A STUDY OF THE MEIOTIC STABILITY OF CERTAIN AGROTRICUM HYBRIDS

by

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INTRODUCTION

Interest in *Triticum* x *Agropyron* hybridization has become very widespread since 1933, when N. V. Tzitzin first reported from Russia concerning his success in crossing of these two genera. He is now generally given credit for the first successful cross although Hillman (9) and McFadden (22) were very near success. In 1929 McFadden did succeed in obtaining two plants which died as seedlings from the crossing of *Triticum vulgare* var. Buffum with an "off-type form" of *Agropyron repens* Beauv.

Today, although *Triticum* x *Agropyron* work has been undertaken by workers in Canada, the United States, Australia, South Africa, Germany, and Italy it is still difficult to evaluate these hybrids. As pointed out by Schmidt (40) and others, the objectives of this hybridization program have been slightly different in the various parts of the world. The Russians have been primarily interested in deriving perennial types, the Canadians in grain types and large-seeded forage types, and workers in this country have been most anxious to transfer genes for disease resistance from the *Agropyron* species to wheat. Schmidt (40) and Schmidt et al. (41) have pointed out that the efforts at the Kansas station have been directed toward securing winter-annual types that are fertile and morphologically-stable, disease- and insect-resistant. Other desirable attributes that might be transferred to the wheats, such as resistance to heat and drought, extreme winter hardiness, dual-purpose type (grain and forage), and wide geographic distribution, have been emphasized by McFadden and Sears (23), Reitz et al. (38), and others.

Schmidt et al. (41) have pointed out that *Triticum-Agropyron* hybrids are now designated as Agrotricum hybrids on the suggestion of Erich von Tschermak-Seysenegg.

Although line breeding, backcrossing, the production of amphidiploids, and other breeding methods have been employed, the problems of obtaining stable lines from these hybrids have not been overcome. The belief has been expressed by some that line breeding and selection for fertility, seed weight, disease reactions, and other morphologic characters would eventually result in lines being obtained that will be stable for both morphological characters and for meiotic regularity.

It is the purpose herein to report on studies of the meiotic stability of certain Agrotricum hybrid lines grown at the Kansas station relative to their fertility, disease reaction, and certain agronomic characters for which they are apparently stabilized to a relatively high degree, and to consider the hypothesis that by selecting for these latter characters meiotic stability will also eventually be obtained.

REVIEW OF LITERATURE

The literature concerned with Triticum x Agropyron hybridization has become very extensive. That prior to 1949 has been reviewed by Schmidt (40), Armstrong and Stevenson (6), Suneson and Pope (51), Smith (45, 46), Pope and Love (34), and others. Aase (1) and Myers (25) have summarized the literature concerned with interspecific and intergeneric relationships of various wheat, rye, and other grass genera. Only the more recent literature or that pertinent to the problem will receive extensive treatment in this paper.

The first successful cross by N. V. Tzitzin (53) in 1930 was made in the North Caucasus, U.S.S.R., using T. vulgare var. Lutescens 962 x A. glaucum Desf. (A. intermedium, Host, Beauv.) Soon after he reported success with other crosses involving A. glaucum, A. elongatum (Host) Beauv., A. tricophorum (Link) Richt., and A. juncecum (L.) Beauv., he published a series of technical and nontechnical papers concerned with these and other hybrids (Tzitzin 54, 55, 56, 57, 58). Khiznjak (14, 15, 16), Lapchenko (17), Vakar (59, 60, 61, 62), Veruschkine (63, 64) and other Russian workers published numerous reports on the progress with Triticum x Agropyron hybrids in that country, but relatively little is known concerning their progress in recent years or just how extensively the hybrids are being grown and utilized. Schmidt (40) has presented a thorough review of the Russian literature that is available.

Results of Triticum x Agropyron hybridization in Canada have been reported by Armstrong (3,4), Armstrong and McLennan (5), Armstrong et al. (7), White (67), Johnson (11), Johnson and McLennan (12), Peto (28, 29, 30, 31), and others. Those in Australia by Raw (37).

The species of Agropyron generally agreed to cross most readily with tetraploid and hexaploid Triticum species are:

A. elongatum (Host) Beauv.	n = 35
A. glaucum (Desf), or	n = 21
A. intermedium (Host) Beauv.[1]	
A. trichophorum (Link) Richt.	n = 21
A. juncecum (L.) Beauv.	n = 14

The crossing relationships of these species with Triticum species have been discussed by Johnson (11), White (67), Smith (45, 46, 47), Armstrong (4),

[1]Agropyron glaucum is treated by Hitchcock as a synonym of Agropyron intermedium (Host) Beauv. Since it appears in the Agrotricum literature and in pedigrees of some of the Agrotricum hybrids reported on in this paper, use of the synonym is necessitated in this paper.

Aase (1), and Myers (25).

The literature discussing the cytology of the various Agropyron species has been reviewed by Schmidt (40) and the interested reader is further referred to Aase (1), Peto (28, 29, 30, 31), Vakar (59, 60, 61,62), Sears (42), and Östergren (27). It will suffice here to say that, apparently, a high degree of instability was present in most species of the Agropyron genus. This is evident from the variability of results obtained by investigators working with the same species and from observations of laggards and univalents during meiosis. Various degrees of success in crossing results when working with different varieties of Triticum and different strains of Agropyron have been reported by Johnson (11), Smith (46, 47), Tzitzin (54), Veruschkine and Shekhurdin (65), and White (67).

Of greater concern is the cytology of the hybrids. The Agrotricum hybrids have shown considerable chromosome pairing, particularly in the cases involving A. elongatum. According to Aase (1) variations in meiotic chromosome configuration occurred in all combinations involving the four Agropyron species most successfully used, indicating incomplete homology between the Triticum and Agropyron genomes, and also a difference in the response of ecotypes and races entering into a particular cross. Vakar (61), investigating the meiotic behavior in the F_1 of T. vulgare x A. elongatum, found the maximum association of chromosomes varied in the different hybrids -- 28_{II}, $21_{II} + 14_{I}$ and $14_{II} + 28_{I}$. As a result, Vakar postulated that the genomes of A. elongatum were A_a, B_a, D_a, X_1 and X_2 where A_a, B_a, and D_a are Agropyron genomes homoeologous with the A, B, and D genomes of T. vulgare. The occurrence of $14_{II} + 28_{I}$ is explained as a failure of one of these genomes to pair in some hybrids because it is less homoeologous that the other two. In the hybrids with 28_{II}, autosyndesis between X_1 and X_2 genomes was assumed. Peto (28) questioned some of Vakar's observations, since he found only about $21_{II} + 14_I$ in T. vulgare x A. elongatum. A. elongatum itself has the cytological appearance of being largely autopolyploid, and Peto, therefore, suggested that A. elongatum is AXXYY (or BXXYY), with only one genome homoeologous with any in wheat. Sears (42) pointed out that, at present, Peto's theory is more acceptable, since it takes into consideration the meiotic behavior of A. elongatum itself.

In the F_1 of T. vulgare x A. glaucum, Vakar (60) reported variations from 6_{II} to 14_{II} with an average of 10_{II}, and concluded that A. glaucum had the genomes A_a, D_a, and X_2. Peto (28) found on the average only 6.2_{II} in T. dicoccum (Vernal emmer) x A. glaucum and 5.5_{II} in T. durum x A. glaucum.

An average of about 7_{II} in hybrids of A. trichophorum with tetraploid and hexaploid wheats was reported by Love and Suneson (20). Apparently one genome in this species may also be homoeologous to the A or B of wheats.

A non-orientation and lagging of univalent chromosomes during meiosis commonly results from the lack of homology between the genomes of the Triticum and Agropyron species. These laggards that fail to enter the daughter nuclei may form chromatin masses or lumps in the cytoplasm and are then called micronuclei.

Myers and Powers (26), working with common wheat, have pointed out the feasibility of using the frequency of occurrence of chromatin loss as a measure of meiotic stability. Previous investigations (Powers 35, 36) had shown chromatin loss to be highly correlated with non-orientation and the occurrence of univalents. It is emphasized that the use of the frequency of occurrence of chromatin loss permitted the collection of data on a larger number of plants than would have been possible if a number of meiotic irregularities had been studied. Chromatin loss was determined by observing immature microspores while still in the form of quartets and recording the number showing micronuclei. These investigators have suggested that meiotic irregularities might arise from genetic factors which govern chromosome behavior and from structural differences between synapsing chromosomes.

Love (19), also working with common wheat, has emphasized that even within intraspecific hybrids and derivatives cytological and genetic abnormalities may lead to difficulty in synthesizing new, stable varieties of the desired genotype. Two major types of abnormalities were involved in his investigations. One was the simple failure of pairing during meiosis which ultimately led to the inclusion of lagging univalents as micronuclei in some of the young pollen quartets. The second type, commonly superimposed on the more common first type of irregularity, was the lagging of bivalents. Love (18) suggested that the percentage of normal pollen quartets be called the meiotic index since this percentage is an index of the regularity of meiotic chromosome behavior. He emphasizes (19) that this index may be affected by any disturbance of the physiological processes of meiosis. The chromosomes from the female parent are adjusted with the general development of the pollen mother cell, and the timing of their development may not coincide with that of the chromosomes from the male parent. Another source of disturbance may be disharmony between the chromosomes of the parents. Thus, Love recognized at least two possible sources of meiotic abnormalities. One was the failure of pairing due to a lack of complete homology and the second was genic disturbance of the meiotic process. The occurrence of a few univalents because of a lack of homology appeared to seldom, if ever, cause complete disintegration of the quartets. Lagging bivalents resulted in many micronuclei and a high frequency of abnormal quartets. This condition was often accompanied by a complete disintegration of the second meiotic division. Love suggested that a plant with a meiotic index of 90 percent or better may be considered cytologically stable for all practical purposes.

In discussing the formation of micronuclei in Agrotricum hybrids, Peto and Boyles (32) stated that univalents lagged at first anaphase and divided equationally in the second division. The half univalents wandered at random, and those that did not happen to be included in the daughter nuclei formed micronuclei which subsequently degenerated. They suggested the possibility that genetic factors capable of causing variation in pairing conditions may exist and that selection might eventually result in forms which form a high percent of bivalents. In spite of a relatively high frequency of micronuclei (average 4 per quartet), the pollen in the plants they studied appeared to be very good. Peto (29) attributed a large part of the pollen degeneration and failure of anther dehiscence to meiotic irregularities caused by random behavior of numerous univalents. In 1939 (30) he reported a relation between the number of univalents and self-fertility. Plants with fourteen or more univalents were self-sterile.

Sax (39) has pointed out that, in general, sterility of interspecific hybrids increased as the proportions of univalent chromosomes in reduction division increased.

Thompson and Grafius (52) stated that the problem relating to differential backcross fertility of closely related plants of an Agropyron species when crossed with T. vulgare was not explained by the observation of normal pollen, micronuclei, or lagging chromosomes. They found that the percent of normal pollen increased with each backcross generation, and the number of lagging chromosomes decreased after the first backcross.

Elliott (8) observed considerable cytological irregularity in 174 derivatives of A. trichophorum x T. durum var. Pentad although they appeared quite uniform in the field. Fertility in the F_2 generation appeared independent of 2n chromosome number or other cytological observations, and morphological variability did not seem to be associated with 2n chromosome number or fertility. He found correlation between the percent fertility and the percent of quartets without micronuclei to be non-significant.

White (67) found a close correspondence between the average proportions of good pollen and the average fertility in the F_1 of tetraploid wheats x A. elongatum. Selection did not have a significant effect upon the fertilities of the progenies.

Johnson (11) and Armstrong et al. (7) reported a correlation between anther dehiscence and the ratio of good to bad pollen. They concluded that there was a "direct correlation between the proportions of good pollen and seed-set when the proportions are sufficient to give anther dehiscence". Johnson further stated that "the degree of chromosomal association is directly related to the degree of efficiency with which chromosomes are distributed to daughter cells in meiotic divisions, which in turn is directly related to the proportions of good and bad pollen produced".

Armstrong (4) suggested that the increasing fertility of Agrotricum hybrids indicated improved cytological stabilization. Armstrong and Stevenson (6) reported the occurrence of improvement in chromosome pairing between the F_1 and F_5 generations. They advanced two theories as an explanation of this improvement. The first is that there may be a recovery of homologues at fertilization, that is, univalents may find mates when the male and female gametes fuse. The second is that there may be a continual elimination of gametes, both male and female, carrying unfavorable chromosome combinations. Plants of low fertility apparently would be eliminated every generation by direct selection. They found that selection for a wheat-like appearance, apparently, reduced the proportion of Agropyron chromosomes.

Jenkins (10) found that the repeated use of the hybrid as the male parent in two backcrosses to wheat resulted in a larger number of plants which resembled wheat than those from any other combination, and yet which displayed an abundance of A. elongatum characteristics. He, also, postulated that the A. elongatum used had three genomes homoeologous with two genomes in wheat and two genomes homoeologous with each other.

Semeniuk (44) studied the chromosomal stability of certain rust-resistant derivatives from a T. vulgare x T. timopheevi cross. While observing the behavior of univalent chromosomes of a 41 chromosome ($20_{II} + 1_{I}$) plant from the variety Steinwedel, the T. vulgare parent, he noted that univalents were found in 76 percent of the cells at metaphase I, and micronuclei in only 25 percent of the diads at interphase. Thus, many of the univalents must have been included in the daughter nuclei at the first division. Highly significant correlations were found between the percentage of metaphase I cells with univalents and the following: total abnormalities at anaphase I, metaphase II, and anaphase II; micronuclei at interphase and in spore quartets; and aborted pollen. Semeniuk pointed out that the percentage of pollen abortion may be useful to the plant breeder in eliminating many of the highly unstable lines. The frequency of pollen quartets with micronuclei might serve as a final check on the most desirable lines.

Allard (2) made extensive cytogenetic studies dealing with the transfer of genes from T. timopheevi to common wheat by backcrossing, and has suggested that incomplete pairing of chromosomes in species hybrids may be determined by chromosome homology, environment, or possibly genes. He also found that when the second backcross was made using the first backcross plants as the pollen parents, the resulting population resembles T. vulgare more closely than did the reciprocal backcross and was more regular cytologically and more fertile. Resistance to stem and leaf rusts and mildew was maintained, but nearly all other characters of T. timopheevi were eliminated rapidly. The genes for the resistance that was retained were evidently on T. timopheevi chromosomes which have nearly exact homologues in T. vulgare. It was suggested that the transfer of genes in chromosomes which completely lack homologues in T. vulgare would depend upon the substitution or addition of a complete chromosome pair.

Smith (48), as a result of his studies between sterility and morphological characters in an interspecific Nicotiana cross, advocated that the percent of pollen abortion was an adequate criterion of the amount of male gamete elimination, with the possible exception of differential selective phenomena that may have occurred between pollen germination and fertilization. He stated that "the genetic factors causing partial isolation of the species through gamete sterility and those governing difference in morphological characters are individually discrete but linked". Pollen sterility, he emphasized, was caused by both chromosomal and genic factors. Genetic factors causing gamete abortion were different from those governing the specific morphologies but linkage occurred between the two gene systems.

MATERIALS AND METHODS

Materials

The Agrotricum hybrids studied trace back, chiefly, to original crosses made by W. J. Sando between 1935 and 1937. Some of the stocks were obtained through other experiment stations, and a more detailed account has been given by Schmidt (40).

Most of the hybrids are from crosses of wheat x A. elongatum although a few were made with A. trichophorum. The latter consists of Mindum x A. trichophorum material that has been backcrossed to wheat and plant selected by C. O. Johnston of the Kansas station. A number of the lines also originated from (wheat-rye x A. elongatum) x Cheyenne material.

The material was handled as bulks until 1948 when ten head selections were made from each. These were planted out in the head row nursery, and in 1949 five heads were selected from the best row and again planted in head rows. This was continued so that each line used in this study can be traced back to single head selections made in the spring of 1948.

Schmidt (40) and Schmidt et al. (41) have presented extensive information concerning the morphological characteristics, disease reactions, and agronomic characteristics of this material. For the most part the lines, apparently, are stable as far as these characters are concerned. The fertility of the lines and their cytology have not been studied prior to this experiment, and there has been no conscious selection for cytological characters.

The lines have been separated into three groups, grasslike, intermediate, and wheatlike, on the basis of morphological characteristics. The grasslike group is characterized by long thin heads with short awns, the intermediate group included lines with more compact heads that were erect and awnletted to awned, and the wheatlike group had lines with still shorter, more compact heads which were awned in some lines and awnletted in others. (Plates I and II).

Cytological Studies

Sporocyte samples used in the study of the meiotic stability were collected at random from 96 of the lines. A number of samples were also taken from the Pawnee check rows. The sporocyte samples in the wheatlike lines were collected at the stage when the boot had just begun to swell noticeably. Preliminary examinations revealed that as the more grasslike types were approached, the samples had to be taken at a considerably later stage, so much so that in the grasslike groups, the samples were collected when the young spike was well up in the boot--in some cases protruding a bit. Thompson and Grafius (52) also noted this in their backcross generations of _T. vulgare_ x _A. trichophorum_. The young spikes were dissected out with a razor blade, fixed and preserved in small corked vials of 6:3:1 Carnoy solution and refrigerated for use in preparing slides later.

Ten spikes were taken at random from each row, or line, sampled, and an attempt was made to collect each of the ten from a different plant. However, this was impossible to do precisely because the stands were in many cases so dense that the task became time consuming, and the interval during which the sporocyte samples could be taken was limited. Samples were collected from all five lines of three families within each of the grasslike, intermediate, and wheatlike groups. These were used later to study the variability between the lines originating from a single head selection.

EXPLANATION OF PLATE I

Comparison of heads from typical Agrotricum lines to those of *Agropyron elongatum* and Pawnee. 1. *A. elongatum*. 2. Grasslike type. 3-5. Intermediate types. 6, 7. Wheatlike types. 8. Pawnee.

PLATE I

EXPLANATION OF PLATE II

Comparison of the grain from the Agrotricum lines of Plate I to that of *Agropyron elongatum* and Pawnee. 1. *A. elongatum*. 2. Grasslike type. 3-5. Intermediate types. 6, 7. Wheatlike types. 8. Pawnee.

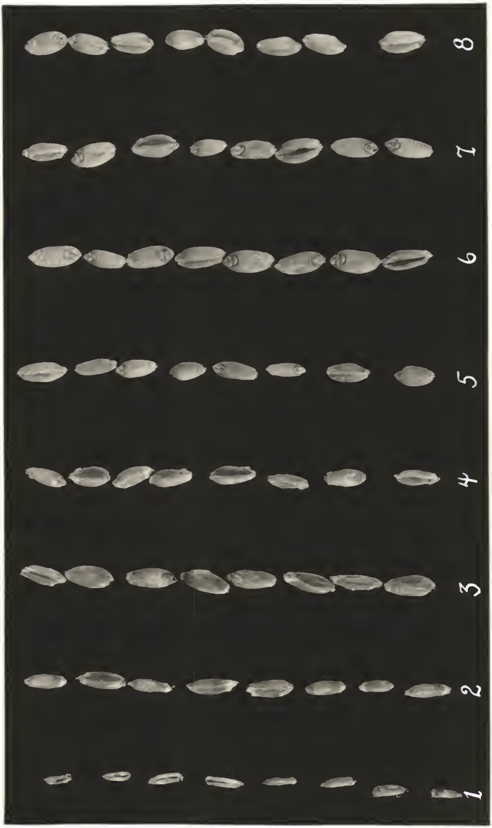


PLATE II

Cytological analyses and studies were made from temporary aceto-carmine smears of pollen quartets according to the method described by Luther Smith (49).

The observation of pollen quartets was, of course, the major interest, but occasionally other stages of microsporogenesis were observed. The chromosome number was also determined for a few lines when a suitable slide was obtained by chance in searching for the quartet stage.

In order that some idea of the sampling variation within a slide, or mount, might be obtained, five hundred pollen quartets were observed in subsamples of one hundred by counting random strips across the slide. The number of pollen quartets with micronuclei was recorded in each case, and a mount was made for each of five lines composing a family in the grasslike, intermediate, and wheatlike groups. Thus, a total of fifteen slides were sampled representing as many lines. It was decided by prior examination that five hundred quartets was about the largest number that could consistently be included on a single slide from a single floret as far as the material being studied was concerned.

Further sampling studies were conducted with the five lines composing one of the grasslike families. Five heads were sampled in each line, two florets in each head (one from an upper spikelet and one from a lower spikelet), and two anthers from each floret. Thus, only one anther was included on any one mount and a total of four mounts were observed for each head. One hundred pollen quartets were observed for each mount, and the number containing micronuclei was recorded.

Meiotic indices were established for 50 of the lines and for a number of Pawnee checks by observing mounts made from a composite of the three anthers from a single floret per head. Four heads per line were sampled and the mean number of quartets with micronuclei was established on the basis of 100 quartets per head—thus, 400 pollen quartets were observed per line. One hundred minus the mean number of pollen quartets with micronuclei for the four heads provided the meiotic indices which were used for the correlation studies.

The average number of micronuclei per quartet was estimated for the lines studied cytologically, and the range for number of micronuclei per quartet was also recorded.

Fertility Studies

Ten heads were bagged at random in 55 of the lines from which sporocyte samples had been collected. These heads were covered with small wax paper bags and clipped to stakes several days in advance of blooming, and the bags were not removed until the latest lines were well past that stage. These heads were used in determining the fertility of the lines when under self-pollination. At the same time 10 additional heads were tagged in the same lines and were used to determine the seed set under conditions of open-pollination.

Following the same scheme as in the collection of the sporocyte samples, heads were bagged and tagged within a group of five lines composing a family within each of the three type groups—grasslike, intermediate, and wheatlike. These families, of course, were ones from which sporocyte samples had been collected previously. Several Pawnee rows were also included as checks.

After the heads were ripe, they were harvested and stored until kernel counts were made on the unthreshed heads by the inspection of the two outside florets of each spikelet. All of the spikelets on the 10 open-pollinated heads for each of 20 lines (taken at random) were examined and the percent seed set thus obtained. These data were compared to that obtained when only 10 spikelets from the center portion of the same spikes were examined. This latter partial count method was used for the remainder of the determinations. It required much less time and labor and eliminated those spikelets near the base and tip of the head which are, apparently, influenced more by certain adverse conditions of the environment.

The values which were recorded for use in the correlations with the meiotic index and percent normal pollen were all percentage values determined on the basis of actual seed set compared to that possible (maximum would be 20 kernels per spike).

Pollen Studies

Two to three heads in early bloom were collected at random from each of the lines for which both meiotic indices and fertility percentages were to be determined, and were preserved in quart mason jars containing 75 percent ethyl alcohol.

The pollen observations were made from mounts prepared by a method similar to that described by Pittinger and Frolik (33). The anthers were prestained in a 2 percent I_2KI solution and were then dissected while in a small drop of the stain on a warmed slide. Dissecting in a drop of stain, rather than in a drop of agar, allowed more time for the operation. After the anther refuse had been removed, a small drop of warm 2 percent aqueous agar was added and stirred vigorously into the pollen and I_2KI mixture until it began to cool and gel. Then a cover slip was dropped vertically onto the preparation, and the slide was inverted and blotted gently on a paper towel.

Pittinger and Frolik's (33) work indicated that a uniform distribution of the pollen is obtained by this method. Blotting the slide results in more of the pollen grains lying in about the same plane and, thus, easier counting is facilitated.

A preliminary test of sampling, similar to the one used previously for the quartet analyses, was conducted on five slides, each representing a line. Five strips were observed across each slide at random and the number of normal and abnormal pollen grains was recorded.

For the remainder of the observations those pollen grains in random strips across each mount were counted until at least 300 had been observed. A single mount was made from the second floret of a spikelet near the center of each head. Therefore, for those lines where two heads were collected, a minimum of 600 pollen grains were observed, and at least 900 were observed when three heads were available.

Both empty and partially stained pollen grains were classified as abnormal. Those which were more than one half to fully stained were classified as normal, and the percent of normal pollen per line was thus established and used in correlation studies with the meiotic index and fertility data.

Rust Experiments

One hundred kernels from each of the lines from which sporocyte samples had been collected were planted in individual rows in sand on a greenhouse bench. The seedlings were inoculated with physiologic race 9 of <u>Puccinia rubigo-vera</u> <u>tritici</u> (Eriks.) by shaking urediospores from infected pots of susceptible seedlings onto them 11 days after planting. The seedlings were moistened with a fine water spray before inoculation, and then were covered with a canvas moisture chamber and left overnight. Pawnee checks were included in the test at regular intervals. The readings were made eight days after the inoculation, and the reactions were based as usual on the classification described by Mains and Jackson (21).

Leaf rust readings in the field were made on the basis of natural infection from the susceptible spreader rows which were inoculated with a composite of leaf rust races. Readings of stem rust infection were also obtained in the field under conditions of natural infection. The lines were classified as highly resistant, HR; resistant, R; moderately resistant, MR; segregating for reaction, Seg.; moderately susceptible, MS; and susceptible, S, on the basis of pustule size and number. The purpose of these readings, as far as this experiment was concerned, was to obtain an indication of the stability of the lines for their reaction to leaf and stem rust.

Determination of Agronomic Characters

Germination percentages and growth ratings were also obtained for the 100 kernels of each line planted in the greenhouse. The germination was determined eight days after planting, and at that time each row was given a growth rating relative to the Pawnee check rows which were given a rating of 0 and were, at the time, four and one-half inches tall. The other rows were then relatively rated as -2, -1, 0, +1 and +2. Leaf counts were also made at the time the seedlings were pulled for the leaf rust readings.

The lines were classified in the field as early, medium, late, or very late for heading on the basis of Pawnee as medium. Stand ratings ranging from one through five were also assigned to the rows on the basis of Pawnee being equal to one.

Threshing percentages were established for all of the lines from which sporocyte samples had been collected and for the Pawnee check rows. After the rows were harvested, they were put through a small head thresher at a constant setting, and the clean threshed grain was separated out by hand picking and screening. The unthreshed portions were re-run through the machine. Several had to be rubbed out by hand. The threshing percentage was determined by dividing the weight of the first threshing by the total weight of the two portions.

Plumpness indices were established for each of the same lines by weighing 500 kernels and rating them relative to the weight of 500 kernels of Pawnee which was given an index of 100.

Methods of Analysis

All of the statistical analyses were performed according to methods given by Snedecor (50).

The data collected by the sub-sampling of pollen quartets and pollen within slides was analyzed by a chi-square test of technique in order to determine how good the sampling procedure was within a single slide. An analysis of variance was performed on the data obtained by the preliminary sampling of anthers within the same floret, head, and line; florets within the same head and line; heads within the same line; and lines.

Correlations between certain characters were computed according to the standard procedures given by Snedecor (50).

EXPERIMENTAL RESULTS

Cytological Studies of Meiosis

The results of the preliminary sampling in which 500 quartets were observed within each of 15 slides in sub-samples of 100 quartets are given in Table 1. Variation between lines was very marked, and a mean of 2.8 quartets per hundred with micronuclei was obtained for the lowest line as compared to a mean of 87.8 for the highest line. The high probabilities of the chi-square values indicated that the variation between the sub-samples of 100 quartets was insignificant. The sum of the chi-square values was 29.7728 (d.f. = 60, P>.50). The close agreement between the sub-samples of 100 quartets within a slide led to the decision to count only 100 quartets per slide for the remainder of the experiment. This is the sample size most generally used by other investigators, even when considerably fewer plants were studied.

In Table 2 are given the results of an analysis of variance conducted on the data obtained by sub-sampling anthers within florets (which actually represented spikelets since only one floret within a spikelet could be obtained in the quartet stage), florets within heads, and heads within lines. All of the F values obtained were significant at the 1 percent level, but the variation was obviously much greater between lines and between heads within the same line than was that between florets within the same head and line. The estimated variance components from the analysis of variance were 5.24 for anthers, same floret, head and line; 8.27 for florets, same head and line; 265.74 for heads, same line; and 40.51 for lines.

Table 1. Test of sampling technique applied to the relative numbers of quartets with micronuclei observed in five sub-samples of 100 within 15 mounts representing as many lines.

Sub-sample	Line (or slide)														
	Grasslike					Intermediate					Wheatlike				
	6424	6425	6426	6427	6428	6608	6609	6611	6612	6613	7122	7123	7124	7121	7125
1	27	34	11	9	16	64	48	89	84	77	7	16	15	6	3
2	30	32	11	9	15	74	53	83	87	75	8	12	14	4	4
3	28	23	8	11	13	73	49	89	88	73	11	12	10	6	3
4	26	31	7	8	19	72	50	91	79	70	10	12	8	6	2
5	29	34	8	9	19	71	52	87	81	72	11	11	12	7	2
Totals	140	154	45	46	82	354	252	439	419	367	47	63	59	29	14
Chi-sq.	.49	3.89	1.70	.60	1.97	3.04	.68	3.45	4.38	1.48	1.52	1.36	3.17	.90	1.11
d. f.	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Probability	.90	.30	.80	.95	.70	.50	.95	.30	.30	.80	.80	.80	.50	.90	.80

Table 2. Analysis of variance of sampling from pollen quartet mounts within five lines of a grasslike family.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Line	4	7,579.1	1894.77	86.996**
Heads, same line	20	21,694.4	1084.72	49.803**
Florets, same head and line	25	544.5	21.78	4.156**
Anthers, same floret, head and line	50	262.0	5.24	
Total	99	30,080.0		

** Exceed 1 percent level of significance.

Since most of the variation obviously consisted of that between lines and between heads within lines, it was decided that four heads would be examined per line for those to be used in correlation studies, but only one floret per head. All three anthers from the floret were included on the slide so that adequate cells were present. In this way it was possible to examine a much larger number of lines in the time available for the study.

All of the cytological data have been summarized in Table 6 in the appendix. The meiotic index, as previously explained, was derived from an average of the data from observation of 100 quartets for each of four heads within a line. Some of the lines showed very little variation between heads while others had very different meiotic indices for each head. Approximately one-half of the 50 lines observed cytologically were, apparently, widely different for meiotic behavior between heads within lines. The meiotic indices for the lines ranged from a low of 30 to a high of 99 with the other lines well distributed between these two extremes. The mean meiotic indices for the grasslike, intermediate, and wheatlike group were 71.5, 56.1, and 84.1 respectively.

The estimated average number of micronuclei per quartet ranged from 1 to 10. However, 28 of the lines were estimated to have an average of only two micronuclei per quartet. Those lines with an average of 2 to 3 micronuclei per quartet had a mean meiotic index of 76.6, a mean percent normal pollen of 88.3, and the mean of the range number of micronuclei per quartet was from 1 to 6. In comparison, the lines with an average of 4 to 10 micronuclei per quartet had a mean meiotic index of 57.9, a mean percent of normal pollen of 77.8, and the mean of the range number of micronuclei per quartet was from 1 to 17.

Various abnormalities were observed while classifying the pollen quartets. Many of the lines had quartets with small extra cells containing one or more micronuclei. In Plate III are shown some normal quartets and some typical abnormalities. The camera lucida drawings of Plate IV represent some of the more extreme examples. In certain of the lines these were common, and these lines, also, tended to have a high average number of micronuclei per quartet, an extreme range number of micronuclei per quartet, and a low meiotic index. In some cases (Plate IV) these extra cells were as large and had nuclei as large as the other cells. Other cells were completely disorganized with chromatin material and chromosomes scattered haphazardly about within the cytoplasm. There was no evidence of an organized spindle ever being formed in these cells, although they had apparently kept pace with normal quartets as far as size was concerned.

In some of the quartets of line 6416 and several other lines, partially-formed additional walls were observed that appeared to be separating off into a separate cell a portion of a nucleus after it had already reached very late telophase II (Fig. 2, Plate IV). The daughter nuclei in these same lines

EXPLANATION OF PLATE III

Fig. 1. A pollen mother cell with $19_{II} + 4_{I}$ from Agrotricum line 6545.

Fig. 2. A pollen quartet showing typical micronuclei.

Fig. 3. A more severely disorganized pollen quartet with two extra cells containing micronuclei.

Fig. 4. A normal pollen quartet.

PLATE III

Fig. 1

Fig. 2

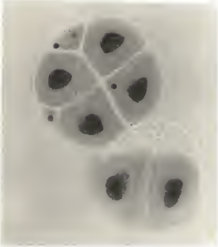


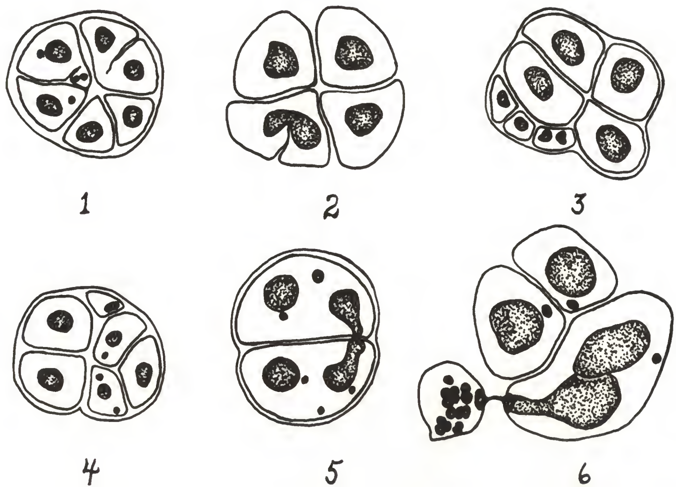
Fig. 3

Fig. 4

EXPLANATION OF PLATE IV

Irregularities of meiosis observed in certain of the Agrotricum hybrids. 1, 3, and 4. Pollen quartets with several micronuclei and extra cells. 2. Pollen quartet with a partially formed extra wall. 5. A disorganized pollen quartet in which meiosis has been completed but only one wall has been formed. There has, apparently, been several bridges between two of the daughter nuclei. 6. A disorganized pollen quartet with one of the daughter nuclei bridged to chromatin in another free cell.

PLATE IV



often had a ragged appearance and some had spine-like projections around their periphery rather than being normally rounded.

In a few of the lines chromatin bridges were commonly observed between the nuclei of the different cells composing the pollen quartet. These were also present between some of the chromosomes in the occasional cells that were observed during anaphase. Bridges between the nucleus of one cell of a quartet and that of a fifth cell, now free from the quartet itself, were also observed on occasion (Fig. 6, Plate IV). Translocation configurations and chains were found at diakinesis in some of the pollen mother cells of line 6415, and quadrivalents were observed in several other lines.

It was noted that those lines with various extremes of meiotic indices could not be distinguished on the basis of morphological characteristics. This is illustrated by Plates V and VI.

Pollen Observations

The results of the preliminary sampling to test the technique used are presented in Table 3. The low chi-square values and their high probabilities indicated that the small amount of variation found between strips could be expected in normal sampling from a homogeneous population.

The summary of the observations of pollen are given in Table 6 in the appendix. The mean percent of normal pollen was 86.3 for the grasslike group, 80.1 for the intermediate group, and 87.6 for the wheatlike group. The range was from 62 percent to 98 percent.

Except for a few cases the empties were a much larger component of the abnormal pollen than were the partials. Some empties were nearly the size of normal pollen grains while others were very small. Many of the very small

EXPLANATION OF PLATE V

Evidence that the meiotic indices are not reflected by the outward appearance of head types. The lines from which the heads were taken had the following indices:

1.	43	grasslike types
2.	88	
3.	34	intermediate types
4.	81	
5.	46	wheatlike types
6.	99	

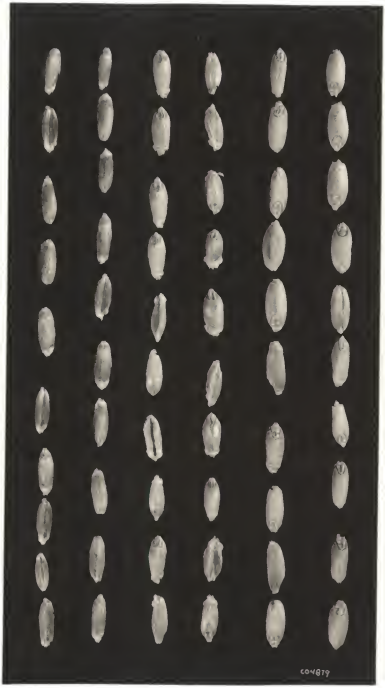
PLATE V

1 2 3 4 5 6

EXPLANATION OF PLATE VI

Grain of the lines from which the Agrotricum heads of Plate V were taken. It is evident that visual observation of the grain gives no indication of the meiotic index.

PLATE VI



1 2 3 4 5 6

Table 3. Test of sampling technique applied to the relative proportions of normal and abnormal pollen in strips across a given mount.

Strip	Slide 1		Slide 2		Slide 3		Slide 4		Slide 5	
	N*	A**	N	A	N	A	N	A	N	A
1	59	1	71	9	63	15	52	8	87	3
2	68	1	61	6	87	18	63	10	77	4
3	70	11	59	7	73	13	58	10	63	5
4	73	0	59	9	63	8	62	8	71	1
5	49	2	69	10	30	4	30	5	20	1
Totals	319	15	319	41	316	58	265	41	318	14
Chi-sq.	.63		1.03		3.45		.49		3.71	
d.f.	4		4		4		4		4	
Probability	.95		.90		.30		.95		.30	

* Normal
** Abnormal

empties were often found joined together in pairs as though the cells of the quartets had never altogether separated. Occasionally all four cells were still joined together. Very small cells filled with starch were sometimes found attached to normal pollen grains.

In 13 of the lines there was wide fluctuation from head to head in the amount of abnormal pollen present.

Fertility Observations

As mentioned previously, both a full count method and a partial count method were used to determine the seed set for 20 of the lines. The two sets of data had a correlation value of $r = 0.85$. Since this significant value indicated that the relative fertility of the lines as determined by the two methods was much the same, the partial count was used for the remainder of the determinations.

The mean percent seed set for the 50 lines studied cytologically was 86.1 under self-pollination as compared to 91.9 under open-pollination. The mean percent seed set for the three groups of lines under both open- and self-pollination is presented in Table 4. The lowest seed set for any line

Table 4. Average seed set under open- and self-pollination.

Group	Self-pollination	Open-pollination
	Percent	Percent
Grasslike	85.2	91.3
Intermediate	89.2	93.9
Wheatlike	84.0	90.7
Over-all mean	86.1	92.0

under self-pollination was 51 percent compared to a low of 73 percent under open-pollination. The highest seed set was 97 percent under self-pollination and 98 percent under open-pollination. It is of interest to note that the five lowest lines under self-pollination had a mean seed set of 59.6 percent which increased to 89.2 percent under open-pollination.

In some of the grasslike lines a few undeveloped spikelets were found at various places on the spike. These undeveloped spikelets were so small that the rachis appeared nearly bare in the areas where they occurred.

Reactions to Rust

Greenhouse Observations. The results of the inoculations with physiologic race 9 of leaf rust are given in Table 6 in the appendix. Most of the lines were resistant although in many cases a few off-type plants were found.

These were probably F_1 plants originating from outcrosses in the field. Specifically, 75 of the lines were resistant, 9 were susceptible, 4 were moderately resistant, and 6 were segregating. Thus, most of the lines were relatively stable for their reaction to this race of leaf rust. All of the Pawnee checks were found to be resistant. The grasslike and intermediate lines were also resistant with the exception of line 6635 which was susceptible.

Observations of Reaction to Leaf Rust in the Field. The Agrotricum lines were found to be very stable for their reaction to leaf rust under the field conditions. Only one line, 7.55, was segregating, 71 were highly resistant, 4 were resistant, 2 were moderately resistant, 5 were moderately susceptible, 14 were susceptible, and the Pawnee check rows were susceptible.

All of the grasslike and intermediate lines were very resistant except line 6635 which was very susceptible. This is the same exception to resistance that was found in the greenhouse.

Observations of Reaction to Stem Rust in the Field. The lines were also very stable for their reaction to stem rust in the field. None of the lines were found to be segregating, 20 were resistant, 33 were moderately resistant, 31 were moderately susceptible, and 12 were susceptible. Seventeen of the resistant lines were in the grasslike group.

It was noted that a number of the lines were not as resistant to stem rust as they had been in previous years, and this was possibly caused by the extremely high temperatures which prevailed during the time the plants were maturing.

Agronomic Characters

Heading and Stand Characteristics in the Field. The grasslike and intermediate lines were all late to very late in heading as compared to the Pawnee checks. Most of the wheatlike lines were also late, but a few were close to Pawnee or of medium earliness. Some of the grasslike lines began to bloom before the heads were more than half emerged from the boot, and, thus, were classed as early as some of the other lines that were actually much more wheat-like. These grasslike lines were in reality much greener and in an active state of growth considerably longer than were any of the wheatlike lines.

The stands of the Agrotricums were considerably poorer, in general, than were those of the Pawnee check rows, and the mean stands for the grasslike, intermediate, and wheatlike groups were 2.5, 2.6, and 2.4 respectively. These ratings were given relative to a rating of 1 for Pawnee.

Specific heading and stand data has been given in Table 6 in the appendix.

Germination and Vigor in the Greenhouse. The data for these two characters has been given in Table 6 in the appendix. In general, the grasslike and intermediate seedlings were found to be less vigorous than the Pawnee checks under the greenhouse conditions. The ratings were assigned primarily on the basis of height differences, but the rows which were shorter than Pawnee also tended to be more spindly. In addition, these rows often had less extensive root systems. The wheatlike seedlings were, in general, equal to or more vigorous than the Pawnee checks.

The mean germination percentages for the grasslike, intermediate, and wheat-like groups were 88.2, 87.3, and 95.5 respectively. The poorest germination, 59 percent, was found for an intermediate line and was completely out of line with the other germination percentages. In fact, this extremely low value was responsible for the mean for the intermediate lines falling below that of the grasslike lines. Two of the wheatlike lines attained the maximum germination of 100 percent.

Plumpness and Threshability of the Grain. Relative to the Pawnee checks, the plumpness of the grain from the grasslike and intermediate groups was very poor. In fact, only one line in these two groups was as good as Pawnee for this character. Many of the 45 wheatlike lines were nearly as plump as Pawnee while 21 were actually superior. The mean plumpness indices, calculated from the data summarized in Table 6, were 50.9, 58.8, and 101.6 for the grasslike, intermediate, and wheatlike groups respectively.

In the same order as above, the mean threshing percentages of the three groups were 40.8, 50.0, and 90.4. A number of the grasslike and intermediate lines were exceedingly difficult to thresh, and it was often necessary to rub out the second run by hand before the weights of the two portions were determined.

Correlations

In Table 5 are summarized the results of the various correlations that were conducted with the data from this experiment. The meiotic index was found to be significantly correlated with the percent of normal pollen, plumpness of the kernels, and germination. As shown by the r values, neither the meiotic index nor the percent of normal pollen was significantly correlated with the percent seed set under either self- or open-pollination. A non-significant r value was also obtained when the seed set under self-pollination was correlated with that under open-pollination. There was a highly significant correlation between plumpness and the two characters — threshing index and germination.

Table 5. Correlations between certain Agrotricum characteristics.

Correlation between	r
Meiotic index and percent normal pollen	.32 †
Meiotic index and plumpness	.48**
Meiotic index and percent germination	.52**
Meiotic index and percent seed set, self-pollination	.12
Meiotic index and percent seed set, open-pollination	-.08
Percent normal pollen and percent seed set, self-pollination	.03
Grasslike group	.40
Intermediate group	.14
Wheatlike group	.08
Percent normal pollen and percent seed set, open-pollination	.09
Threshing index and plumpness	.78**
Percent germination and plumpness	.53**
Percent seed set, self-pollination and percent seed set, open-pollination	.22

† r value exceeds 2 percent level of significance.
** r value exceeds 1 percent level of significance.

When the percent of normal pollen and the seed set under self-pollination within the three groups of hybrids were investigated, r values of .4041, .1386, and .0765 were obtained for the grasslike, intermediate, and wheatlike groups respectively. Although all three of these values are non-significant, it is of interest to note the trend.

DISCUSSION

Preliminary Sampling

Throughout this experiment an attempt was made to keep the cytological analyses on a practical basis since these studies tend to become very time consuming, and must usually be kept on such a level if they are to be in accord with the facilities, personnel, and time allotted to most plant breeding programs.

The number of pollen quartets observed by different investigators has varied considerably, as has the number of plants, depending upon the purpose and nature of their studies. Love and Suneson (20) studied 200 quartets per plant; Thompson and Grafius (52), Love (19), and Elliott (8) studied 100 quartets per plant. Other investigators have not studied any definite number of quartets per plant. There was little evidence presented in the literature which was reviewed to support the size of sample or method of sampling employed. Admittedly, the preliminary sampling experiments used in this study were limited, but they do give some idea as to the reliability of the sampling techniques employed for this Agrotricum material.

The results of sub-sampling in random strips of 100 pollen quartets within a given slide were presented in Table 1. The results of the chi-square test of technique, which was applied to the data, indicated that there was relatively little variation between the sub-samples of 100, and that any strip of 100 quartets taken at random across a slide could confidently be expected to be representative of the total population a high percentage of the time. The total sample of 500 quartets approached the maximum population that could be consistently included on a slide from a single floret in this material.

Thus, it seems that for practical purposes, in the case of the material studied, the additional accuracy gained by observing more than 100 pollen quartets within a single slide would not justify the additional time and labor required. By limiting the sample to this size it was possible to study many more heads and lines, and this was desirable from the standpoint of the correlation studies. The results of the analysis of variance (Table 2) bear out this need to study relatively greater numbers of heads and lines. The estimated variance components were very much larger for these two than were those for anthers and florets. It should be emphasized that the data collected for other characters of the lines were actually averages from several plants, and that the meiotic index finally used for correlations with these characters was an average of four plants from each line. If it were possible to work with individual plants, only a few heads would be available per plant for determination of the various characters, and a larger sample within a head would probably be justified. Thus, correlations could be made on the basis of individual plants and should be more exact than those made with sets of data, such as collected in this experiment, which probably represented the averages of a different group of plants for each character.

The preliminary sampling and test of technique applied to the pollen studies (Table 3) gave similar results to those obtained for the quartets. It was apparent that random strips across the slide gave very similar results and that a good distribution of pollen over the slide was being obtained by the method used. Since 100 quartets should theoretically give rise to 400 pollen grains, it was decided that a minimum of 300 pollen grains should be observed per slide in the random strips.

Meiotic Stability and Other Characters

There was wide fluctuation between the meiotic indices of the various lines studied in this experiment. This was more or less expected since there were also obvious differences between the lines in morphology and other characters. However, differences in these characters were not generally apparent between the five lines originating from a single head selection the previous year and composing what has been called a family. The wide variation for meiotic regularity found between these lines was more surprising and might possibly suggest that segregation for meiotic behavior was occurring in some of the material. The variability that was found between heads in many of the lines accentuated this possibility, and the question arises as to whether the meiotic behavior might be under genic control. Sears (42) has reported at least one major, dominant factor in hexaploid wheats for normal synapsis of chromosomes. Partial desynapsis due to single recessive factors has also been reported, and the existence of minor factors affecting meiotic stability is suggested by the work of Myers and Powers (26). Allard (2) has also suggested the possibility of genic control of chromosome pairing. Segregation for such a factor or factors is a possibility suggested by the results obtained in this experiment.

Various numbers of unpaired chromosomes were observed in the few lines for which slides in the proper stage for such observations were obtained. Several of the intermediate lines were found to have $n = 28$ chromosomes; however, varying numbers of univalents were present and insufficient observations were made to present any data as to the frequency of univalents in this material. The fact that some of the intermediate lines are approaching the chromosome number of common wheat very closely is emphasized by the $n = 21$

number observed for 6545 (Fig. 1, Plate III). However, this line is still very unstable meiotically as shown by a meiotic index of 33. Further cytological studies in these lines should include the determination of univalent frequency.

It has been noted that there was very marked variation in the average number and range number of micronuclei found in these lines. While reviewing the Agrotricum literature, no evidence was found of anyone correlating the frequency of univalents with that of micronuclei. However, a close correlation should not necessarily be expected in this material since it seems apparent that several chromosomes may unite to form a single micronucleus. A single univalent occurring at metaphase I may also divide and produce more than one lagging chromosome at anaphase II. In addition a certain number of univalents can be expected to be included by chance in the daughter nuclei. A much closer correlation would be expected between the number of metaphase I cells with univalents and the number of pollen quartets with micronuclei. Semeniuk (44) found this to be true in the derivatives of a T. vulgare x T. timopheevi cross. He emphasized that in his material differences in chromosomal stability were inherited as indicated by the fact that parent-offspring correlations for abnormalities at corresponding stages were highly significant and that lines differing in stability were established.

As previously mentioned, several univalents may evidently unite to form large micronuclei, and the large size of some micronuclei is evident in the camera lucida drawings of Plate IV. Whether these large micronuclei always result from several chromosomes just happening to be excluded together is debatable. It may be that some of the laggard chromosomes, after failing to get into the daughter nuclei, migrate together, especially if they happen to lie near each other in the cytoplasm. Another possibility is that the forces operating within the cell during separation of the chromosomes and the formation of the cell plate may push lagging chromosomes together by chance. The fact that micronuclei are often found out at the extreme edges of the cell, in an extra cell or not, suggests that they are moved about in the cell by some force.

In quartets such as the ones pictured in Figs. 1 and 4 of Plate III, the additional cells had nuclei that were so large that it was difficult to postulate about what had occurred to upset the normal condition so radically. It may be that during metaphase II and anaphase II a block of adjacent chromosomes failed to separate at disjunction, or lagged closely together at the plate, and eventually rounded up into a separate nucleus during telophase. Should such a phenomenon occur in both halves of a dyad, six cells of about equal size such as those pictured in Fig. 1 of Plate III could result. Such a condition might arise as a result of additional mitotic divisions in part of the cells composing a quartet. Certainly some of the large micronuclei which were walled off into separate cells must have resulted from the union of a number of chromosomes, and at least limited migration or pushing together of chromosomes at times does not seem impossible.

The observation of translocation figures during diakinesis in one of the lines (6415), and the presence of chromatin bridges between the nuclei of the cells composing pollen quartets of other lines was encouraging, since structural alterations may prove to be the most satisfactory means of transferring characters from the Agrotricums to a satisfactory wheat. A very short segment from an _Agropyron_ chromosome attached to a nearly complete wheat chromosome might provide the desired factors without having a disturbing or disrupting effect on normal pairing and disjunction during meiosis. It is becoming more and more evident that the retention of complete Agropyron chromosomes in a good wheat type may be impossible. As pointed out by Allard (2), the transfer of genes in chromosomes which completely lack homologues would depend upon the substitution or addition of a complete chromosome pair. It may be that none of the Agropyron chromosomes are homologous enough with T. vulgare to pair consistently and be retained in a stable state from generation to generation.

Many of the extreme abnormalities and deviations from normal microsporogenesis that were observed are unexplainable on the basis of this study, but they all emphasize the fact that most of the lines studied are still far from meiotic stability relative to that expected of common wheat. According to Love (19) a wheat plant must have a meiotic index of 90 percent or better if it is to be considered stable enough for practical purposes. A definite line between what is stable and unstable is difficult to establish, but, in general, wheat plants with meiotic indices below this 90 percent level are likely to give the plant breeder trouble.

Just where should the line be drawn for the Agrotricum hybrids? A definite answer to this question is dependent upon further investigations, but certain facts can be considered at the present time. If those lines above 90 percent were to be saved or selected from the material studied, only 15 of the 50 would be good enough to retain. These 15 lines are all within the wheatlike group, and this, plus the relatively high mean meiotic index (84.1) for the wheatlike group, indicates that by selecting for wheatlike characters, a suitable meiotic stability will in general, eventually be expected for at least part of the lines. However, it is to be emphasized that these 15 lines are, for the most part, less desirable for their reactions to leaf and stem rust than are the majority of the lines that would be eliminated because of their meiotic instability. Evidently, selection for wheatlike characters in these instances has tended to reduce the resistance of the plants, and did so by eliminating certain Agropyron chromosomes which carry the factors for resistance.

This is in agreement with the postulations of Armstrong (4) and Armstrong and Stevenson (6) that by making selections which incline toward wheat in appearance, the proportion of Agropyron chromosomes are also reduced. These investigators also feel that increasing fertility indicates improved cytological stabilization. This may be true in the very early generations of Agrotricum hybrids, but it does not seem to apply to late generations such as the ones included in these studies. This is emphasized by the fact that there was no significant correlation between the meiotic index and fertility. It also seems doubtful that selection for any morphological characters by visual observation will be accompanied by a definite trend, either up or down, for meiotic stability. Certainly the photographs in Plates V and VI provide ample evidence that nothing concerning the nature of meiotic stability could be conceived from a visual observation of the heads or the grain from these heads.

Jenkins (10) has demonstrated that the repeated use of the Agrotricum hybrid as the male parent in backcrosses to wheat resulted in a larger number of plants which resembled wheat than when other methods were used and yet an abundance of A. elongatum characteristics were retained. His work suggests that unpaired Agropyron chromosomes are probably eliminated more quickly by this method of crossing because of the elimination of male gametes which have unfavorable chromosome combinations and are non-functional. Armstrong and Stevenson (6) have proposed the theory that the decided improvement in chromosome pairing in advanced generations of Agrotricums may be caused by a continual elimination of both male and female gametes carrying unfavorable chromosome combinations. This is undoubtedly true, but Jenkins' work indicated that elimination through the male gametes may be more rapid.

Allard (2) also found that when he used backcross plants as the pollen parents, the resulting populations resembled wheat more closely and were more fertile and regular cytologically than when the populations came from the recriprocal backcrosses. He postulated that functional male gametes of backcross plants were genetically and cytologically similar to common wheat gametes and that backcrosses in that direction acted as a fine sieve which passed certain genes but screened out nearly all _T. timopheevi_ genes.

A more rapid loss of unfavorable chromosome and gene combinations, conceivably, could increase the chances of retaining other _Agropyron_ chromosomes. This would especially be true if some of the unfavorable chromosomes were carrying factors from the _Agropyron_ parent for abnormal synapsis or for other detriments to normal meiosis. It is conceivable that in every generation retaining these factors certain _Agropyron_ chromosomes might fail to pair and, thus, be eliminated although they had previously paired with wheat chromosomes. To date the fact persists that breeders have been disappointed to find that their selection of the Agrotricums for wheatlike characters has led to an accompanying loss of desirable _Agropyron_ characters. It remains to be seen whether or not any of the _Agropyron_ chromosomes and wheat chromosomes are homologous enough with each other to pair consistently enough that one or a few of the former can be retained in a suitable wheat.

Another possible explanation of why these advanced generations of Agrotricums are still so meiotically unstable might be that enough unfavorable chromosome combinations or unpaired chromosomes are getting through microsporogenesis and being carried along to maintain the condition. However, it seems evident that gametes are being eliminated continuously, and before too many generations most of the unfavorable combinations should theoretically be eliminated. The elimination of gametes could result from natural selection operating through such factors as differences in the rate of pollen tube growth, differences in germination, and differences in competitive ability of seedlings produced by shriveled and by plump kernels. The close correlation found in this experiment between the meiotic index and both plumpness and germination suggested that unfavorable chromosome combinations had been transmitted to the zygote and were producing an adverse effect on plumpness, and, in turn, on germination. The reduced germination of lines with low meiotic indices indicated that elimination of gametes with unfavorable chromosome combinations was probably occurring.

The formation of the pollen is another place where unfavorable chromosome combinations may be eliminated through the loss of male gametes. It has been noted previously that a significant correlation was found between the percent of normal pollen and the meiotic index. This means that as the meiotic irregularity increased the amount of non-functional pollen also increased. Some of the microspores with irregularities, evidently, are able to form pollen that is normal in appearance, but, probably, are subject to further selection against unfavorable combinations at pollenization. Part of these could conceivably be eliminated as a result of slow pollen tube growth as compared to that of normal pollen. Selective fertilization may be another possible factor in elimination.

Thus, there are a number of apparent places in the life cycle of a plant where unfavorable chromosome combinations can be eliminated. It seems highly probable that elimination did occur at several stages in the life cycle of the Agrotricums studied. The question arises again as to why most of the lines studied are highly unstable for meiotic regularity although they have been grown nearly every year since the original crosses were made in 1935-37, and are, apparently, quite stable for morphologic and agronomic characters. It is possible that a certain amount of outcrossing has been continuously going on in the Agrotricum material studied, and, if so, this would be another factor contributing to irregularity.

Therefore, it is possible that the continued meiotic irregularity might be attributed to any one of the following or a combination thereof:

1. Genes or factors which influence synapsis or chromosome pairing may be present and are being maintained in the populations.

2. A portion of unfavorable chromosome combinations and unpaired chromosomes may always be passing through megasporogenesis and microsporogenesis into the following generation.

3. A certain amount of outcrossing may be continuously occurring and contributing to the meiotic irregularity.

The authenticity of these possibilities should be subjected to further study. This could probably best be accomplished by space planting the material to be studied, and by bagging to assure selfing, so that the various characters could be determined on the basis of individual plants. It would be of interest to select on the basis of meiotic regularity and observe the effects on this character for a number of generations. If it should prove possible to stabilize lines at a certain level for meiotic stability, crossing experiments would be of interest. In addition, a more detailed study of the chromosome numbers, pairing, and behavior during meiosis should be conducted.

A number of the other correlations are of interest and warrant some discussion. The lack of a significant correlation between the meiotic index and the seed set under either self- or open-pollination was not surprising in view of the fact that the correlation between seed set and the percent of normal pollen was also insignificant. Any effect of meiotic irregularity during microsporogenesis on fertility would evidently have to be expressed through the pollen, and even when there was a high percentage of abnormal pollen, there was, evidently, enough normal pollen present for fertilization. The seed set under conditions of self-fertilization was a reflection of the compatibility of both the male and female gametes of any given plant, and should not be expected to correlate very closely with the meiotic index which is a measure of the irregularity of the male gametes only. Also, female gametes may be irregular and still function normally. Thus, it was not surprising that there was no correlation between the seed set under conditions of open-pollination and that under self-pollination.

This lack of a correlation between meiotic irregularity and fertility has also been reported by other investigators. Peto (30) and Elliott (8) found no correlation between fertility and the number of univalents. Elliott also reported a lack of correlation between the percent fertility and the percent of quartets with no micronuclei.

The fact that the fertility of the wheatlike group was the lowest under both open- and self-pollination indicated that selection for wheatlike characters does not assure high fertility in this material. White (67) and Allard (2) found that little was gained by selecting the more fertile or more cytologically regular plants as far as meiotic regularity and fertility was concerned.

The remainder of the observations are essentially in agreement with those made by Schmidt (40) in 1949 from the Agrotricum material preceeding the lines used in this study. There is evidently an abundance of genes in these lines for resistance to both leaf and stem rust. They tend to be later, in general, than common wheats such as Pawnee, and the stands in the field are poorer. This poor stand probably can not be attributed to inferior germination, and the possibility that the Agrotricum hybrids fail to develop sufficient top and root growth in the fall for overwintering is under investigation.

In general, the grasslike and intermediate Agrotricum seedlings appeared to be less vigorous than Pawnee in the greenhouse tests. However, many of the wheatlike hybrids were equal to or exceeded Pawnee in vigor. The vigor of the seedlings, evidently, was closely related to the plumpness of the kernels as would be expected since they were grown in sand, and no fertilizer was applied until after the vigor ratings had been made. Thus, the seedlings were probably almost entirely dependent upon the endosperm for nourishment.

The close correlation between plumpness and threshability indicated that although many of the lines were very difficult to thresh, this should be no problem for the breeder. Grain which is plump enough to meet the other requirements which are demanded will surely thresh freely.

SUMMARY

Preliminary sampling indicated that for the material studied the variation in the numbers of quartets with micronuclei was much greater between heads and between lines than was that between anthers and between florets. Therefore, only 100 quartets, from the three anthers of a single floret, were

observed per head so that it was possible to observe a larger number of heads and lines.

The material was found, in general, to be still highly irregular for meiotic stability regardless of the fact that morphological and agronomic characters are apparently well stabilized. Wide differences for meiotic stability were found between the lines that had originated from a single head selection the previous year, and also between heads within many of the lines. The presence of univalents and laggard chromosomes, as well as other abnormalities during microsporogenesis, emphasized the fact that many of the lines were cytologically unstable.

The meiotic index was found to be significantly correlated with the percent of normal pollen, plumpness of the grain, and germination. Neither the meiotic index nor the percent of normal pollen was significantly correlated with the seed set under either self- or open-pollination. The plumpness of the kernels was found to be significantly correlated with both the threshing index and germination.

The correlation of the meiotic index with the three characters above indicated that male gamete elimination, probably, was occurring in this material. Part of the unfavorable chromosome combinations, obviously, were being eliminated during male gametogenesis but others were effective in fertilization which later affected plumpness, and germination of the seed.

Three explanations of the failure of these lines to stabilize for meiotic irregularity were postulated as follows:

1. Genes or factors which influence synapsis or chromosome pairing may be present and are being maintained in the population.

2. A portion of unfavorable chromosome combinations and unpaired chromosomes may always be passing through from one generation into the next.

3. A certain amount of outcrossing may have been occurring continuously and contributing to the meiotic irregularity.

Further study of the chromosomal condition in these lines has been suggested in the hope of determining the authenticity of the above postulations. Such studies could best be made on the basis of individual plants, and selection for meiotic stability should be attempted.

It was concluded that these Agrotricum hybrids can not be evaluated according to the meiotic index of 90 that Love has given as the level below which common wheat is unsatisfactory cytologically.

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APPENDIX

Table 6. Data on various characters of certain Agrotricum hybrids and Pawnee checks.

Line	Meiotic Index	No. Micro-nuclei per quartet: Ave.	No. Micro-nuclei per quartet: Range	% Normal Pollen	% Seed Set, Self	% Seed Set, Open	Growth Rating1/	% Germi-nation	Plump-ness Index2/	% Thresh-ing	Head-ing3/	Field stand4/	Stem rust5/	Leaf rust5/	Reaction to Pr 9 in G.H.6/
	Wheat x A. elongatum														
6395	76	4	1-9	69	74	82	-1	80	45	3	L	3	MR	HR	R
6545	33	2	1-5	90	74	87	0	95	101	75	L	4	MR	HR	R
6604	50	6	1-28	83	94	98	—	—	—	—	L	2	MR	HR	—
6608							-2	79	49	50	L	3	S	HR	R
6609							-1	92	62	51	L	2	MS	HR	R
6611							-1	90	54	58	L	2	S	HR	R
6612							-1	87	44	52	L	3	MS	HR	R
6613							-1	94	57	55	L	3	MR	HR	R
6614							-1	98	55	68	L	3-4	MR	HR	R
6615							-2	80	48	58	L	4	MR	HR	R
6616							-1	97	49	69	L	2-3	MR	HR	R
6617							-1	91	55	57	L	2-3	MR	HR	R
6618	81	4	1-8	93	95	97	-1	89	62	66	L	3	MR	HR	R
6635	45	2	1-9	95	90	96	-2†	91	20	92	L	3-4	S	S	S,13=R,2=X
6656	72	2	1-6	85	90	90	-1	85	62	20	L	3	MS	HR	R
6657	34	4	1-12	62	83	87	-1	83	64	24	L	3	MS	HR	R
6658	30	4	1-14	76	68	87	-1	86	50	20	L	3	MS	HR	R
6659	64	4	1-10	93	94	91	0	87	61	23	L	3	MS	HR	R
6660	67	3	1-7	86	92	93	0	97	61	32	L	2-3	MS	HR	R
6665							-1	84	64	32	L	2-3	MS	HR	R
6667							-1	72	64	46	L	3	MS	HR	R
6674	51	5	1-28	69	94	97	0	89	65	53	L	3	S	HR	R
6698	43	4	1-12	88	96	97	0	91	69	70	L	1	MS	HR	R
6736	76	3	1-12	69	91	97	0	89	65	67	L	1	MR	HR	R

Table 6. Cont.

Line	Meiotic Index	No. Micronuclei per quartet Ave.	No. Micronuclei per quartet Range	% Normal Pollen	% Seed Set, Self	% Seed Set, Open	Growth Rating	% Germination	Plumpness Index	% Threshing	Heading	Field stand	Stem rust	Leaf rust	Reaction to Pr 9 in G.H.
	Wheat x <u>A. elongatum</u>														
6782	57	4	1-30	73	94	95	-1	87	69	50	L	2	MS	HR	R
6787	57	5	1-28	74	95	97	-1	90	59	50	L	1	MS	HR	R
6796					92	95	-1	88	66	41	L	2	S	HR	R
6799							-2	59	54	22	L	4	MS	HR	R
6807					81	87	-1	91	68	53	L	2	MS	HR	R, 1=S
6815	62	3	1-16	86	93	93	-1	87	55	33	L	3	MS	HR	R
6819	66	4	1-12	87	89	97	-1	84	54	44	L	1	MS	HR	R
6821	59	10	1-30	69	79	93	-1	84	49	44	L	2	MS	HR	R
6828	63			64	94	98	0	91	78	75	L	2	MR	HR	R
7017	46	2	1-7	89	62	95	+1	88	103	79	L	2	MR	HR	MR,2=R
7091	90			85	85	97	0	98	124	100	M	1	MR	HR	R
7094	81	2	1-4	98	89		0	93	65	77	L	3	MR	MR	R,1=MR
7097	73	2	1-7	66	90	88	0	97	106	34	L	1	S	S	S,7=R,3=MR
7104	99	2	1-3	92	84	90	-1	96	99	87	L	2	S	MS	R
7111	90	1	1-6	93	85	89	-1	98	135	93	L	2	MR	S	S,1=R
7114							0	98	119	94	L	3	MR	S	MR,11=R,7=X
7117							-1	99	87	85	L	3	MR	MS	R
7120							0	94	96	89	L	4	MR	MS	R,13=MR,2=X
7121							-1	95	118	92	L	2	MR	S	R,5=MR
7122							-1	93	99	90	L	2	MR	S	R,1=S
7123							-1	94	106	88	L	2	MR	S	R,5=MR
7124							-1	94	95	81	L	3	MR	S	R,6=MR
7125	98	2	1-3	78	81	73	0	95	109	95	L	3	MR	MS	MR,11=X
7131	43	2	1-4	77	88	85	-1	97	61	95	L	2	S	S	S,2=R

Table 6. Cont.

Line	Meiotic Index	No. Micro-nuclei per quartet Ave.	No. Micro-nuclei per quartet Range	% Normal Pollen	% Seed Set, Self	% Seed Set, Open	Growth Rating	% Germi-nation	Plump-ness Index	% Thresh-ing	Head-ing	Field rust	Stem rust	Leaf rust	Reaction to Pr 9 in G.H.
	Wheat x *A. elongatum*														
7137							-1	94	82	88	L	3	MS	S	MR,2=S,5=X
7141	94	2	1-4	98	95	92	0	96	105	90	L	2	MR	S	R,13=MR
7146							-1	90	92	91	L	3	MS	S	R,4=MR
7155	69	2	1-3	96	92	90	+2	97	103	99	L	1	S	Seg.	R,2=MR
	(Wheat-rye x *A. elongatum*) x Cheyenne														
6398							-1	91	51	54	L	3	R	ER	R
6399							-1	86	54	44	L	4	R	HR	R,1=S,2=X
6400							-1	83	53	49	L	3	R	HR	R,1=X,1=S
6401							-1	78	52	37	L	2	R	HR	R,3=S,2=X
6402	77	2	1-4	93	91	92	-1	93	51	52	L	2	R	HR	R,2=X
6403	88	2	1-4	93	84	93	-1	92	49	37	L	2	R	HR	R,5=X,1=S
6408	57	2	1-5	93	91	96	-1	88	48	40	VL	3	R	HR	R,10=X
6414							-1	85	65	45	L	1	R	HR	R, 7=S
6415							0	96	55	42	L	4	R	HR	R,1=X
6416							-1	92	53	45	VL	3	R	HR	R,2=X
6417	62	3	1-6	94	80	90	-1	81	50	36	VL	2	R	HR	R,6=X,1=S
6418							-2	88	43	33	VL	3	R	HR	R
6424	83	1	1-4	92	88	95	-1	90	52	33	L	1	R	HR	R
6425	68	2	1-7	91	86	92	-1	93	50	45	L	2	R	HR	R
6426	80	2	1-6	90	89	92	-1	94	50	47	L	2	R	HR	R,4=X,2=S
6427	71	2	1-4	87	85	93	-1	87	52	48	L	2	R	HR	R
6428	81	2	1-6	64	88	90			43	36	VL	3	R	HR	
6996	96	2	1-4		57	74	+2	94	106	87	L	1	MR	S	R

Table 6. Cont.

Line	Meiotic Index	No. Micro-nuclei per quartet Ave.	Range	% Normal Pollen	% Seed Set Self	% Seed Set Open	Growth rating	% Germi-nation	Plump-ness Index	% Thresh-ing	Head-ing	Field stand	Stem rust	Leaf rust	Reaction to Pr 9 in G.H.
	(Chinese-rye x Chinese) x (*A. elongatum* x Forward)														
7021	81	4	1-9	75	85	92	+1	99	99	94	L	3	S	HR	R
7027	61	5	1-12	79	60	94	+1	97	117	96	L	1	MR	HR	R
7034	99	3	2-4	84	92	95	+2	95	115	92	L	1	MS	HR	S,2=R
7036	95	2	1-7	94	51	96	0	96	117	89	M	3	MS	HR	S
7044	98	2	1-6	89	87	96	+2	94	108	89	L	1	MS	R	S,1=MR
7169							+1	96	81	93	VL	3	R	HR	S,42=R
7171							+1	95	98	93	VL	2-3	MR	HR	S,27=R
7172							+1	98	97	92	VL	3	MR	HR	S,28=R
7173							+1	96	94	92	VL	4	MS	HR	S,50=R
7174							+1	95	98	94	VL	3	S	HR	R,22=S
7175	93	2	1-5	90	87	93	+1	98	87	92	L	3	S	HR	R,5=S
7176	94	2	1-5	89	97	98	+1	98	79	86	L	3	MS	HR	R,7=S
7177	93	2	1-4	96	91	81	+1	96	83	93	L	3	MS	HR	R,1=S
7178	93	2	1-4	90	89	91	+1	99	89	93	L	3	MS	HR	R,2=S
7179	96	2	1-7	96	87	92	+1	94	92	97	L	3	MS	HR	R,9=S
7181							+1	99	97	95	L	3	MS	HR	R,15=S
7185							+1	98	92	95	L	2-3	MS	HR	R
	{(Mindum x *A. trichophorum*) x (Med.-Hope x Paw.)} x (Nebred x Ceres H-44)														
7048	70	1	1-6	98	90	91	-1	87	79	80	L	3	MR	HR	R
7056							+1	98	105	97	M	2	R	R	S,9=X
	Pawnee Checks														
6730	98	1	1-2				0	97	100	99	M	1	S	S	R
6810	98						0	96	100	99	M	1	MS	S	R
7050	98						0	98	100	99	M	1	MS	S	R
7090							0	99	100	99	M	1	MS	S	R

Table 6. Cont.

Line	Meiotic Index	No. Micro-nuclei per quartet Ave.	No. Micro-nuclei per quartet Range	% Normal Pollen	% Seed Set, Solf	% Seed Set, Open	Growth Rating	% Germi-nation	Plump-ness Index	% Thresh-ing	Head-ing	Field stand	Stem rust	Leaf rust	Reaction to Pr 9 in G.H.
	Aegilops triuncialis x Peliss x Hard Fed. x *A. elongatum* x VPI 131 and/or Harvest Queen														
6420	43	3	1-6	84	81	89	-1	91	52	50	L	3	MR	HR	R,9=X
	+(Mindum x *A. trichophorum*) x Red Chief+ x (Med.-Hope x Paw.)														
7060							+2	95	141	98	M	1	R	S	S
7062							0	89	82	86	L	3	MR	R	R,1=MR
7071							+2	89	153	92	M	3	MR	R	S,35=R,2=X
7076							+1	96	112	98	L	3	MS	HR	R
7082	91	2	1-7	86	86	86	+1	100	115	98	L	2	MR	MR	R
7086	98	2	1-5		86	95	+1	100	134	98	M	2	MR	MR	R

1 Ratings on the basis of Pawnee being equal to 0.
2 Index derived on the basis of Pawnee being equal to 100.
3 M - Medium
L - Late
VL - Very late
4 Ratings on the basis of Pawnee being equal to 1.
5 HR - Highly resistant
R - Resistant
MR - Moderately susceptible
S - Susceptible
6 X - Intermediate type
S - Susceptible, 3-4 infection type
MR - Moderate resistance, 1+ to 2+ infection type
R - Near immunity 0-1 infection type

A STUDY OF THE MEIOTIC STABILITY OF CERTAIN AGROTRICUM HYBRIDS

by

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The Agrotricum (Triticum x Agropyron) material used in this experiment previously had been studied and found fairly stable for disease reactions and agronomic and morphological characteristics. However, little was known about the fertility of these lines and nothing concerning their chromosomal stability. The purpose of this experiment was to study their meiotic stability in relation to fertility, disease reaction, and certain agronomic characters, and to test the hypothesis that by selecting for these latter characters meiotic stability would also be obtained.

Various investigators have used the frequency of chromatin loss in the form of micronuclei within pollen quartets as a measure of meiotic stability. These micronuclei result from abnormalities in chromosomal pairing, and it has been suggested that genetic factors capable of causing variation in pairing conditions may exist. Low self-fertility and pollen degeneration has been attributed to the meiotic irregularity of the Agrotricum hybrids.

Meiotic indices and percentages of normal pollen were determined for 50 Agrotricum lines. Preliminary sampling experiments indicated that the observation of 100 pollen quartets in temporary aceto-carmine smears for each of four plants per line and 300 pollen grains in temporary I_2KI-agar mounts for each of two or three plants per line would provide satisfactory samples for these determinations. The percent seed set was determined on the basis of the number of florets filled in ten heads per line under both self- and open-pollination. The threshability, plumpness, and germination of the grain was determined. Stem rust reactions under field conditions and leaf rust reactions under both field and greenhouse conditions were recorded. Correlation studies were conducted with these various Agrotricum characteristics.

In general, the hybrid lines were found to be highly irregular for meiotic stability. Various abnormalities were observed in the microsporocytes and pollen quartets. Wide differences for meiotic stability were found between plants within lines which appeared similar for other characteristics. Head and grain type were of no value for predicting the meiotic regularity of the hybrid lines studied.

The percent normal pollen, fertility, and percent germination were found to be relatively higher than expected on the basis of the meiotic indices. The mean seed set under open-pollination was found to be about six percent higher than that under self-pollination.

The meiotic index was found to be significantly correlated with the percent normal pollen, plumpness, and the percent germination. Plumpness was significantly correlated with both the threshing index and percent germination.

It was suggested that the following factors were contributing to the persistence of meiotic irregularity:

1. Genes or factors were present which were influencing chromosome synapsis or meiotic regularity in some manner, and segregation for these factors could be independent of those controlling morphological characters.
2. A number of unfavorable chromosome combinations could continually be passing into the following generation.
3. A certain amount of outcrossing could continually be occurring in these hybrid lines.

It was pointed out that selection for stability of agronomic characters and/or disease reactions will not assure meiotic regularity, and that the lines studied could not be selected for meiotic stability using the same criteria as for common wheat.