk	6/11	50	Medium erect	1
4773	"	"	Like Centurk	6/9	55	" "	1
4774	"	Centurk	" "	6/9	58	" "	1
4775	"	"	" "	6/10	58	" "	1
4776	"	Centurk++	" "	6/10	59	" "	1
4777	"	"	" "	6/12	65	" "	1
47732	B	Centurk	Narrower than Ctk	6/10	72	Medium erect	1
47733	"	" +	" " "	6/10	65	" "	1
47734	"	" ++	" " "	6/8	62	" "	1-
4778	C	Centurk+	Broader than Ctk	6/11	69	Erect	1
4779	D	Centurk+	" " "	6/8	63	Medium erect	2
47710	"	"	" " "	6/8	64	" "	2
47711	"	Centurk++	" " "	6/12	67	" "	2
47712	"	Centurk	" " "	6/12	64	" "	2
47713	"	Centurk+	" " "	6/13	71	Erect	1
47714	"	Centurk++	" " "	6/12	66	" "	2
47715	"	" ++	" " "	6/11	65	" "	2
47716	"	" ++	" " "	6/12	66	" "	2
47717	"	Centurk+	" " "	6/9	62	" "	2
47718	"	"	Like Centurk	6/10	67	" "	2+
47719	"	" ++	" " "	6/9	68	" "	2+
47720	"	" +, soft	" " "	6/11	70	" "	3
47721	"	Centurk, soft	" " "	6/11	71	" "	3
47722	E	Centurk+	" " "	6/14	64	Spreading	0
47723	"	"	" " "	6/15	60	" "	0
47724	"	"	" " "	6/12	69	" "	0
47725	"	"	" " "	6/13	62	" "	0
47726	F	"	Narrower than Ctk	6/7	58	Erect	1
47727	"	"	" " "	6/7	57	" "	1
47728	"	Centurk	" " "	6/7	55	" "	1
47729	"	Centurk+	" " "	6/8	60	" "	1
47730	"	Centurk+	" ck" "	6/8	55	" "	1
47731	Ctk	Centurk ck	Centurk ck	6/13	64	Spreading	1

\*Ctk=Centurk check, \*\*Streaking was apparently due to the bacterium Xanthomonas translucens, 0=No streaking, 4=Heavily streaked, Centurk+=Better than Centurk

Figure 4. Comparison of the average height of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.

Figure 5. Comparison of average number of days to half headed of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.



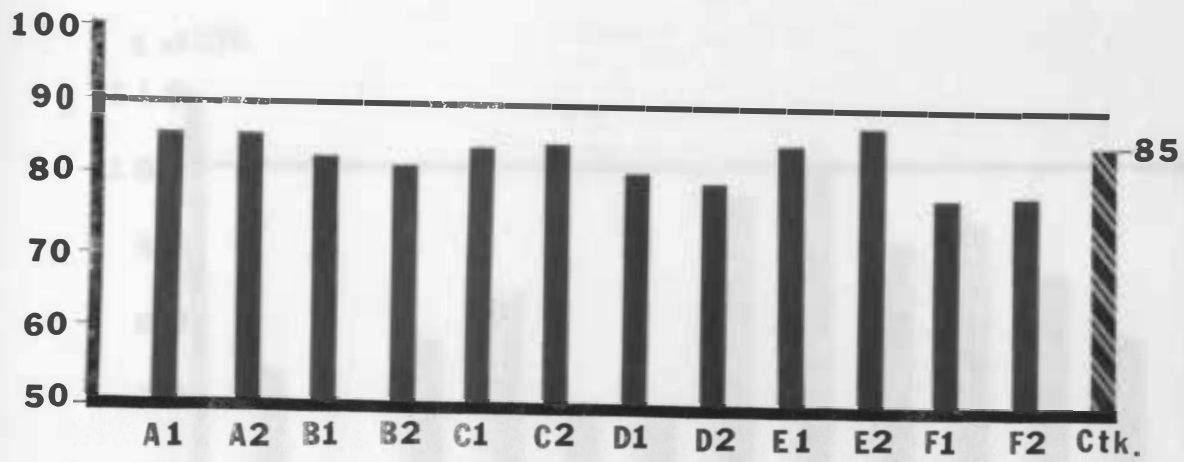


Fig. 5 No. of days to half headed.

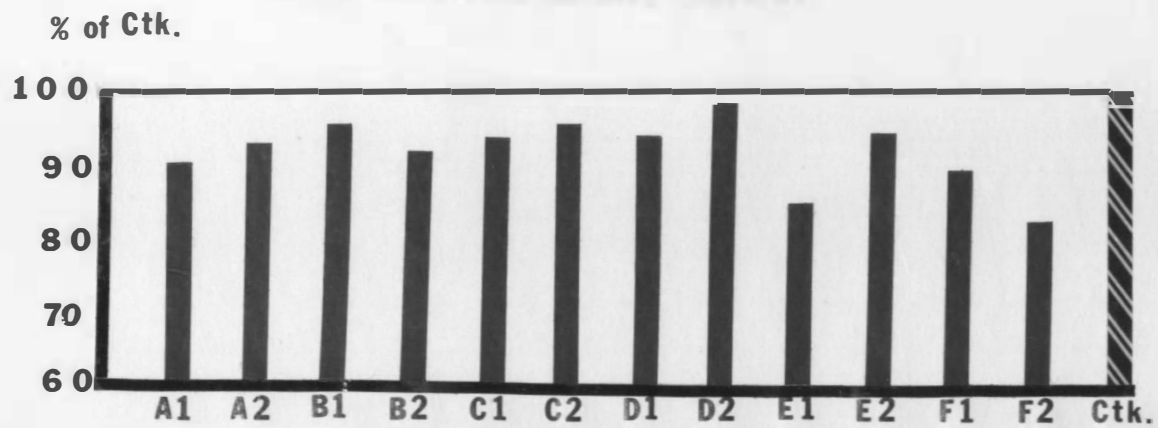


Fig. 4 Average height.

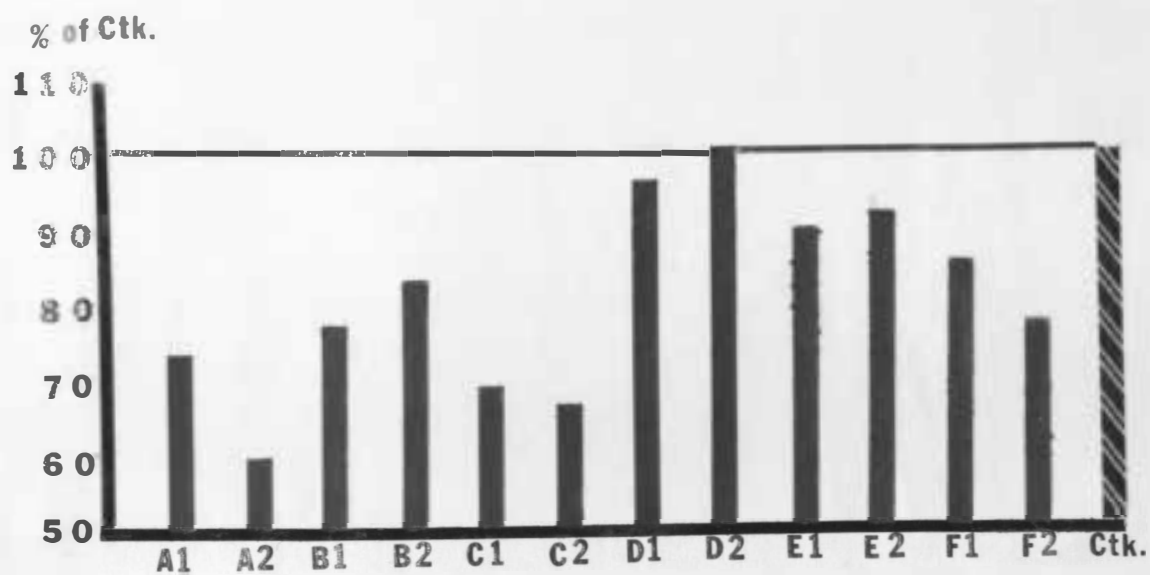


Fig. 6 No. of tillers per plant.

Figure 6. Comparison of the average number of tillers per plant of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.

Figure 7. Comparison of fertility in the main spike of different lines and their sibs in percent of the recurrent parent, Centurk.

Figure 8. Comparison of number of seeds in the main spike of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.

% of Ctk.

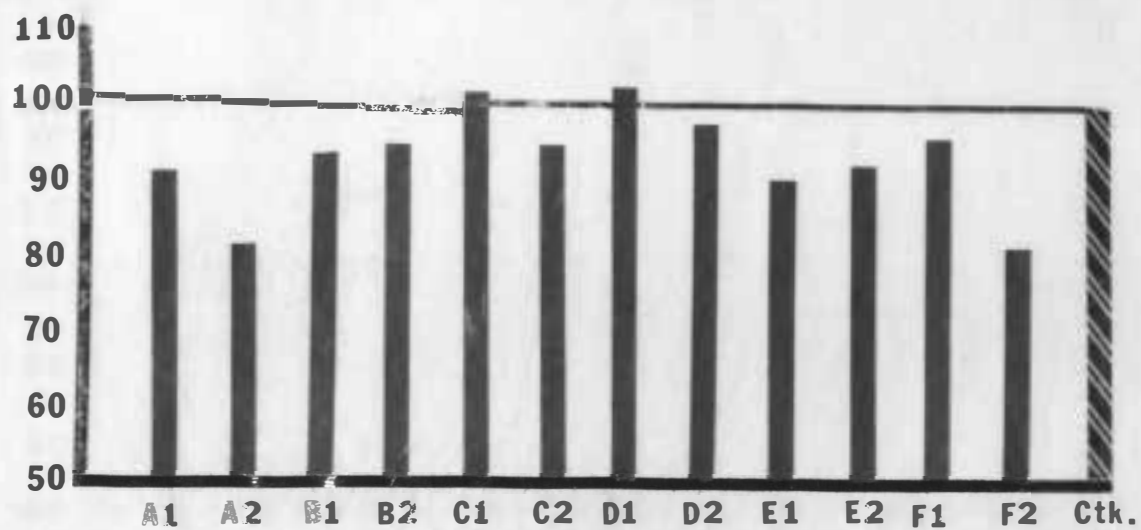


Fig. 7 Fertility of main spike.

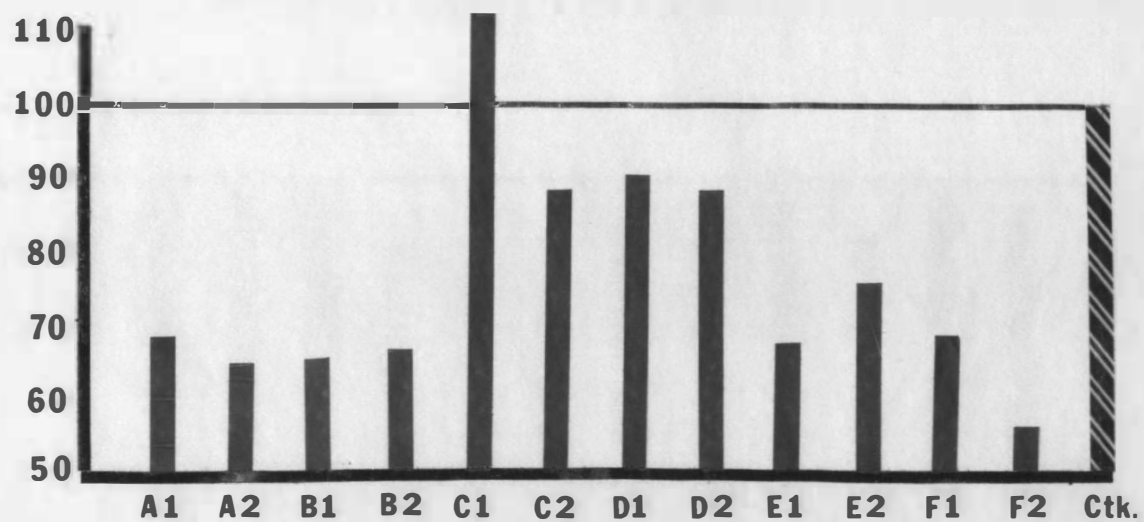


Fig. 8 No. of seeds in main spike.




Figure 9. - Comparison of mean yield per plant of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.

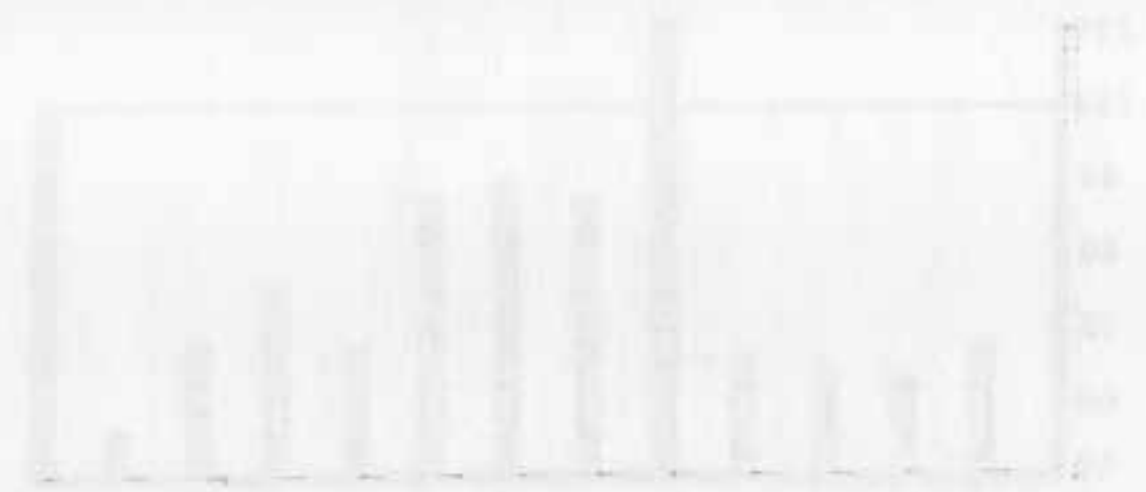


Figure 10. Comparison of weight of 100 seeds in grams per plant of different lines and their sibs in  $F_5BC_4$  with that of the recurrent parent, Centurk.

% of Ctk.

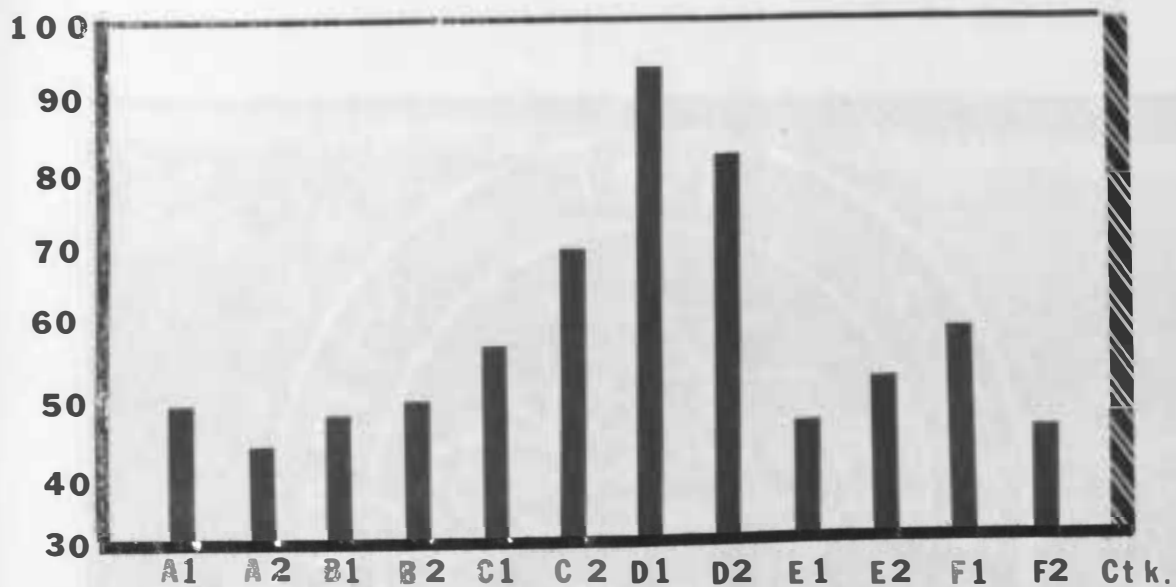


Fig. 9 Yield Per Plant.

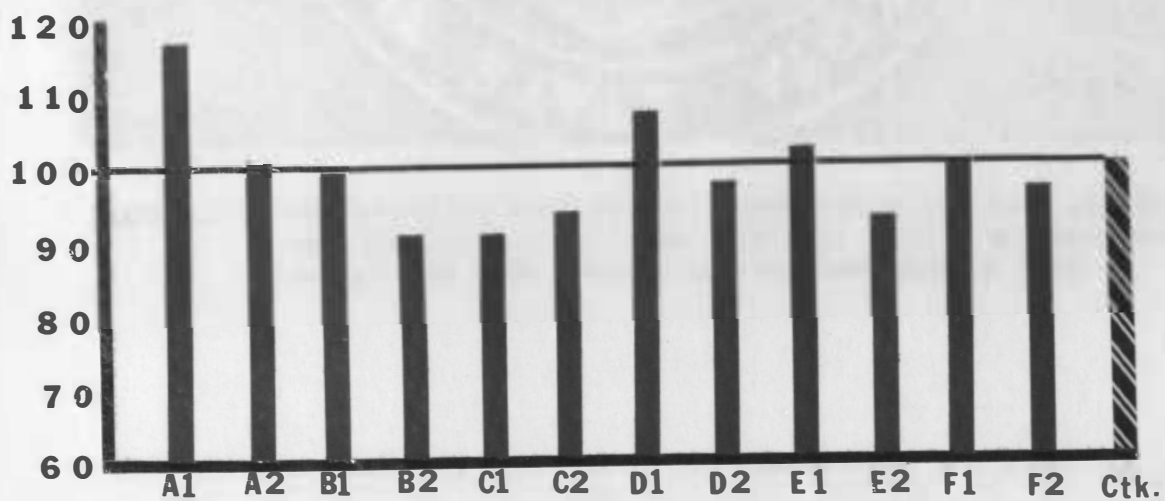


Fig. 10 Seed weight.



Figure 11. Variation in leaf attitude (erectness and leaf width) of two lines and their sibs. Sibs of line C are more erect, taller and have broader leaves than sibs of line A.



Figure 12. Variation in leaf attitude of two lines and their sibs. Sibs of line C are more erect than sibs of line D. Sibs of line D have broader leaves than sibs of line C.





Figure 13. Variation in leaf attitude (erectness and width) and height of two lines and their sibs. Sibs of line D are more erect, taller and have broader leaves than sibs of line E.



Figure 13b. Variation in leaf attitude (erectness), height and maturity at a later date between the sibs of lines D and E. Sibs of line D are more erect, taller and earlier than sibs of line E.

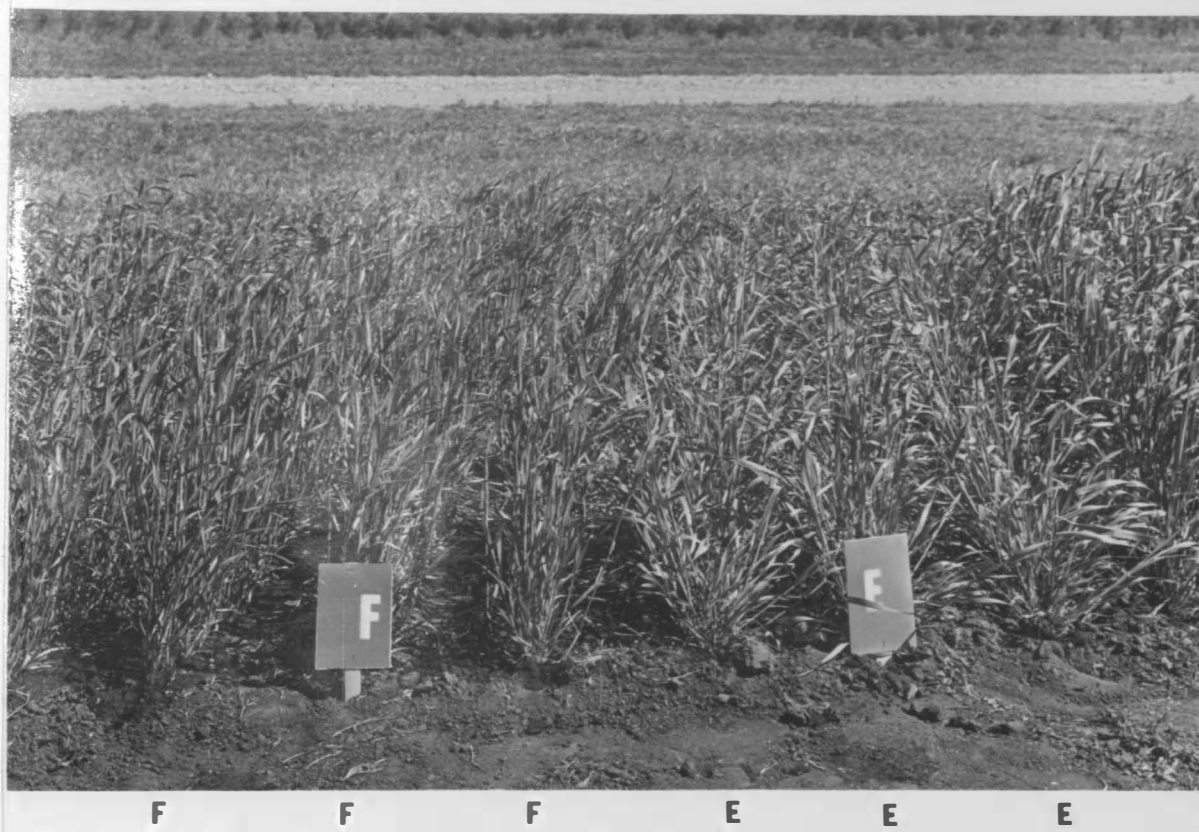


Figure 14. Variation in leaf attitude (erectness) and height of two lines and their sibs. Sibs of line F are more erect, taller and earlier than sibs of line E.



**Ctk.**      **Ctk.**      **Ctk.**      **F**      **F**      **F**

Figure 15. Variation in leaf attitude (erectness) between sibs of line F and Centurk check. Sibs of line F are more erect and earlier than Centurk.



Figure 16. Variation in leaf attitude (erectness) and maturity between sibs of line B and Centurk check. Sibs of line B are semi-erect and earlier than Centurk.



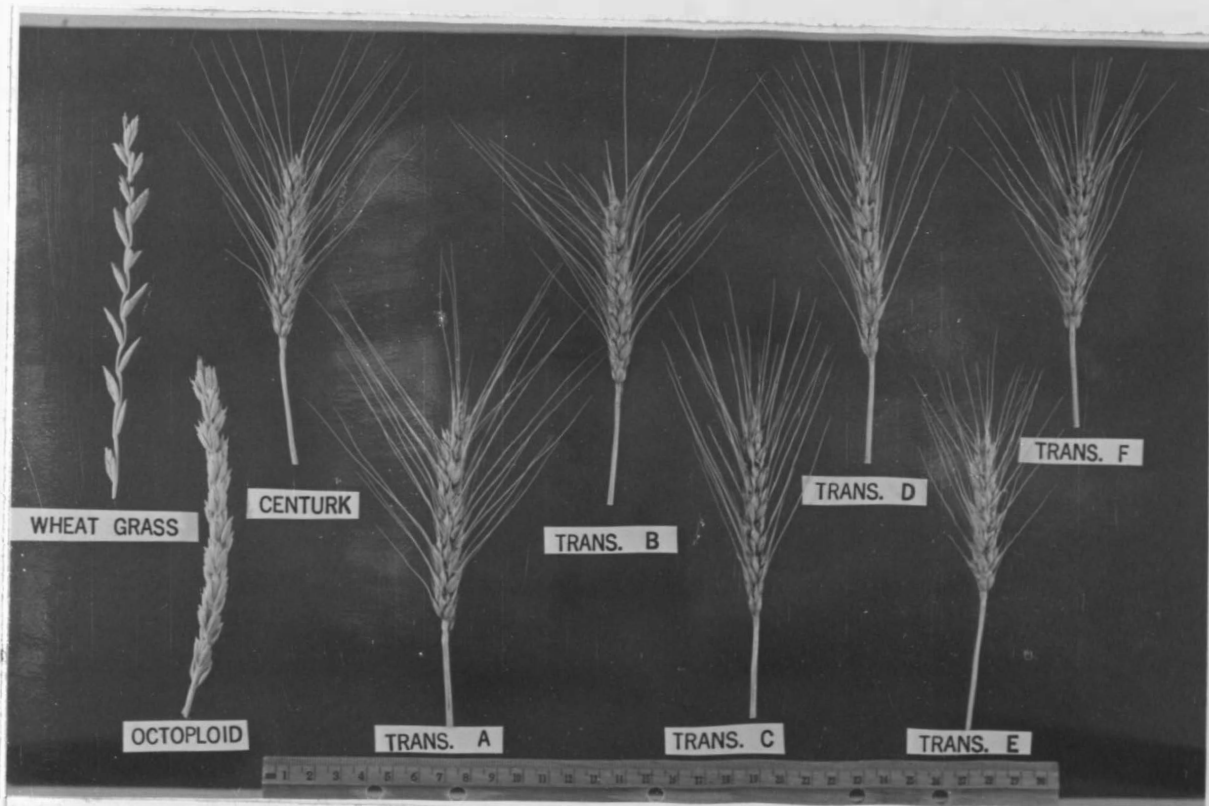


Figure 17. Comparison of spikes from different lines, the Centurk check, wheatgrass (*A. intermedium*) and the octoploid, TA 25. Heads of lines C, D and E had more erect awns than Centurk. Lines A, B and F had medium spreading awns.

## DISCUSSION

It is a well established fact that among all species related to wheat, Agropyron has resistance not only against leaf, stem and yellow rust, but also against wheat streak mosaic virus (WSMV). As a matter of fact, none of our winter wheat varieties has sufficient resistance to WSMV. It is a worthwhile project to attempt transferring immunity from Agropyron to cultivated wheat. Sebesta (Martin et al., 1976) has transferred immunity from A. elongatum via an Agrotricum. That immunity is recessive in the greenhouse so is unlike the immunity involved in the present study.

Various complexities involved in the utilization of lines derived from intergeneric crosses are decreased fertility, lack of pairing between the chromosomes of the two species precluding a natural exchange of genes through crossing over, and incorporation of undesirable characteristics along with resistance due to the presence of the whole alien chromosome. These problems can be overcome by subtle application of scientific knowledge and techniques to produce translocation lines.

According to Sears (1956), a univalent chromosome is lost about half the time at meiosis to male and female gametophytes expected to receive it. It is then included in only 25% of the gametes, producing a ratio of about 44% immune to 56% susceptible progeny. In contrast, the occurrence of ratios of 75% immune to 25% susceptible plants in progeny tests from selfing heterozygotes can be used as an indication of the

occurrence of translocations between the wheat and Agropyron chromosomes.

Sears (1956), Knott (1961), Sharma and Knott (1966) and Wienhues (1973) have found differential transmission of translocated chromosomes through male and female gametes of some translocation lines involving both A. elongatum and A. intermedium chromosomes. A frequency of 50% resistant plants may result if a translocation is transmitted only through female gametes. Frequencies of immune plants bearing a translocation have ranged from 50-75% depending on the rate of transmission of the translocation through male and female gametes.

In the present study, the treatment of seeds with fast neutrons induced chromosomal interchanges, which is in agreement with reports by Larter and Elliott (1956), Knott (1961), Qureshi *et al.* (1961), Sharma and Knott (1966) and Wienhues (1963, 1973).

The transfer of a resistance gene or genes from an immune Agro-tricum to Centurk, a common winter wheat variety, was indicated in fourteen different lines by ratios approaching three immune to one susceptible progeny. Due to limitations of space in the greenhouse, only nine of the 14 suspected translocations were studied in detail.

The  $F_2BC_4$ ,  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_2$  ratios and cytological examination gave evidence that lines A, B, C, D, F and G had translocations. In lines B and F, the data show that some of the families may have had an alien chromosome addition. In line E, the data do not indicate conclusively the presence of a translocation.

The translocation of a chromatin segment from A. intermedium to one of the Centurk chromosome did not change the level of expression of



immunity. The expression of resistance in each of the nine lines carrying a suspected translocation appeared to be identical to that of the immune check, CI 15092. The wheat chromosome involved in the translocation is not known.

In some cases, homozygous immune  $F_3BC_4$  plants, when progeny tested, produced a small number of susceptible plants (18:1, 20:1, Table 4,  $F_4BC_4$ ). The reason for this instability is not known. Wienhues (1973) reported instability in translocation lines in different generations. In translocation homozygotes, reported Wienhues, the chromosome carrying a gene or genes for resistance sometimes lagged behind in meiosis and was lost. Evidence for this was not observed in the present study. Some of the susceptible plants were dwarf and sterile which is an indication of loss of a whole chromosome pair.

None of the immune selections appeared to be agronomically equal to or superior to Centurk. Most of the lines are as early or earlier than Centurk. All the lines are shorter than Centurk, and all but D2 had fewer tillers per plant. Fertility of all but C1 and D1 was less than Centurk. Self-fertility might improve through pedigree selection. Only C1 exceeded Centurk in number of seeds in the main tiller. Yield per plant was usually less than for Centurk.

Most of the lines had larger seeds than Centurk. Earliness, shorter straw and larger seeds are a bonus which could be exploited along with immunity by using these lines as parents.

Plants of line D were earlier, shorter, had more tillers, higher fertility, larger seeds and higher yield than other lines. Dissimilarity of the phenotypes of the lines probably depended upon the loss of

different amounts of a Centurk chromosome as well as the addition of different amounts of the A. intermedium chromosome. Four doses of Centurk are present on the average in these lines so they potentially are much alike.

Knott (1958) noted that certain Thatcher substitution lines in which a pair of Thatcher chromosomes was replaced by a pair of A. elongatum chromosomes resembled Thatcher in yield and vigor. Among a large number of translocation lines, one may occur having no deleterious effect on the phenotype of Centurk; but such a line was not found among the few tested agronomically.

Most of the resistant progeny at the beginning in  $F_2BC_4$  had the entire alien chromosome. The unchanged A. intermedium chromosome had no apparent deleterious effects on gametes. In contrast, Sears (1956), in working with Aegilops umbellulata, found that the unchanged Ae. umbellulata chromosome carrying the gene or genes for leaf rust resistance was deleterious to gametophytes and was transmitted through pollen at a rate of only four percent. The selection pressure against the unchanged Ae. umbellulata chromosome increased the frequency with which translocations were found. In the present study, the absence of selection pressure against gametes having the alien chromosome reduced the frequency with which translocations were found.

The program to transfer wheat streak mosaic virus resistance from an immune Agroticum having A. intermedium as a parent to Centurk was facilitated by two things. Firstly, the resistance of A. intermedium was dominant over the susceptibility of Centurk. This provided a ready means of detection of the gene or genes for resistance. If the

susceptibility of the Centurk parent had been dominant, then a delaying procedure of progeny testing would have had to be adopted to detect resistance. Secondly, the A. intermedium resistance was due to a single gene or genes very closely linked.

The objective of transferring a gene for immunity to wheat streak mosaic virus from an Agropyron intermedium chromosome to one of the Centurk chromosomes by irradiation appears to have been achieved. Fourteen suspected translocations of the A. intermedium chromosome to Centurk were obtained, and nine of them (A, B, C, D, E, F, G, H and N) have been studied in some detail. Seven of these nine (A, B, C, D, E, F and G) have been crossed as parents with different commercial varieties and advanced lines in the winter wheat improvement program.

The immune translocation lines should be further tested for performance and quality and the best one considered for release.

## SUMMARY AND CONCLUSIONS

$F_1BC_3$  monosomic alien addition seeds having three doses of Centurk were irradiated with fast neutrons to translocate a segment of the alien chromosome accounting for immunity from wheat streak mosaic virus to a Centurk chromosome. Immune plants from the irradiated seeds were used as male parents onto Centurk and about 2,000  $F_1BC_4$  seeds obtained.

Cytological examination of pollen mother cells of 151 resistant  $F_1BC_4$  plants indicated that the majority of the plants continued to have an apparent alien univalent present in addition to the wheat complement.

Fourteen suspected translocations were identified in  $F_2BC_4$  on the basis of genetic segregation. The breeding behavior of nine of these 14 was studied in  $F_3BC_4$ ,  $F_4BC_4$ ,  $F_6BC_4$  and  $F_2$  generations. Most of these lines became more stable with advancing generations. Pollen mother cells of 37 plants in  $F_3BC_4$  and  $F_4BC_4$  were examined cytologically and 21 bivalents counted.

The frequency of transmission of the translocations through male and female gametes of translocation heterozygotes was found to be about 50 percent since in the  $F_2$  generation involving translocation lines A, B, C, D and G, 81, 75, 75, 78 and 78 percent of the progeny were resistant. In line F, however, immunity was transmitted with a reduced frequency of 68 percent.

A test to evaluate the effects of the suspected translocations on agronomic qualities and yield components of the plants indicated that all the translocation lines except D1 had less tillers per plant than the recurrent parent, Centurk. Fertility in the main tiller was higher in translocation lines C1 and D1 than Centurk. All the resistant lines tested in the field were shorter and headed earlier than Centurk except line E2, which headed three days after Centurk. Seeds were larger in all the lines than Centurk except lines B and C. Number of seeds in the main spike was lower in all the lines except C1. Yield per plant was also lower in all the lines.

Variation in the frequency of transmission of resistance through male and female gametes, plant height, tillers per plant, percent fertility in the main spike, number of seeds in the main tiller, seed size, yield and heading date of the six suspected translocation lines indicate that the substitution of the A. intermedium chromatin for the different segments of a Centurk chromosome had varying effects.

The genetic data show that resistance is controlled by a single dominant gene. Translocation of the gene from A. intermedium to a Centurk chromosome did not affect the expression of resistance.

The study provided at least six translocation lines, some of which may possibly be used as direct releases or certainly as parents to incorporate resistance to wheat streak mosaic virus into commercial varieties.

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Table A1. Comparison of number of tillers by replicates per mature plant grown from vernalized seedlings of six lines and their sibs in the field in 1977.

Plant No.	Line A1			Line B1			Line C1			Line D1			Line E1			Line F1			Ctk. Ck. I			Ctk. Ck. II		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
1	10	10	7	12	5	14	6	6	8	5	13	7	15	7	10	8	10	8	13	10	9	9	14	9
2	8	9	7	8	10	7	6	4	6	11	14	12	8	14	8	12	12	16	10	10	11	11	18	13
3	6	8	11	7	8	14	7	11	8	8	12	12	9	6	13	14	8	7	10	8	14	9	11	14
4	10	11	6	8	12	8	8	6	11	11	13	12	11	13	12	13	12	6	11	10	17	8	14	13
5	6	12	6	12	9	8	3	7	5	11	14	10	4	11	13	11	10	7	7	10	13	14	5	14
6	12	12	5	11	6	11	6	10	5	8	12	7	9	11	12	10	4	13	7	4	10	13	21	9
7	3	8	10	6	7	7	8	9	9	14	13	12	12	9	10	10	10	5	12	8	5	9	15	13
8	6	8	6	6	9	11	8	7	13	13	8	10	12	5	7	9	9	9	9	7	13	5	11	12
9	9	9	7	8	5	8	9	12	7	11	9	12	9	13	12	4	13	14	11	5	6	11	16	10
10	9	9	7	8	6	8	7	8	12	11	11	9	6	9	9	9	8	8	22	15	12	14	19	9
Rep. Total	79	96	72	86	77	96	68	80	84	103	119	103	95	98	108	100	96	93	112	87	110	105	144	116
Line Total	247			259			232			325			301			289			309			365		
Line Mean $\bar{x}$	8.2			8.6			7.7			10.8			10.0			9.6			10.3			12.1		
Plant No.	Line A2			Line B2			Line C2			Line D2			Line E2			Line F2			Ctk. Ck. I			Ctk. Ck. II		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
1	5	8	7	9	9	10	8	9	8	14	13	8	9	5	10	10	6	9	11	17	9	8	13	9
2	5	8	7	8	13	6	6	7	5	17	8	5	8	13	12	7	9	9	14	7	4	11	14	12
3	7	3	5	9	9	10	7	3	11	13	10	9	9	9	13	5	13	11	10	16	12	9	10	18
4	9	13	11	9	7	9	9	7	4	12	10	11	11	10	14	3	16	9	8	14	13	11	15	9
5	9	8	9	5	7	11	8	10	15	13	9	9	10	7	11	11	3	8	15	13	12	15	10	11
6	6	7	6	8	10	10	13	7	6	14	13	16	11	12	5	7	7	11	8	4	13	8	11	9
7	5	5	5	8	10	12	6	5	7	13	10	14	6	12	11	7	11	5	12	14	12	10	18	14
8	4	7	5	9	13	10	10	4	4	14	11	9	16	12	16	11	10	11	12	7	9	7	13	14
9	5	7	6	9	12	6	7	6	7	8	10	8	10	9	2	7	5	9	11	9	17	10	3	8
10	7	7	7	10	11	9	11	7	4	13	12	13	12	12	14	11	9	7	13	14	9	9	17	8
Rep. Total	62	71	68	84	101	93	85	65	71	131	106	102	102	101	108	79	89	89	114	115	110	98	124	112
Line Total	201			278			221			339			311			257			339			334		
Line Mean $\bar{x}$	6.7			9.3			7.4			11.3			10.3			8.6			11.3			11.1		

\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a suspected translocation source.



Table A2. Comparison of percent fertility of the main spike of plants grown from vernalized seedlings of six lines and their sibs with those of the recurrent parent, Centurk, in the field in 1977.

Plant No.	A1			B1			C1			D1			E1			F1			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	86.0	76.5	75.0	85.7	100.0	77.1	97.3	96.4	70.9	100.0	97.1	94.6	100.0	100.0	63.3	75.0	93.9	97.2	97.6	85.0	95.0	97.7	55.6	100.0
2	100.0	100.0	92.9	96.4	80.0	76.7	100.0	100.0	100.0	100.0	100.0	100.0	96.4	20.0	96.7	100.0	85.7	96.9	96.4	100.0	100.0	98.1	97.7	97.7
3	100.0	96.7	94.1	75.0	90.0	100.0	100.0	100.0	100.0	94.7	100.0	97.1	100.0	100.0	76.7	97.6	96.9	89.3	100.0	62.5	97.8	90.0	80.0	97.6
4	85.0	46.7	66.7	100.0	89.3	74.3	86.8	100.0	100.0	100.0	92.1	100.0	95.8	93.3	94.6	95.0	83.3	91.7	94.6	97.5	96.0	97.7	88.6	97.5
5	84.2	70.0	76.7	96.7	81.8	80.0	100.0	91.9	100.0	97.4	84.2	97.5	75.0	93.9	100.0	88.9	78.6	94.4	100.0	93.2	98.0	97.5	100.0	94.4
6	31.6	96.9	100.0	93.8	85.7	72.7	83.3	97.8	91.7	84.2	80.0	100.0	100.0	56.7	93.8	93.8	88.0	97.4	98.0	94.6	100.0	97.8	97.9	97.4
7	100.0	78.9	95.7	100.0	63.3	84.4	100.0	98.3	100.0	100.0	100.0	97.7	78.1	55.3	75.0	56.2	74.1	92.9	97.8	98.0	96.4	100.0	100.0	97.6
8	65.7	76.4	96.0	93.3	97.1	69.7	100.0	77.2	98.1	100.0	100.0	97.7	86.7	97.4	46.7	90.6	86.7	100.0	97.8	95.4	94.7	97.5	80.9	96.0
9	100.0	93.3	96.4	90.0	100.0	90.6	100.0	98.2	100.0	95.2	97.4	97.5	97.1	100.0	82.9	100.0	100.0	94.1	95.6	90.0	96.9	97.6	88.1	97.5
10	95.7	90.6	100.0	100.0	100.0	96.4	100.0	92.3	97.8	81.8	97.3	100.0	96.7	91.1	97.1	97.7	92.6	77.8	96.2	90.5	100.0	97.7	100.0	100.0
Rep. Total	849.2	826.0	893.5	930.9	907.2	821.9	967.4	952.1	957.6	953.3	948.1	982.1	925.8	807.7	826.8	894.8	879.8	931.7	974.0	906.7	974.8	971.6	888.8	975.7
Line Total	2,567.7			2,600.0			2,877.1			2,883.5			2,560.3			2,706.3			2,855.5			2,836.1		
Line Mean	85.6			88.7			95.9			96.1			85.3			90.2			95.2			94.5		
Plant No.	A2			B2			C2			D2			E2			F2			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	68.4	76.7	72.5	95.8	84.6	100.0	100.0	93.8	97.4	91.9	100.0	46.9	70.3	97.2	97.2	93.3	66.7	97.6	100.0	97.5	85.4	91.9	97.5	100.0
2	46.9	100.0	73.4	86.7	95.4	77.8	77.1	58.0	100.0	100.0	100.0	100.0	90.0	100.0	100.0	32.0	100.0	100.0	97.5	97.5	100.0	97.9	100.0	100.0
3	73.7	69.2	71.4	90.9	100.0	90.0	100.0	91.9	100.0	97.2	97.5	83.8	100.0	100.0	74.3	42.9	100.0	50.0	97.6	100.0	85.7	82.6	90.0	97.6
4	71.4	91.4	81.4	75.8	75.0	100.0	100.0	96.3	78.6	95.2	97.6	95.2	100.0	89.5	89.2	40.0	96.7	100.0	94.1	98.3	100.0	92.6	93.3	95.0
5	65.8	90.6	78.2	84.8	96.3	83.3	100.0	98.2	95.5	100.0	96.9	100.0	68.6	78.8	81.8	54.3	90.0	40.1	97.5	98.1	80.0	97.5	97.3	97.6
6	84.2	97.6	90.0	100.0	97.1	100.0	100.0	62.5	91.4	89.9	67.9	72.6	87.5	76.3	100.0	60.7	100.0	46.7	98.1	81.1	100.0	100.0	94.6	100.0
7	57.6	85.7	71.7	100.0	100.0	96.9	100.0	100.0	97.6	100.0	100.0	88.1	90.6	76.3	85.7	96.9	76.9	66.7	100.0	100.0	83.3	79.4	84.6	90.4
8	70.0	94.4	82.2	93.9	77.3	84.8	97.9	98.0	63.6	96.1	97.7	92.9	96.2	100.0	100.0	80.0	96.7	90.9	90.9	97.9	97.1	96.0	93.2	97.7
9	72.9	78.6	75.8	85.7	100.0	100.0	100.0	97.7	90.0	100.0	91.4	59.5	100.0	97.1	86.9	78.6	63.6	90.0	97.7	93.8	93.8	100.0	96.9	100.0
10	75.6	76.7	76.2	42.4	90.0	87.9	50.0	92.5	74.3	97.8	97.3	80.9	96.9	97.1	97.9	100.0	80.0	81.5	97.7	97.7	100.0	94.0	95.4	100.0
Rep. Total	686.5	860.9	773.7	857.0	916.7	920.7	925.0	888.9	888.4	968.1	946.3	869.9	801.0	912.3	913.0	678.7	870.6	763.5	971.1	961.9	925.3	931.9	942.8	978.3
Line Total	2,321.1			2,694.4			2,702.3			2,784.3			2,626.3			2,312.8			2,858.3			2,853.0		
Line Mean	77.4			89.8			90.0			92.8			87.5			77.1			95.3			95.1		

\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a suspected translocation source.

Table A3. Comparison of number of seeds in the main spike of plants grown from vernalized seedlings of six lines and their sibs with those of the recurrent parent, Centurk, in the field in 1977.

Plant No.	A1			B1			C1			D1			F1			F1			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	37	26	21	24	29	27	36	54	28	35	34	35	37	30	19	21	31	35	41	34	57	43	20	54
2	38	30	26	27	24	23	41	40	42	42	29	40	27	7	29	28	30	31	54	48	44	51	43	43
3	46	29	32	30	27	35	67	44	57	36	42	34	34	35	23	40	32	25	58	25	45	36	32	41
4	34	14	16	24	25	26	33	48	48	42	35	46	23	28	35	38	25	22	35	39	48	43	39	39
5	32	21	23	29	27	28	57	34	46	37	32	39	24	31	32	24	22	34	42	41	49	39	37	34
6	12	31	32	30	24	24	25	45	44	32	36	44	40	17	30	30	22	37	49	35	38	45	47	37
7	43	30	44	28	19	27	68	58	63	41	42	43	25	21	24	18	20	26	45	49	54	44	44	41
8	23	26	24	28	34	23	54	27	53	42	41	43	26	37	14	29	26	36	45	42	36	39	34	48
9	32	28	27	27	36	29	51	55	56	40	37	39	33	46	29	30	31	32	43	36	31	41	37	39
10	29	29	30	28	29	27	48	48	44	27	36	36	29	31	34	42	25	21	50	38	54	43	46	40
Rep. Total	326	264	275	275	274	269	480	453	481	374	364	399	298	283	269	300	264	299	462	387	456	424	379	416
Line Total	865			818			1,414			1,137			850			863			1,305			1,219		
Line Mean	28.8			27.3			47.1			37.9			28.3			28.8			43.5			40.6		
Plant No.	A2			B2			C2			D2			E2			F2			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	26	23	25	30	22	32	40	30	37	34	40	31	26	35	35	28	20	40	40	39	41	34	43	40
2	24	23	24	26	27	21	27	29	28	46	36	46	30	36	35	8	32	27	39	39	51	47	40	42
3	28	30	29	30	34	27	51	34	32	35	39	31	34	36	26	12	30	10	41	52	30	38	36	41
4	25	18	22	25	18	39	42	52	25	40	41	40	37	34	33	8	29	28	32	57	40	50	42	38
5	25	32	28	28	26	25	42	55	42	37	31	42	24	26	27	19	27	18	39	53	36	39	36	41
6	32	29	31	38	33	28	43	20	32	34	19	30	21	29	40	17	33	14	51	30	45	46	35	52
7	19	41	30	31	30	31	50	33	41	38	36	37	29	29	30	31	20	20	56	40	35	27	38	47
8	28	24	26	31	17	28	47	49	14	50	43	39	25	35	37	24	29	30	40	47	47	48	41	43
9	27	34	31	24	32	27	52	43	36	45	32	25	37	34	20	22	14	27	43	30	45	50	31	46
10	28	22	25	14	27	29	19	37	26	44	36	34	31	33	46	39	24	22	43	43	50	47	42	46
Rep. Total	262	276	271	277	266	287	413	382	313	403	353	355	294	327	329	208	258	236	424	430	420	426	384	436
Line Total	809			830			1,109			1,111			950			702			1,274			1,274		
Line Mean	26.9			27.7			36.97			37.02			31.66			23.4			42.5			41.5		

\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a suspected translocation source.



Table A4. Comparison of 100 seed weight (g) of plants grown from vernalized seedlings of six lines and their sibs with those of the recurrent parent, Centurk, in the field in 1977.

Plant No.	A1			B1			C1			D1			E1			F1			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	2.66	2.67	2.78	2.37	1.90	2.33	1.85	1.94	2.52	2.04	2.28	2.67	2.23	2.12	2.57	2.26	2.03	1.90	2.25	2.09	2.32	2.07	2.15	2.33
2	2.61	2.67	2.98	2.16	2.20	2.27	1.59	1.79	1.91	1.95	2.40	2.82	2.31	2.31	2.28	2.54	2.23	2.31	2.07	2.08	2.07	2.13	2.24	2.34
3	2.92	3.09	2.67	2.09	2.11	2.42	1.75	1.93	2.28	2.10	2.27	2.56	2.26	2.15	2.13	2.31	2.22	2.20	2.21	2.29	2.39	2.34	2.45	2.71
4	2.03	2.56	3.30	2.21	2.16	2.48	2.16	2.10	1.96	2.28	2.54	2.78	2.33	2.43	2.16	2.49	2.13	1.91	2.68	2.36	2.15	2.26	2.37	2.27
5	2.24	3.07	2.78	2.29	2.17	2.27	2.16	2.17	2.14	2.46	2.30	2.58	2.24	2.21	2.45	2.89	2.09	2.12	2.44	1.98	2.17	2.53	1.90	2.27
6	2.37	2.38	2.92	2.38	2.09	2.36	1.92	2.15	1.76	2.08	2.32	2.51	2.42	2.39	2.66	2.43	2.71	2.09	2.46	1.98	1.92	2.39	1.84	2.92
7	2.07	2.46	2.71	2.04	2.11	2.40	1.88	2.14	2.03	1.82	2.32	2.37	2.44	2.48	2.39	2.31	2.06	1.89	2.45	1.92	2.34	2.27	2.02	2.04
8	2.16	2.74	2.45	2.26	2.07	2.13	1.90	2.10	2.04	2.76	2.37	2.84	2.11	2.10	2.31	2.46	2.42	2.40	2.30	2.18	2.34	2.51	2.16	2.37
9	2.38	2.62	2.64	2.12	2.38	2.38	2.20	2.36	2.07	2.23	2.38	2.61	2.29	2.40	1.90	2.46	1.81	2.40	2.12	2.22	2.22	2.15	2.42	2.25
10	2.44	2.63	2.78	2.24	2.17	2.30	1.95	2.16	2.01	2.38	2.36	2.67	2.32	2.35	2.14	2.01	2.31	2.30	2.13	2.38	2.04	1.92	2.21	2.27
Rep. Total	23.88	26.94	28.01	22.16	21.36	23.36	19.36	20.84	20.72	22.10	23.54	26.41	22.95	22.94	22.99	24.16	22.01	21.52	23.12	21.47	22.02	22.68	21.76	23.77
Line Total	78.83			66.88			60.92			72.05			68.88			67.69			66.61			68.21		
Line Mean	2.62			2.23			2.03			2.40			2.29			2.25			2.22			2.27		
Plant No.	A2			B2			C2			D2			E2			F2			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	2.28	2.50	2.39	2.15	2.16	2.23	2.36	2.28	2.16	2.07	2.60	1.96	2.30	2.17	1.99	2.24	2.30	1.81	2.23	2.23	1.86	2.65	2.42	2.43
2	2.17	2.24	2.21	2.20	2.06	2.07	2.21	2.11	2.00	2.38	2.65	2.19	2.24	2.08	2.08	2.10	2.27	2.28	2.25	2.39	2.05	2.59	2.14	2.69
3	2.42	2.47	2.45	2.21	2.14	2.09	2.58	2.30	2.49	2.66	2.36	2.14	2.26	2.03	2.24	2.10	2.21	2.29	2.63	2.40	2.17	2.51	2.08	2.54
4	2.35	2.48	2.42	2.06	2.15	2.15	2.03	2.41	1.44	2.30	2.30	1.89	2.34	1.98	2.42	2.08	2.57	2.30	2.07	2.25	1.96	1.94	2.27	2.67
5	2.50	2.15	2.33	1.92	1.95	2.01	2.23	2.21	2.03	2.36	2.38	1.91	2.17	2.06	2.36	2.58	2.09	2.31	2.55	2.40	2.20	2.23	2.53	2.54
6	2.34	2.16	2.25	2.35	2.18	1.98	1.96	2.30	1.86	2.44	2.56	1.97	1.72	1.84	2.72	2.04	2.12	2.17	2.50	2.36	1.69	2.24	2.37	2.50
7	2.10	2.44	2.27	1.99	2.19	2.18	2.16	2.50	2.03	2.38	2.63	2.19	1.96	2.34	2.72	2.59	2.20	2.31	2.37	2.30	1.92	2.40	2.55	2.64
8	2.24	2.36	2.30	2.14	2.01	1.94	2.23	2.20	2.30	2.23	2.67	1.98	2.13	2.04	1.85	2.46	2.23	2.14	2.22	2.10	1.91	2.25	2.33	2.58
9	2.42	2.58	2.50	1.97	2.06	2.12	2.23	2.00	2.04	2.50	2.10	1.70	2.11	1.96	2.08	2.32	2.26	1.96	2.36	2.85	2.05	2.16	2.64	2.58
10	2.35	2.36	2.36	2.23	2.14	1.86	2.06	2.36	1.72	2.15	2.24	1.57	2.14	2.04	2.14	2.20	2.30	2.14	2.18	2.56	2.07	2.05	2.40	1.96
Rep. Total	23.17	23.74	23.48	21.22	21.04	20.64	22.05	22.67	20.07	23.47	24.49	19.50	21.37	20.34	22.59	22.71	22.55	21.71	23.36	23.84	19.88	23.02	23.73	25.19
Line Total	70.39			62.50			54.79			67.46			64.30			66.97			67.08			71.94		
Line Mean	2.35			2.09			2.16			2.25			2.14			2.23			2.24			2.39		

\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a suspected translocation source.

Table A5. Comparison of yield per plant (g) of plants grown from vernalized seedlings of six lines and their sibs with those of the recurrent parent, Centurk, in the field in 1977.

Plant No.	A1			B1			C1			D1			E1			F1			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	7.7	7.8	3.8	4.2	1.5	7.9	2.4	5.0	1.4	1.5	11.4	6.3	8.6	3.9	3.7	3.8	6.5	5.6	14.9	10.8	9.5	8.1	9.1	7.6
2	5.5	6.6	4.0	6.6	5.2	3.7	3.1	2.8	4.2	6.5	12.5	12.7	4.4	6.6	3.6	10.7	7.8	9.5	4.5	13.1	11.8	10.1	11.9	9.2
3	3.2	4.9	4.7	2.9	3.7	8.3	4.7	8.0	7.6	6.8	10.4	11.9	4.5	2.4	4.9	6.3	3.1	3.7	15.6	9.0	9.4	15.2	14.4	6.4
4	6.0	5.0	3.0	3.8	5.7	5.3	6.8	3.9	6.1	8.5	12.3	12.7	4.1	7.2	5.0	8.1	5.4	2.7	8.3	10.9	12.2	17.6	10.2	9.8
5	1.4	6.3	8.7	5.6	5.8	5.1	3.4	8.5	3.8	9.4	8.5	10.8	1.5	4.6	7.2	8.0	5.2	2.3	9.1	15.8	7.9	10.4	2.9	9.6
6	5.0	1.7	6.3	6.5	2.8	6.0	2.7	5.3	3.0	4.8	10.2	6.6	3.5	3.6	3.3	4.2	10.5	9.9	14.4	7.5	14.2	7.4	3.8	3.4
7	3.0	4.6	4.7	3.0	3.3	3.7	6.6	7.4	7.0	7.6	11.4	12.6	4.9	3.7	4.9	4.0	4.5	2.1	15.4	5.9	9.6	6.0	5.9	7.9
8	1.9	4.8	4.2	3.4	4.0	5.2	8.7	2.6	7.4	12.8	7.7	10.2	5.2	2.3	5.0	5.5	2.4	6.0	8.3	14.8	16.9	16.0	7.7	6.1
9	4.6	4.8	4.6	4.6	3.1	4.4	6.8	9.4	4.9	8.8	8.6	11.4	4.4	7.1	1.2	3.0	7.3	10.3	6.6	10.2	14.4	3.6	10.8	3.5
10	4.3	4.8	4.9	4.5	3.3	4.6	6.9	5.5	8.3	4.5	8.9	7.8	3.8	4.5	2.2	5.2	4.1	3.4	11.2	11.2	1.7	9.4	7.9	12.5
Rep. Total	42.6	51.3	48.9	45.1	38.4	55.0	52.1	58.4	53.7	71.2	102.4	103.0	44.9	45.9	44.1	58.8	56.8	55.5	108.3	109.2	107.6	103.8	84.6	76.0
Line Total	142.8			138.5			164.2			276.6			134.9			171.1			325.1			264.4		
Line Mean	4.8			4.6			5.5			9.2			4.5			5.7			10.8			8.8		
Plant No.	A2			B2			C2			D2			E2			F2			Ctk. Ck. I			Ctk. Ck. II		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
1	4.7	3.4	4.1	4.9	4.7	6.2	3.3	7.3	5.0	8.2	12.8	3.7	6.2	2.9	5.0	6.5	3.3	4.8	8.3	12.5	8.4	10.2	6.9	8.3
2	4.6	4.9	4.8	4.5	7.7	2.6	2.8	3.7	3.1	13.1	6.3	4.3	4.5	6.1	5.8	1.4	6.2	6.4	11.7	8.5	13.5	11.8	8.9	8.6
3	5.6	4.3	4.9	5.1	5.3	4.4	8.9	2.1	10.2	10.2	7.9	4.0	4.2	5.3	5.1	1.2	5.2	3.1	14.1	10.0	6.4	9.7	7.4	16.1
4	3.1	2.6	2.9	6.0	3.9	5.7	7.4	8.1	1.8	8.3	6.0	4.9	5.6	5.5	7.4	0.7	4.4	5.4	11.2	10.5	10.7	7.9	6.4	8.8
5	4.9	5.7	5.3	2.0	3.4	5.0	8.6	10.7	13.3	10.8	5.7	5.2	5.0	3.1	5.9	8.2	9.1	3.3	13.3	8.7	2.7	20.5	8.8	9.3
6	4.0	3.2	3.6	5.3	4.0	5.4	13.7	4.1	2.5	12.2	8.2	10.0	3.6	4.7	2.1	2.2	0.7	4.3	9.4	9.1	14.4	10.7	7.8	6.8
7	7.1	5.1	6.1	3.8	5.2	6.7	4.8	3.9	6.5	11.4	8.7	11.4	5.4	5.5	6.8	4.5	5.9	2.8	9.8	10.8	14.8	8.8	11.5	14.0
8	1.2	5.9	3.5	5.0	6.9	4.9	9.5	4.6	7.2	11.2	12.4	7.0	2.6	4.8	9.1	7.7	2.7	3.2	11.1	9.5	13.4	7.4	8.4	12.0
9	4.4	3.1	3.7	2.8	6.4	3.0	7.2	6.2	2.6	7.3	7.5	7.0	6.2	6.0	0.9	2.5	8.5	6.3	8.6	7.5	6.4	13.8	12.6	8.4
10	4.4	4.3	4.4	3.9	5.9	4.8	5.6	6.1	1.9	10.3	8.2	2.6	5.1	6.8	8.5	8.3	4.5	1.5	8.4	13.1	9.7	9.3	12.1	6.0
Rep. Total	44.0	42.5	43.3	46.3	53.4	48.7	71.8	56.8	54.1	103.0	83.7	69.1	48.4	50.7	56.6	43.2	50.5	41.1	105.9	100.2	100.4	110.1	90.8	98.3
Line Total	129.8			148.4			182.7			246.8			155.7			134.8			306.5			299.2		
Line Mean	4.3			4.9			6.1			8.2			5.2			4.5			10.2			9.9		

\*Numbers 1 and 2, as in A1 and A2, identify different sibs within a suspected translocation source.

Table A6. Progeny test to wheat streak mosaic virus (WSMV) in F<sub>2</sub> of seedlings from the plants used in the agronomic study in the field and of immune and susceptible checks grown in the greenhouse.

Plant No.	A1			B1			C1			D1			E1			F1			Immune check	Susc. check
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	I:S	I:S
1	6:0	6:0	6:0	6:0	6:0	7:0	7:0	6:0	6:0	7:0	7:0	7:0	5:1	7:0	7:0	6:0	7:0	8:0	5:0	0:7
2	6:0	6:0	5:1	7:0	7:0	7:0	6:0	6:1	7:0	7:0	7:0	7:0	7:0	6:1	7:0	7:0	7:0	8:0	7:0	0:7
3	6:0	5:0	5:0	7:0	6:0	7:0	6:0	6:1	6:0	7:0	6:0	7:0	7:0	6:0	7:0	7:0	7:0	9:0	6:1	0:7
4	6:0	5:0	6:0	5:1	7:0	5:1	6:0	5:1	5:1	7:0	7:0	7:0	7:0	6:0	7:0	7:0	6:0	9:0	5:1	0:7
5	5:0	4:1	6:0	7:0	5:0	7:0	7:0	6:0	6:0	7:0	7:0	7:0	6:1	6:0	7:0	7:0	7:0	6:0	7:0	0:6
6	6:0	4:0	5:0	7:0	7:0	6:0	7:0	6:0	5:1	7:0	7:0	7:0	7:0	6:1	5:2	7:0	7:0	8:0	6:0	0:6
7	5:0	6:0	5:0	6:0	6:0	6:0	6:0	6:0	6:0	7:0	7:0	6:0	7:0	7:0	6:0	7:0	7:0	9:0	3:0	0:6
8	4:0	4:0	5:0	7:0	5:0	7:0	7:0	5:0	6:0	7:0	7:0	7:0	6:1	7:0	6:0	7:0	7:0	8:0	6:0	0:6
9	6:0	---	---	6:0	6:0	6:0	5:2	6:0	6:0	7:0	7:0	7:0	6:0	7:0	6:1	7:0	7:0	6:0	5:0	0:6
10	---	---	---	---	7:0	6:0	7:0	7:0	6:0	7:0	7:0	7:0	6:1	---	4:3	7:0	7:0	7:0	6:0	0:3
Rep. Total	53:0	40:1	43:1	50:1	63:0	64:1	64:2	59:3	59:2	70:0	69:0	69:0	64:4	58:2	62:6	69:0	69:0	78:0	56:2	0:61
Line Total	136:2			185:2			182:7			204:0			184:12			216:0			56:2	0:61
I:S	98.6:1.4			98.9:1.1			96.3:3.7			100.0:0.0			93.9:6.1			100.0:0.0			96.6:3.4	0.0:100.0
Plant No.	A2		B2			C2			D2			E2			F2			Immune check	Susc. check	
	R1	R2	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3	I:S	I:S	
1	6:0	6:0	5:0	6:0	4:1	6:0	6:0	7:0	7:0	6:1	5:1	6:1	7:0	6:0	7:2	6:0	7:0	5:0	0:7	
2	6:0	6:0	6:1	5:0	5:0	6:0	6:0	6:0	7:0	6:1	7:0	7:0	7:0	7:0	7:0	7:0	6:0	7:0	0:7	
3	6:0	6:0	6:0	8:0	6:0	6:0	6:0	6:0	7:0	5:2	7:0	7:0	6:1	5:2	7:0	7:0	6:0	6:1	0:7	
4	5:0	4:0	7:0	6:0	6:0	4:2	6:0	6:0	7:0	6:1	3:4	6:2	7:0	7:0	8:0	7:0	6:0	5:1	0:7	
5	4:0	5:0	5:0	5:0	5:0	4:2	6:0	7:0	7:0	6:1	5:2	7:0	7:0	7:0	8:0	7:0	6:0	7:0	0:6	
6	4:0	6:0	6:0	6:0	5:0	5:1	6:0	7:0	7:0	6:1	5:2	7:0	7:0	7:0	5:0	7:0	6:0	6:0	0:6	
7	6:0	6:0	5:0	6:0	7:0	6:0	6:0	7:0	7:0	7:0	7:0	7:0	6:1	7:0	7:0	7:0	7:0	3:0	0:6	
8	4:0	6:0	7:0	6:1	6:0	5:1	6:0	7:0	6:1	6:1	7:0	7:0	6:1	7:0	8:0	7:0	4:0	6:0	0:6	
9	4:0	6:0	7:0	5:0	6:0	6:0	5:0	7:0	6:1	6:1	7:0	7:0	7:0	7:0	7:0	7:0	6:0	5:0	0:6	
10	5:0	4:0	6:0	5:1	7:0	5:1	6:0	7:0	7:0	6:1	7:0	6:0	---	7:0	9:0	7:0	5:0	6:0	0:3	
Rep. Total	50:0	59:0	60:1	58:1	57:1	53:7	59:0	67:0	68:2	60:10	60:9	67:3	60:3	67:2	73:2	69:0	59:0	56:2	0:61	
Line Total	109:0		175:3			179:7			188:21			194:8			201:2			56:2	0:61	
I:S	100.0:0.0		98.3:1.7			96.2:3.8			90.0:10.0			96.0:4.0			99.0:1.0			96.6:3.4	0.0:100.0	

\*Numbers 1 and 2, as in A1 and A2, identify different sites within a suspected translocation source. b I=Immune and S and Susc.=Susceptible.