Progress in Wheat-Grass Breeding

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McFadden (McFadden and Sears, 1947) of the United States who began crossing wheat with *Agropyron* (tall wheatgrass) as early as 1914, called attention to numerous characters in the genus *Agropyron* that would be of value in the cultivated wheats. Among the *Agropyron* characters specifically mentioned were perennial nature, extreme winterhardiness, and resistance to heat and drought, frost, and to rust and smuts.

After many years of effort by numerous researchers, N. V. Tzitzin of the U.S.S.R. achieved success in making a *Triticum* X *Agropyron* cross in 1930 (Schmidt et al., 1953). Canadian and U.S. breeders produced their first fertile *Triticum* X *Agropyron* hybrids in 1935 (Reitz et al., 1945). This opened up a new field of wheat breeding and after numerous efforts in the U.S. and Canada to produce high yielding, disease resistant, perennial types this objective came almost to a standstill. The Russians have claimed success in the production of commercially useful perennial wheat (Anonymous, 1936). From about 1940 up to the present, the major emphasis in the U.S. and Canada shifted to the production of desirable annual types with disease resistance. Various difficulties have been encountered: the transfer of disease resistance to wheat-like types, various degrees of sterility, and failure to breed true in subsequent generations.

WORK AT THE OKLAHOMA STATION

Materials and Methods

Work with *Agropyron-Triticum* breeding was initiated at the Oklahoma Station in 1947. It was a modest beginning in that only 15 *Triticum* sp. X *Agropyron elongatum* advanced generation lines were received from the Kansas Station, Manhattan. These lines resulted from earlier hybridization work by W. J. Sando of the United States Department of Agriculture.

The first planting of these lines in March, 1947 showed they were highly variable; and a few produced normal-appearing wheat-like heads with viable seeds. The most promising line carried the Kansas number '464708. In the fall of 1947 the bulk of the seed derived from the spring-sown material was seeded in the field and was used for (1) crossing and (2) further selection.

Crosses were made with 4 recommended varieties of hard red winter wheat: Cheyenne C.I.[1] 8885, Comanche C.I. 11673, Pawnee C.I. 11669 and Tenmarq C.I. 6936. A total of 102 head selections varying from completely awnless to fully awned were selected for future studies. In later crosses only a few of the more promising of certain derived lines, based on winter survival, awn type, head shape, and leaf rust resistance, were used.

Results of First Crosses

First crosses were made in the spring of 1948 with Cheyenne, Comanche, Pawnee, and Tenmarq hard red winter wheats. Viable crossed seeds were obtained only in the combination with Pawnee. Studies in advanced generations of this material led to the production of types with

[1] C.I. refers to the accession number of the Field Crops Research Branch, A.R.S., U.S.D.A. (Formerly Cereal Investigations).

wheat-like characters, leaf rust resistance (immunity), fair yield and test weight, but all had a soft grain texture unsuitable for bread-making. Even so, the successful transfer of leaf-rust resistance, one of the chief objectives, to wheat-like types was most encouraging, particularly since this had proved to be a major stumbling block in numerous previous experiments.

Additional crosses and backcrosses involving Comanche, Concho, Pawnee, Ponca and Westar, both with lines of the reselected *Triticum* sp.-*A. elongatum* and with selected *Triticum* sp.-*A. elongatum* X Pawnee lines, produced wheat-like, leaf-rust resistant types, but none was satisfactory for hard wheat milling and baking qualities. Also, studies involving inheritance of leaf rust resistance in segregating generations frequently showed non-Mendelian ratios with a segregation for wheat and *Agropyron* chromosomes rather than a normal gene segregation.

Triumph X *Triticum* sp.-*Agropyron elongatum*

Agronomic characters and Quality. Triumph C.I. 12132 is presently the most widely grown wheat in Oklahoma. According to the last (1954) wheat varietal survey conducted by U. S. Department of Agriculture (Salmon and Reitz, 1957), Triumph occupied 41.5% and 40.5% of the total wheat acreage in Oklahoma in 1949 and in 1954, respectively. Unofficial estimates by Oklahoma State University wheat research and extension workers and by wheat growers have been made since 1954. These indicate that at present Triumph is grown on from 60 to 65% of the total acreage. It is an early maturing variety, a much sought-after character by growers, and the grain produces a family type flour classed as mellow. In the higher protein ranges (13.5 to 16%) it produces a satisfactory flour for bakery bread if blended with strong gluten wheats. Since Triumph is the best available early-maturing, hard red winter wheat, it has been used in many wheat breeding programs, including the one with wheat-grass.

Triumph was crossed with a reselection of *Triticum* sp.-*Agropyron elongatum*, Kans. 464708, in 1950. In 1955 as an F_6, one hybrid head row, based on its uniformity of plant type and leaf-rust resistance, was harvested in bulk. In 1956 this strain was first grown in a preliminary yield and seed-increase plot at which time it again showed its uniform reaction to plant type and leaf-rust reaction. In 1958, in the F_7 generation, this strain, Stillwater Sel. 554494, C.I. 13523, was grown in a yield nursery of 3 replications on the Agronomy Farm, OSU. In this test of 22 varieties and strains, the average yield of all 22 entries was 33.5 bushels per acre and the range in yield was from 42.8 bushels for C.I. 13523 to only 15.6 bushels for Harvest Queen (Rosette Resistant). Triumph, the female parent of C.I. 13523, produced 37.6 bushels. No leaf rust pustules were produced on C.I. 13523, but Triumph showed 60% severity and 100% prevalence.

One criterion of bread quality is dough mixing time measured with a farinograph. A typical farinograph curve of Triumph wheat flour with medium to high protein content is presented in Fig. 1 which shows a desirable curve with much stability. A farinograph curve of C.I. 13523 grown in the same test with Triumph is shown in Fig. 2. It can be noted that these 2 curves are almost identical. Further, bread baked from these 2 flours produced almost identical loaves. These loaves, while somewhat deficient in volume, were otherwise acceptable.

The chief point of interest lies in the fact that, out of the literally thousands of selections of *Triticum* sp.-*A. elongatum* X different wheat varieties tested previously, C.I. 13523 is the first and only strain in which wheat-like characters, high leaf-rust resistance, high yield, and acceptable (Triumph-like) flour quality have been recombined in our program. All other similar strains or selections (produced by crossing wheat once, i.e., no backcrossing, with *Triticum* sp.-*A. elongatum),* which possessed high leaf-rust resistance, also possessed inferior bread quality. A farinograph curve representative of the extremely poor quality types is shown in Fig. 3, which illustrates, as an example, a selection from the cross Concho X *Triticum* sp.-*A. elongatum.*

CYTOLOGY

Review of Pertinent Literature

There are three taxonomic groups of wheat—the einkorns, the emmers, and the bread wheats. These groups have 7, 14, and 21 pairs of chromosomes respectively. Extensive research by various investigators has shown that wheats comprise an allopolyploid series in which the 7 pairs of chromosomes of the einkorns plus an additional set of 7 pairs constitute the 14 pairs of chromosomes of the emmer group. These 14 pairs plus an additional 7 pairs make up the complement of 21 pairs of the bread wheats. The various sets of chromosomes have been designated as the A, B, and C genomes (McFadden and Sears, 1947).

The genus *Agropyron,* which is taxonomically related to wheat, is a large and complex group of plants. As in *Triticum,* the species for which chromosome numbers have been determined, also form a polyploid series starting with a basic number of 7 chromosomes. The degree of polyploidy exhibited by this genus is greater than is the case with *Triticum,* extending to $2n = 70$ for one species (Sears, 1948). Within the genus a few species also exhibit a polyploid series. For example, *A. cristatum* is comprised of diploid, tetraploid, and hexaploid races (Aase, 1946). *Agropyron elongatum,* which frequently has been used in hybridization with wheat, also has forms with different chromosome numbers viz., $n = 35$ (Peto, 1930) and $n = 7$ (Simonet, 1936).

Many different species of *Agropyron* have been crossed with wheat, but the greatest success has been obtained with *A. elongatum* ($n = 35$), *A. glaucum* ($n = 21$), and *A. tricophorum* ($n = 21$).

Cytological studies of chromosome number and pairing relationships in *Triticum-Agropyron* hybrids were first reported by Vakar according to McFadden and Sears (1947). Similar studies were published about the same time by Peto (1936, 1939) and the conclusion was reached that they have at least one genome in common with the tetraploid and hexaploid wheats. Sears (1948) reviewed the whole problem of genome homologies in *Agropyron* and stated that no good evidence exists that the homoeology observed by various investigators does not involve chromosomes of the A and B genomes of wheat.

More recently Riley *et al.* (1958) considered both cytogenetic evidence and other researches involving hybrids of polyploid *Agropyrons* with tetraploid and hexaploid wheat. Since there has apparently been no character transfer from *Agropyron* to wheat, he stated that "the bulk of the evidence indicates that there is no genome in *Agropyron* closely related to a wheat genome."

Other cytological reports on parents, hybrids and derivatives have been made by Armstrong and McLennan (1944), Armstrong and Stevenson (1947), and Love and Suneson (1945), which illustrate the variable chromosome numbers that may be observed in *Triticum-Agropyron* hybrids.

Results of backcrossing onto either the F_1 or a line selection have been reported by several workers. Armstrong and Stevenson (1947) crossed some F_1 plants of Kharkov ($2n = 42$) X *A. elongatum* ($2n = 70$)

with hexaploid wheat and obtained F_1 plants with chromosome numbers ranging from 42 to 48 (2n). F_3 plants of the hybrid used in the backcross had 54 (2n) chromosomes. Thompson and Grafius (1950) studied the F_1 and two backcross generations of hexaploid wheat with *A. tricophorum* (2n = 42). The F_1 had 42 (2n) chromosomes while the backcross plants of several different lines had 63 chromosomes (2n). Second backcross plants from three lines had 46, 50, and 50 (2n) chromosomes respectively.

A similar reduction in chromosome number in hybrid derivatives obtained by backcrossing to wheat is shown in the work of Ohlendorf (1955), who studied the F_2 to F_9 backcross progenies of hybrids of hexaploid wheat with tetraploid *A. intermedium*. The backcross progeny were extremely variable in fertility, morphological characters and grain quality. Chromosome numbers ranged from 41 to 63 in the F_2 generation plants. Chromosome numbers tended to stabilize at 42 and 56 by F_6 - F_7 generation. Lines with other chromosome numbers survived, but they were considerably inferior in vitality to the two main groups. According to Ohlendorf's observations plants with many *Agropyron* characters possessed high chromosome numbers while those closely resembling wheat possessed a low chromosome number. Further, this worker reported that a substitution line with 2n = 42 chromosomes had been isolated.

Marshall and Schmidt (1954) studied the meiotic behavior of a number of *Triticum-Agropyron* hybrids in advanced generations. These authors reported that, although the material was fairly stable for disease reaction and morphological characteristics, the hybrids were generally highly unstable meiotically.

Cytological Observations on Hybrids at the Oklahoma Station

Cytological studies on some of the original *Triticum* sp.-*Agropyron* material as well as on early generation backcross derivatives of certain of these hybrids to wheat were made by the junior author in 1952-53 (Sebesta, 1953). These first observations were primarily concerned with the over-all meiotic stability of the hybrids, but in certain cases chromosome numbers were determined.

A few of the *Triticum* sp.-*A. elongatum* lines examined were found to have 42 (2n) chromosomes, or the same number as common wheat. These were, in general, predominantly wheat-like in character. Another derivative of similar origin was more grass-like. Plants of this hybrid had 49 (2n) chromosomes.

The backcross derivatives showed to a lesser degree the influence of the *Agropyron* parent and were found generally to possess 42 (2n) chromosomes. Occasionally plants with 41 and 43 (2n) chromosomes were observed.

Of particular interest were two lines of *Triticum* sp.-*A. elongatum* X Pawnee in the F_4 generation. These lines were very wheat-like in appearance and were highly resistant to wheat-leaf rust. One of these lines was stabilized at a chromosome number of 44 while the other had 42 (2n) chromosomes.

These observations and others relating to plant type and grain characteristics indicated that the excellent source of wheat-leaf rust resistance present in these hybrids could easily be utilized in developing resistant strains of wheat of the desired quality. However, this has not been the case as was pointed out previously.

The observation noted above that a rust-resistant line of Triumph X *Triticum* sp.*A. elongatum* was superior to other hybrid derivatives thus far developed, both in quality of the grain and in yield potential, prompted the determination of the chromosome number of this particular strain.

This was accomplished by cytological examination of root tips obtained from germinated seeds of the hybrid line. These observations revealed that this line has a somatic complement of 42 (2n) chromosomes, the same number as common wheat. The chromosomes as observed in Triumph (the wheat parent) are shown in Figure 4, and those of the hybrid in Figure 5.

Detailed cytogenetic analysis of this particular strain has been initiated with a two-fold purpose: (1) to determine, if possible, the cytological basis for the apparent combination of leaf rust resistance, high yield and good quality and (2) to determine whether or not the inheritance pattern of the genetic factors governing rust resistance in this material can be effectively used in wheat breeding by employing conventional plant breeding procedures. So far this has not been possible with another stable, 42-chromosome, resistant, hybrid line, the cytology of which is reported on in these meetings by Mr. Joginder Bakshi.

DISCUSSION

The results from the use of *Triticum* sp.-*Agropyron* derivatives as breeding stock, until the advent of C.I. 13523, have been disappointing. The failure to develop strains of wheat with combined leaf rust resistance, high yielding potential and high quality grain is related to the behavior of the chromosomes in the hybrids and its derivatives. Various published reports have shown that the chromosomes of wheat and Agropyron fail to pair. Therefore, the chance of getting a natural transfer of the genes governing rust resistance or any other desirable character from this material is remote.

The breeding procedures as followed in the development of the present hybrids have produced stable 42 and 44 (2n) chromosome resistant strains. These represent alien substitution and alien addition lines in which an *Agropyron* chromosome has been substituted in or added to the wheat complement. However, as Sears (1956) pointed out, such derived lines are likely to prove unsatisfactory from the practical point of view because so much genetic material has been introduced from the foreign species. This affords a logical explanation for the poor quality as observed in C.I. 13014, the 44 chromosome line, as well as in C.I. 13020, a 42 (2n) chromosome line.

However, another mechanism in reducing quality in the substitution lines may be in operation. This is related to the loss of the substituted wheat chromosome which may carry genes governing quality. Hence, in the substitution lines two different, but additive, processes may be responsible for the production of poor quality grains.

These processes may serve to explain the reason for the inferior nature of some of the hybrid lines, but we are faced with the question as to why another hybrid, presumably also an addition line with 42 chromosomes, should possess superior quality and high yield potential.

At present it is not known whether there are other *Agropyron* chromosomes carrying genes for leaf rust resistance which might not affect quality so adversely. Neither is it known whether or not certain of the chromosomes of the wheat complement can be substituted with less deleterious effect on quality. From the work of Sears (1954) with nullisomics and monosomics, one might suspect that this might be so.

Answers to these questions certainly would be valuable to the plant breeder. However, systematic cytogenetic studies of each of the possible

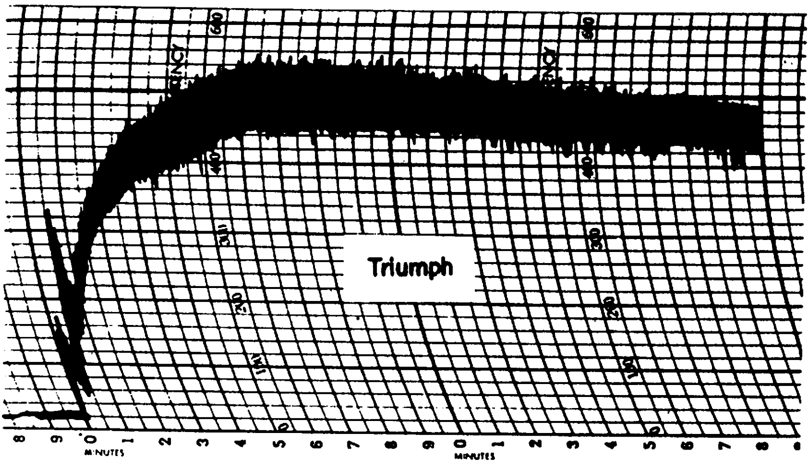

Figure 1. Farinograph curve of a dough made from Triumph wheat grown at Stillwater, Oklahoma in 1958.

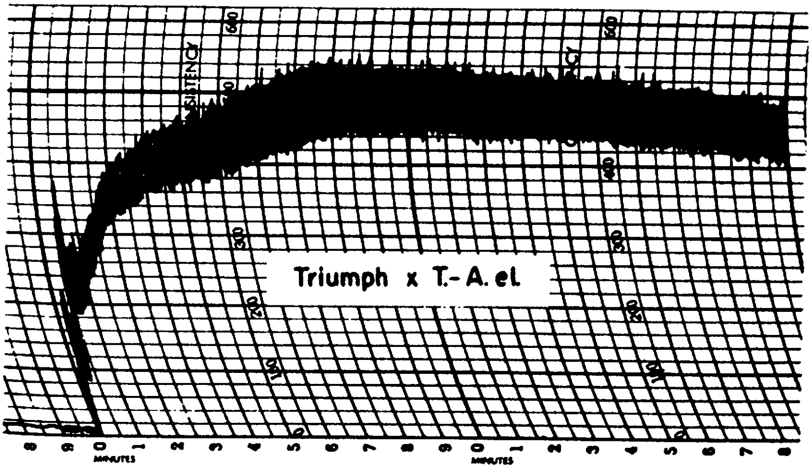

Figure 2. Farinograph curve of a dough made from Triumph X *Triticum* sp.-*A. elongatum* C.I. 13523 grown at Stillwater, Oklahoma in 1958.

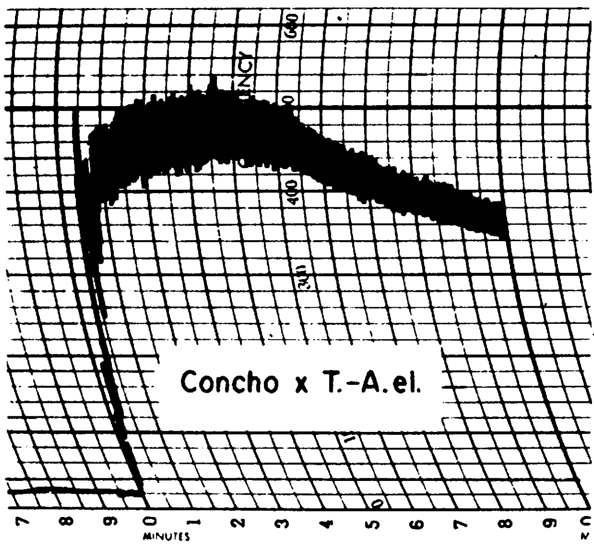

Figure 3. Farinograph curve of a dough made from Concho X *Triticum* sp.-*A. elongatum* grown at Stillwater, Oklahoma in 1958. Note short mixing time of this hybrid in contrast to the longer mixing times shown in Figs. 1 and 2.

Figure 4. Somatic chromosomes (2n = 42) from root tips of Triumph wheat. Alpha monobromonaphthalene pretreatment and Feulgen stain. 1500 X.

Figure 5. Somatic chromosomes ($2n = 42$) from root tips of Triumph X *Triticum* sp.-*A. elongatum* C.I. 13523. Treatment and stain same as in Figure 4. 1500 X. Differential shortening caused by pretreatment is responsible for apparent morphological differences of the two sets of chromosomes.

addition and substitution types possible with *Triticum-Agropyron* hybrids is a costly and time consuming procedure.

Perhaps a more economical and practical means of utilization of this material would be through the use of radiation to effect transfer of the genes for resistance from the hybrids already at hand to a wheat of good quality.

Such a method of transfer has been described by Sears (1956), who successfully transferred the resistance for leaf rust from a *Triticum-Aegilops* derivative to common wheat with the use of X-rays.

Work with certain of these hybrids is proceeding in two directions: (1) studies are underway to transfer the resistance from certain of these hybrids to wheat according to the method of Sears (1956) and (2) detailed cytogenetic studies of the good quality, 42-chromosome derivative.

Studies with this hybrid are designed to determine whether it represents an alien substitution line, or whether the genes for resistance have been transferred to the wheat complement. Although the probability of transfer is low it may be possible, since Ohlendorf (1955) reported that he found a *Triticum-Agropyron* line in which a small segment of *Agropyron* chromosome had replaced the corresponding segment of a wheat chromosome.

Concurrently a comparison of this line, should it prove to be a substitution, with another substitution line (C.I. 13020) will indicate whether the *Agropyron* chromosome in each are one and the same. Similarly, information may be obtained as to whether or not the same wheat chromosome has been replaced in the respective lines.

It is hoped that these studies will shed some light as to why this particular line alone, among so many others, reflects an apparent recombination of rust resistance with high yield and quality potential.

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