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CYTOLOGICAL OBSERVATIONS OF THE F_1 AND TWO BACKCROSS GENERATIONS OF T.VULGARE X AGROPYRON SPP.

By

Donald L. Thompson

SOUTH DAKOTA STATE COLLEGE

A thesis submitted to the faculty of South Dakota State College of Agriculture and Mechanic Arts in partial fulfillment of the requirements for the degree of Master of Science.

March 1949

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ACKNOWLEDGMENT

The author wishes to extend his sincere appreciation to Dr. J. E. Grafius for the helpful suggestions and valuable guidance in the pursuance of this investigation. Also the assistance given by Dr. W. L. Miller is gratefully acknowledged.

This is to certify that, in accordance with the requirements of South Dakota State College for the Master of Science Degree, Donald L. Thompson has presented to this committee three bound copies of an acceptable thesis, done in the major field; and has satisfactorily passed a two-hour oral examination on the thesis, the major field, Agronomy, and the minor field, Botany.

Head of Major Department

March 24, 1949
Date

Head of Minor Department

Rep. of Graduate Committee

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INTRODUCTION

Interspecific and intergeneric crosses have been widely used in the improvement of Triticum vulgare Vill. Especially noteworthy are the interspecific crosses between T.vulgare and T.dicoccum Schrank., var. Yaroslav and between T.vulgare and T.durum Desf., var. Iumillo. The progeny from these two crosses, Hope and Marquillo, respectively, have been widely used as sources of stem rust resistance, Puccinia graminis tritici E. & H. Another interspecific cross, T.vulgare x T.timopheevi Zhuk. has produced promising results by having resistance to stem rust and other pathogens. The classic work of Sears and McFadden in tracing the origin of common hexaploid wheat is also illustrative of the use of intergeneric and interspecific crosses. Many programs have been organized involving Triticum-Agropyron hybrids, but as yet commercially important progenies have not been released.

The crosses between T.vulgare and Agropyron spp. offer tremendous possibilities as a means of improving winter wheat by increasing its winterhardiness, drought resistance, and disease resistance. It is also possible that a perennial type may be developed from the cross of these two genera.

Cytological information of this type would be valuable in ascertaining the number of backcrosses to make and in using the various progenies for the continuation of the breeding program.

This cytological study was undertaken to (1) obtain basic knowledge of these two genera and observe the chromosome compatability in the F_1, and (2) to note the trend and the rate of return toward chromosomal stability in the subsequent backcross generations. As this study was necessarily limited to the parent plants, the F_1's, and two backcross generations, complete chromosomal stability was not reached.

LITERATURE REVIEW

The first successful attempts at hybridizing wheat and Agropyron spp. were made by Tzitsin of the U.S.S.R. in 1930(1). His chief aim was the production of a perennial wheat. Further reports by Smith(15) state that Tzitsin obtained crosses with A.glaucum Desf., A.trichophorum Link., A.elongatum(Host) Beauv., and A.junceum(L.)Beauv. The A.elongatum hybrids had vigorous root systems and were resistant to rust, smut, mildew, cold, and drought. Many plants were of perennial type and increased in yield in later generations.

The Canadians were next to attempt these crosses and their program was initiated in 1935 at the Central Experimental Farm, Ottawa as reported by Armstrong(1). The production of a heavy seeded forage crop was one of the aims. Projects now are under way in the United States, South Africa, and Australia designed to develop both heavy seeded forage types and improved wheat varieties. Many of the Agropyron spp., but mainly A.glaucum and A.elongatum, have been used in crossing programs with wheat. T.vulgare-A.trichophorum hybrids (the type crosses used in this study) have been reported by Smith(15), Suneson and Pope(17), Love and Suneson(7), and White(18).

T.vulgare has been successfully crossed with A.elongatum, A.glaucum, A.intermedium(Host.) Beauv., A.trichophorum(Link.) Richt., A.cristatum(L.) Gaertn., and A.repens (L.) Beauv. (1)(6)(15)(17)(18).

Failures were reported in crosses involving A.caninum(L.) Beauv., A.ciliare(Trin.) Franch., A.dasystachyum(Hook) Scribn., A.pungens(Pers.) Roem. and Schult., A.semicostatum(Steud.) Nees., A.sibiricum (Willd.) Beauv. A.smithii Rybd., A.spicatum(Pursh.) Scribn. and Smith, A.trachycaulum (Link.) Malte., A.subsecundum(Link.) Hitchc., A.desertorum(Fisch.)Schult., and A.obtusiusculum Lange. (1)(6)(15)(18).

Varying degrees of success has been experienced in obtaining successful crosses and in the germination of this seed. The usual F_o seed-set has varied from 0 - 20%; however, unusual cases have been reported in which as high as 70% of the florets pollinated produced seed(18). Varieties of wheat vary in their cross compatability with an Agropyron spp., and conversely, different strains of an Agropyron spp. vary in their crossability with a variety of wheat. Germination of the F_o seeds has generally been good with instances of germination in excess of 90%. Poor germination followed by the death of many of the seedlings has been reported; however, in some instances, the addition of a glucose solution to the germinating tray has helped the survival rate of the seedlings(6). The absence of embryos in the seed has been one cause of poor germination. A correlation of germination percentage with seed weight has also been reported.

Phenotypic characters of the F_1's have been generally dominantly Agropyron with some characters intermediate or exhibiting Triticum dominance(1)(6)(17)(18). Some of the dominant Agropyron characters noted are rootlet number, coleoptile color, susceptibility to ergot, perennial habit, glume adherence, waxy bloom, leaf posture, and the period from spike emergence to anthesis. Several of the intermediate characters reported are spike density, leaf margin pubescence, glume width, leaf width, and leaf scabrousness. Triticum dominance has been expressed in the secondary glume character, auricle color, leaf hairiness, and barbs on the keel.

Perennial character, as observed by Armstrong and Stevenson(3) was well fixed in advanced generations, and this perennial nature appeared to be conditioned by a multiple series of dominant genes. In many lines of these Vernal x A.elongatum crosses, plants attained fair uniformity for many spike characters in the F_5. Meiotic behavior of the F_1 and the F_5 showed

a trend toward chromosome stabilization and complete and regular pairing. Backcross results indicated that lines showing wheat characters also possessed mostly wheat chromosomes.

A complete absence of rust was noted by White(18) in the F_1, F_2, F_3, and F_4 generations of intergeneric crosses of wheat and A.glaucum or A.elongatum during periods of severe leaf and stem rust epidemics. However, during seven generations, both homozygous and heterozygous reactions for several types of rust resistance have been observed by Suneson and Pope(17) in crosses involving various species of Triticum crossed with A.trichophorum and A.elongatum. Rust resistance varied from susceptible to resistant. Perennial strains having the gluten properties of wheat yielded 60% of wheat during the first season; however, the yield of these decreased by more than one-half the second year.

Although self-sterility is the general rule in the F_1's, a small amount of self-fertility has been reported (1)(6)(18). Fertility occurring as a result of the union of unreduced or partially reduced gametes or by the natural or artificial production of amphiploids have also been reported (2)(7)(12)(17). The self-sterility in the F_1 is accompanied by a lack of complete pairing at meiosis, a large number of micronuclei in the quartet stage, and a low percentage of normal pollen which prevents dehiscence (1)(3)(6)(7)(11)(12)(18).

One partially fertile F_1 (an A.elongatum cross) was observed to have 50-60% normal pollen, whereas the sterile F_1's had only 5% normal pollen. An example of comparatively good fertility was reported in which over one-third of 113 F_1 plants (A.elongatum crosses) possessed some degree of fertility during one year's growth(1).

The F_1 of a Vernal x A.glaucum cross (2N=35)(12) averaged 6.2 bivalents, 20.4 univalents, and 0.8 trivalents and had only 2% normal pollen, which did

not dehisce. Colchicine treated F_1's developed into amphiploids (2N=70) which had 92-97% normal dehiscent pollen and set seed in 77% of their florets. Expectations of observing 35 bivalents in these amphiploids were not realized as the five amphiploid F_2 plants examined averaged only 27 to 30 bivalents.

A few seeds were observed during six years growth in the F_1's (2N=42) of two A.trichophorum strains crossed with T.macha(7), but these were thought to be crossed rather than selfed seeds. Cytological examinations revealed 7.7 bivalents, 22.6 univalents, and some multivalent association. An average of 2.11 micronuclei was observed per quartet. Several fertile derivatives had a double complement of chromosomes, but bivalent associations were different from that expected in a true amphiploid. They were thought to be the product of random fertilization of partially reduced or unreduced gametes.

These same two strains of A.trichophorum crossed with T.durum, set 33 seeds during six years growth. From the one strain the F_1's averaged 1.6 bivalents and 31.8 univalents. An average of 3.35 micronuclei were observed per quartet. The F_1's from the other strain averaged 6.1 bivalents and 20.2 univalents plus some multivalent associations. An average of 2.31 micronuclei was observed per quartet.

Another typical example of low pairing relationship is found in a Kharkov x A.glaucum cross (2N=42)(11) which had 5.6 bivalents, 30.0 univalents, and 0.01 trivalents, again indicating a partial homology with one genome of wheat.

Pollen studies (6) indicated that field grown plants had a higher pollen fertility than greenhouse plants. It was also observed that pollen dehiscence was correlated with the ratio of normal pollen to

aborted pollen; and seed-set was correlated with the percentage of normal pollen, providing dehiscence occurred.

Pollen and micronuclei observations have been used extensively as a criterion of chromosomal stability. It is known that temperature and weather conditions at the time of collection can affect these observations and result in considerable variation even within lines. However, Semeniuk (14) found the correlation between certain meiotic abnormalities with micronuclei and aborted pollen high enough to conclude that these could be used to indicate chromosomal instability and to identify highly abnormal plants. However, certain cases were observed in which high frequencies of abnormalities at meiosis were accompanied by a low percentage of normal pollen. He concluded that pollen sterility could be used to eliminate unstable plants and then the number of micronuclei could be used as a final check.

MATERIALS AND METHODS

One winter wheat variety and two Agropyron spp. were used in this study.

Triticum vulgare variety Minter is a winter wheat. This variety was derived from a cross of Hope x Minturki, backcrossed to Minturki. It is winter hardy, stem rust resistant, moderately susceptible to leaf rust, and has good milling qualities. It was released jointly by the U.S.D.A. and the Minnesota and South Dakota Agriculture Experiment Stations in 1948 and is one of four winter wheat varieties presently recommended for South Dakota.

Agropyron trichophorum (Link) Richt. is an erect perennial with creeping rhizomes; culms glabrous, 30-40 inches tall; sheaths glabrous; blades flat, hirsute on both surfaces; spike erect, 4-18 inches long;

spikelets 15-20 mm. apart, 15-20 mm. long, 5-8 flowered, glumes hispid; lemmas hispid, abruptly mucronate; palea about as long as lemma, evenly hispid-ciliate. It is quite variable in habit, varying from short to tall, and from coarse to slender. This species is drought resistant, stiff stemmed, and disease resistant. It is native to the steppes and mountain slopes of eastern Europe, central Asia, the Caucasus, and Asia Minor. It was introduced into this country by the United States Department of Agriculture.

Ree Wheatgrass(4) is an erect perennial with abundant slender rhizomes; culms 30-40 inches high; sheaths glabrous; blades flat, glabrous on lower surface, villous on upper; spike erect to slightly nodding, lax, 6-14 inches long, spikelets 15 to 20 mm. long, 6-8 flowered; glumes abruptly subacute; lemma ciliate, some awned others awnless or nearly so; palea shorter or equal in length to lemma. Considerable variation in minor characters exists in this variety. It was developed by C. J. Franzke from a plant introduction (P.I. 98,568, from the Maikop regions of Russia) of the United States Department of Agriculture, Bureau of Plant Industry. Material collected in July, 1941 was classified by J. R. Swallen, U. S. D. A., B. P. I., as a combination cross of Agropyron intermedium and Agropyron trichophorum.

T. vulgare, var. Minter was used as the female in the first cross because it was easy to emasculate; partial self-sterility evident in some Agropyron plants was not a factor; the main florets of the spike mature at about the same time; and a large number of plants were available. Pollen was secured from various plants in the Agropyron plant selection nursery. These plants differed somewhat in observable characters, but all were vigorous, stiff stemmed, erect, and were shedding abundant pollen.

Crossing was accomplished by emasculating, waiting two days, and

pollinating daily for three consecutive days. This method of using three pollinations was followed in making the first cross and the first backcross.

The custom of writing the female of a cross first is used throughout. T.vulgare x Agropyron trichophorum and T.vulgare x Ree Wheatgrass are the F_1's. F_1 x T.vulgare, the first backcross generation, is abbreviated BC-1. (F_1 x T.vulgare) x T.vulgare, the second backcross generation, is abbreviated BC-2. (F_1 x T.vulgare) selfed plants are abbreviated BC-1 Self. No backcross seeds were obtained in crossing attempts with F_1's of T.vulgare x Ree Wheatgrass. As backcrosses were only obtained from one group of F_1's (T.vulgare x A.trichophorum #4), it is unnecessary to differentiate the backcrosses other than by the F_1 plant number in their parentage. Backcross lines are referred to by the F_1 plant number in their parentage, i.e., Line 9 is those plants derived from F_1 9. Where two backcross lines were derived from a single F_1 plant, the letters A and B were added to differentiate the two lines.

To speed the program, seeds planted in the greenhouse and in the field in the spring were vernalized as described by Peltier and Kisselback(9). This consisted of germinating the seeds and then storing them at 35°F for at least 30 days before planting.

Plants started in the greenhouse were later transplanted to the field. Some plants were returned to the greenhouse for the winter study. When it was desirous to increase the number of plants, the tillers were separated and planted in individual pots.

The percentage of normal pollen was determined by staining the pollen grains with iodine-potassium iodide (13). Anthers were selected at the time of pollen dehiscence and observed immediately or were stored in 70% ethyl alcohol for future observation. The anthers were macerated

on a slide in the reagent, the anther wall removed, the cover glass added, and the observations made. Normal pollen grains were those in which one-half or more of the grain was stained dark blue or black, indicating the presence of starch.

The acetocarmine smear technique of pollen mother cells was used for making cytological observations(16). Although temperature and weather conditions affect cell division, entire spikes collected in the following period of development were generally at the correct stage of division for good observations:

T.vulgare	very early boot stage
A.trichophorum	4-5 spikelets extending above the collar of the boot
Ree Wheatgrass	6-8 spikelets extending above the collar of the boot
F_1 plants	3 spikelets extending above the collar of the boot
BC-1 and BC-2 plants	quite variable but usually early to late boot stage

Material collected for smears was fixed in Carnoy's Fluid A and stored in the fixative at room temperature. Most of this material was still in excellent condition after being stored for a year. Some of the material was killed and fixed for two days in Carnoy's A, then transferred to 70% ethyl alcohol for storage. This gave about the same results as that which was stored directly in the fixative.

Acetocarmine stain was prepared as directed by Smith (16). This solution was diluted as follows: 1 part acetocarmine with 2 parts 45% acetic acid. Smears were made in the usual manner by placing the three anthers of a floret on a slide and macerating them in the stain.

A satisfactory water soluble, temporary slide seal was used to preserve slides for later examination. This seal (16) containing water, glycerin, gum arabic, and chloral hydrate was placed around the edge

of the cover slip and was entirely satisfactory, providing the humidity stayed below 50%.

Temporary slides were made permanent by the method developed by Sears which is presented in Smith's paper (16). The temporary seal was chipped off with a razor blade, the cover slip soaked off in an acetic acid-ethyl alcohol solution, and the mount treated with various concentrations of tertiary butyl alcohol and remounted in balsam.

Observations were made to determine the pairing relationship of the various plants, percentage of normal pollen, number of micronuclei per quartet, and the number of laggards at metaphase I and anaphase I. Pairing observations were made at diakinesis whenever possible. The percentage of normal pollen was determined by the proportion of pollen grains staining dark blue or black in IKI to those not stained, Fig. 1. Micronuclei, which usually result from lagging chromosomes or from supernumary nuclei in the anaphse II division, were observed in the quartet stage, Fig. 2. Laggards at metaphase I were mainly univalents which were slow to orient themselves on the plate, Fig. 3. Laggards at anaphase I are mainly univalents which are slow in being drawn to the poles, Fig. 4.

Photomicrographs were made on Commercial Ortho or Contrast Process Panchromatic film, using a Wratten B filter No. 58 in front of the light source. Development was with Kodak Dektol developer. Camera lucida drawings were used for recording and interpreting observations.

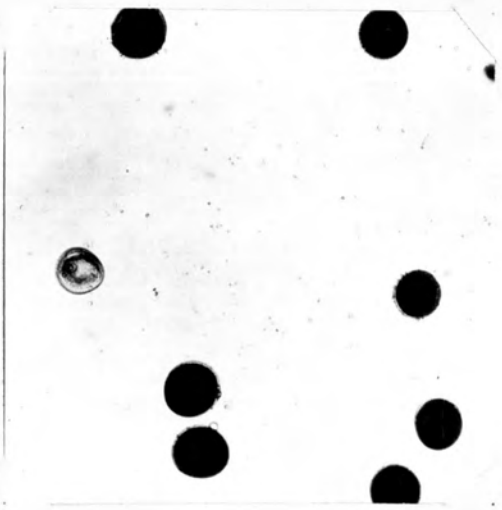

Fig. 1. Normal pollen stained by IKI and one aborted pollen grain not affected by the stain. X450.

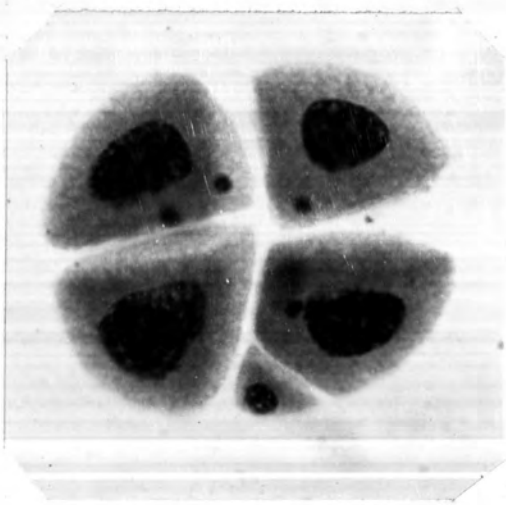

Fig. 2. BC-1. Quartet showing presence of micronuclei. X980.

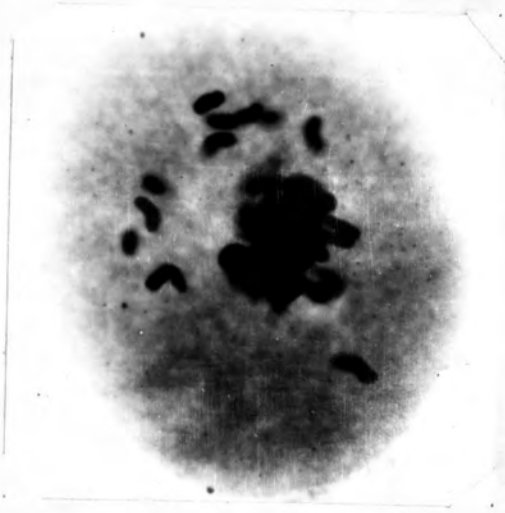

Fig. 3. A metaphase I cell containing lagging chromosomes. X 980.

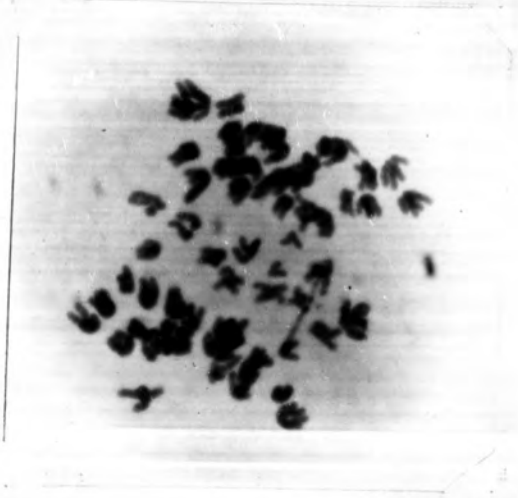

Fig. 4. BC-1. An anaphase I cell showing lagging chromosomes and one bridge. Several of these lagging univalents are splitting. X980.

EXPERIMENTAL RESULTS

F_o Seed

T.vulgare, var. Minter, was crossed with Ree Wheatgrass and various plant selections of A.trichophorum.

The F_o seeds obtained are listed in Table I.

Table I: Total seeds and number of hybrid seeds obtained from crosses of T.vulgare x indicated Agropyron spp.

AGROPYRON PARENT	No. spikes which set seed	Av. No. seeds per fertile spike	Total Seeds No.	Hybrid Seeds No.
Ree Wheatgrass	12	3.5	42	14
Agropyron trichophorum #2	2	1.0	2	0
Agropyron trichophorum #4	10	5.8	58	50
Agropyron trichophorum #5	15	2.9	43	23
Agropyron trichophorum #6	2	1.0	2	0
Agropyron trichophorum #7	6	2.0	12	10

Not all spikes which were pollinated produced seed, and many of the seeds obtained were Minter selfs. The crossing technique of removing the covering sack daily for 3 consecutive days, in order to pollinate, allowed wind blown pollen a chance to enter. Germination of these seeds was quite good. Of 91 surviving plants from 102 seeds, 38 proved to be Minter selfs. Several very abnormal, short lived plants were observed in the seeding stage.

A.trichophorum #4 not only gave greater cross-fertility according to the number of seeds obtained and number of seeds per spike, but also fewer selfs appeared when the seeds were grown.

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F_1 Generation

The F_1 plants were generally intermediate to the wheat and the Agropyron parents. Some of the characters were dominantly Agropyron. A photograph of spikes of the F_1 and the parents is presented in Fig. 5. Perennial in nature, the F_1's were successfully grown in the field for two years. During the winter, several of the plants were removed to the greenhouse where they grew vigorously and produced many spikes. They are less rhizomnous than the Agropyron parents; however, new shoots were continuously produced until late summer. This resulted in a bunch type plant.

Approximately one-fourth of the F_1 plants were dwarf type (12 inches or less), one-fourth were medium in height (12 to 24 inches), and one-half were tall (24-36 inches or taller). Some dwarf plants failed to produce spikes and several of these died as a result of a severe rust infestation. Approximately one-half of the overwintering plants in the field failed to survive until the following spring. In most instances the taller, more vigorous plants gave the highest survival rate.

The leaf and glume pubescence of the Agropyron parent was evident in all F_1's. Spike density was intermediate to the parents. Awns were lacking.

Of all F_1 plants, about one-half exhibited evidence of leaf rust. The infestation varied from a trace to 70% on individual plants. Those F_1's having A.trichophorum #4 in their parentage, varied from a trace to 10%. Only one plant of seven, having Ree Wheatgrass as the Agropyron parent, developed rust and this was classified as 2% of type 2 rust. A rather severe ergot infestation developed both summers in the field.

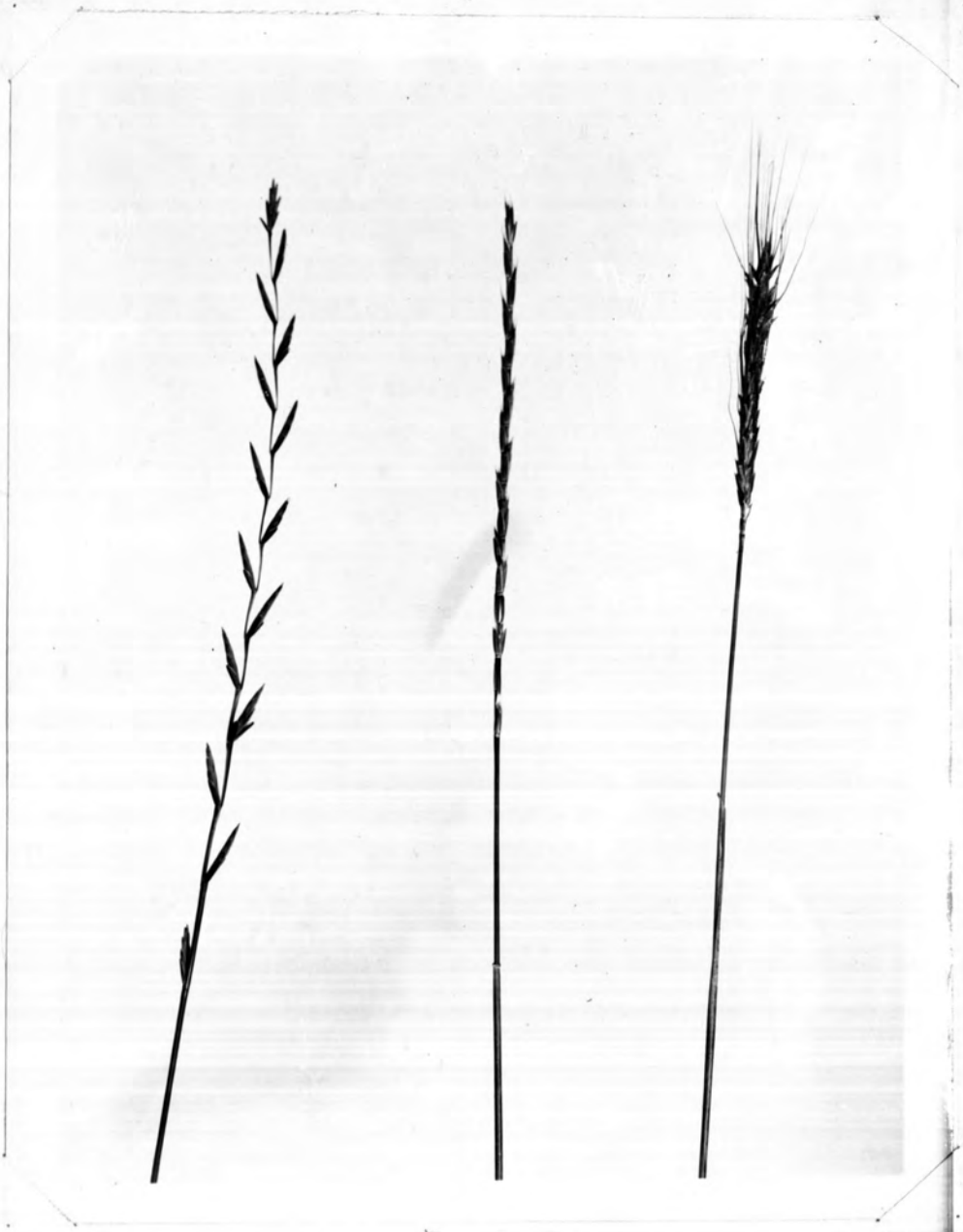


Fig. 5. Spike of T. vulgare x A. trichophorum hybrid and parents. Left to right, A. trichophorum #4, F_1 hybrid, and T. vulgare, Variety Minter. Approximately 2/5 actual size.

The plants are entirely self-sterile as evidenced by the fact that no selfed seeds were observed during two years of continuous growth. Pollen dehiscence was observed in only three F_1 plants.

By using T.vulgare as the pollen parent, several backcross seeds were obtained. In this program F_1 plants having different Agropyron parents were pollinated. It soon became evident that backcross seed was being obtained only on those F_1's having A.trichophorum #4 as their Agropyron parent. Subsequent crossings were concentrated on these plants. Under field conditions only one-half of the plants pollinated produced seed. Other evidence of varying backcross fertility is shown by the fact that two plants yielded over one-half of the seeds obtained. The usual seed-set was one seed per spike (approximately 25 florets pollinated); however, not all spikes pollinated produced seed. Thirteen backcross seeds were obtained in the greenhouse, and forty were obtained during the summer after the plants were removed to the field. The ergot infestation also affected the number of normal seeds obtained. The backcross seeds were larger than the F_0 seeds or those of either parent.

BC-1 Generation

The BC-1 plants were also perennial and were grown for a year in the greenhouse and field where they continuously sent up new shoots and produced spikes and had only short periods of dormancy. Their height varied from 24 to 36 inches. There were a few of the dwarf type but most of them were tall and vigorous. Pubescence, which was evident on the glumes and leaves of the F_1, occurred on all BC-1 plants. Spikes, more dense than the F_1's, varied from awnless to fully awned.

Ergot and leaf rust also appeared in this generation; however, the late transplanting to the field prevented accurate observations on the percentage of leaf rust.

Self-fertility varied from near 100% to almost sterile. Using wheat as the pollen parent, BC-2 seeds were obtained quite easily. Here again, plants varied in crossing fertility. The seeds secured were smaller than those of the previous generation.

Selfed seeds obtained from these BC-1 plants in the greenhouse were vernalised and planted in the field. These resulting plants were perennial and varied in height from dwarf non-vigorous to tall (30 inches) vigorous types. Pubescence occurred on the glumes and to a lesser extent on the leaves as compared to the parent, BC-1. Spike density was similar to that of the parent. As these seeds were planted in the field very late, the extreme hot weather during flowering may have accounted for the absence of fertility.

BC-2 Generation

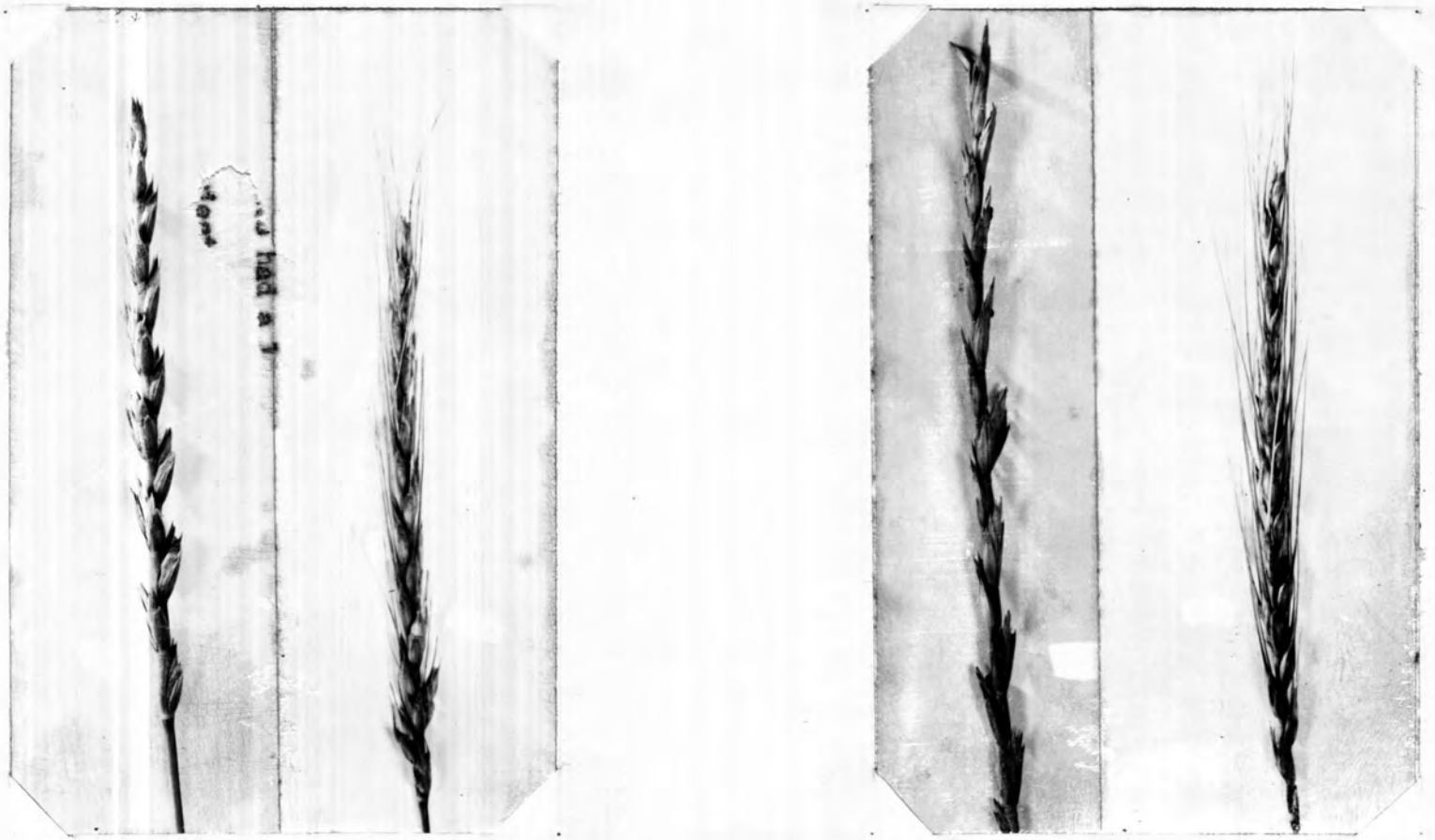
The plants of the second backcross generation were perennial and produced many shoots and spikes during the summer and again when transplanted to the greenhouse. They were generally equal to or a little shorter in height than their female parent, BC-1.

Pubescence on leaves and glumes varied from none to as much as in the F_1 generation. Spike density approached that of the wheat parent, and the plants varied from awnless to fully awned as in the wheat parent.

These plants ... late start in the field and matured during the hottest and dr... part of the summer; therefore, good observations of their fertility could not be made. Self-fertility and fertility with wheat pollen (for BC-3), nevertheless, were quite good.

This generation, BC-2, showed considerable evidence of an approach to the recurrent parent, T.vulgare, in the following characters: Spike density, absence of pubescence, awns, self-fertility and stem type.

A comparison of spikes of BC-1 and BC-2 is shown in Fig. 6 and 7.



BC-1 BC-2 BC-1 BC-2

Fig. 6. Spikes of first and second backcross of T. vulgare x A. trichophorum with T. vulgare as the recurrent parent. Left to right in each picture, Backcross 1 and the Backcross 2 offspring.

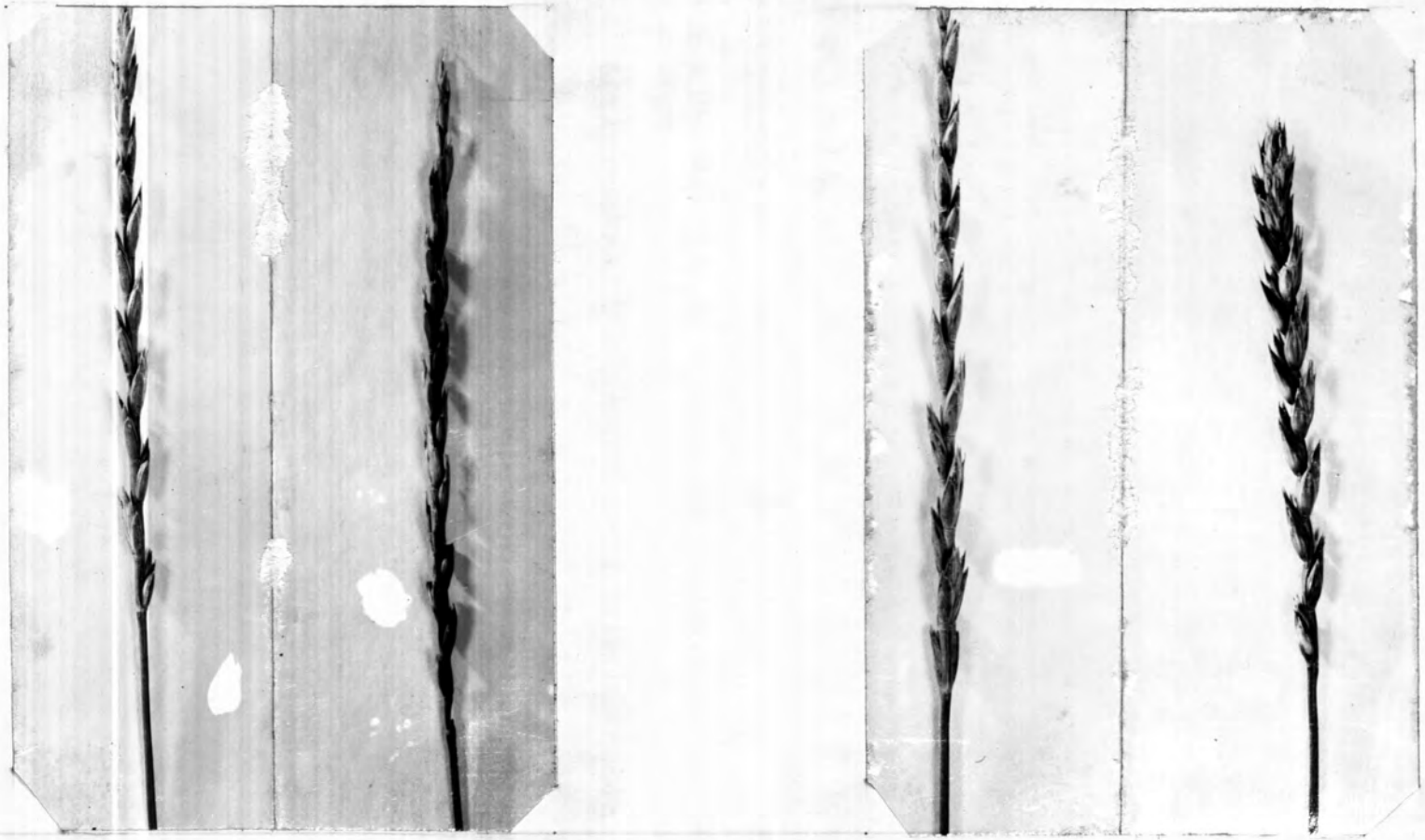


Fig. 7. Spikes of first and second backcross of T. vulgare x A. trichophorum with T. vulgare as the recurrent parent. Left to right in each picture, Backcross 1 and the Backcross 2 off spring. Approximately 2/3 actual size.

Cytological Observations of the Parents

Cytological observations were made of the chromosome number, percentage normal pollen, number of micronuclei per quartet, and the number of laggards at metaphase I and anaphase I.

These cytological observations of the parents are presented in Table II.

Table II: Average percentage normal pollen, number of micronuclei per quartet, and number laggards at metaphase I and anaphase I as observed in the parents.

Parent	Chromosome No.	Normal Pollen %	Micronuclei per quartet	Laggards per cell	
				Metaphase I	Anaphase I
Ree Wheatgrass	42	84.2	0.30	0.90	1.90
A.trichophorum #4	42	79.8	0.13	0.22	0.39
A.trichophorum #5	42	87.2	0.08	0.10	0.11
A.trichophorum #7	42	93.0	2.20	2.00	1.30
T.vulgare, var. Minter	42	96.9	0.04	0.04	0.28

T.vulgare shows the greatest stability, having the highest percentage of normal pollen and with one exception the lowest number of abnormalities as indicated by the observations of micronuclei and laggards. This one exception is that A.trichophorum #5 had the fewest laggards at anaphase I. The Agropyrons exhibit less stability than the wheat, but these differences do not account for their varying cross-fertility with the wheat or the different backcross fertility of their F_1 progeny.

A.trichophorum #4, which crossed most readily with wheat, was the only Agropyron which produced F_1's that were backcross fertile, yet it had the lowest percentage of normal pollen.

Pollen observations of F_1's

Pollen fertility of the F_1's, as indicated by the percentage of normal pollen, was grouped and averaged according to the Agropyron parent of the cross. As only F_1's of A.trichophorum #4 gave backcross seed, it was thought that pollen observations would give some indication of the relative fertility of the four groups. The observations are presented in Table III.

Table III: The average percentage normal pollen of F_1 plants grouped according to Agropyron parent.

Agropyron Parent	Plants observed No.	Normal Pollen %	% Normal Pollen Range	Standard Deviation
Ree Wheatgrass	4	3.4	0.2-8.1	3.41
A.trichophorum #4	24	16.4	3.2-35.2	9.46
A.trichophorum #5	9	5.2	0.7-11.7	3.84
A.trichophorum #7	1	4.4	----	—

Offspring of A.trichophorum #4 had a higher average percentage of normal pollen than the other F_1 groups. The F_1 plant with the highest percentage of normal pollen of all plants occurred in this group. Also the average of this group exceeds the maximum percentage of normal pollen observed in any of the other three lines.

Pollen fertility, as indicated by observations of normal pollen, is highest in the backcross fertile group of F_1's — those from A.trichophorum #4. The F_1's in the other three groups have a very low pollen fertility, and all attempts to obtain backcross seed in these three groups failed. Thus, these pollen observations did differentiate between the group which was backcross fertile and those which were not backcross fertile. However, the percentage of normal pollen was not well correlated with backcross fertility of individual plants in this backcross fertile group. Some plants having

less than 10% normal pollen were noted to be more backcross fertile than plants having over 25% normal pollen. However, ergot infestation and the small number of plants pollinated undoubtedly influenced these observations. The most backcross fertile plant had 8.3% normal pollen. The success obtained in these backcrossing attempts was 0-12% seed-set in the florets pollinated.

Generation Trends - Cytological.

Cytological observations of 3 F_1 plants and 6 BC-1 and BC-2 plants are compared to note the trend effected by backcrossing. Averages of these observations are presented in Table IV and are presented graphically in Figure 8.

Table IV: Average percentage normal pollen, number of micronuclei per quartet and number of laggards at metaphase I and anaphase I as compared in the F_1 and the two backcross generations.

	No. of Plants	Normal Pollen %	Micronuclei per quartet	Laggards	
				Metaphase I	Anaphase I
F_1	3	11.4	4.3	7.9	12.5
BC-1	6	57.6	8.5	7.0	11.1
BC-2	6	62.3	2.4	3.4	6.4
L.S.D. at 5% level		4.2	2.2	3.5	3.5

It will be noted that the percentage of normal pollen increased with each backcross generation, and the number of lagging chromosomes decreased as indicated by observations at metaphase I and anaphase I. The average number of micronuclei per quartet increased in BC-1 and decreased in BC-2.

It is difficult to explain the large number of micronuclei present in BC-1 as compared to the F_1 generation. It should be pointed out, however, that there are two facts which may have a bearing on this, (1) the increase

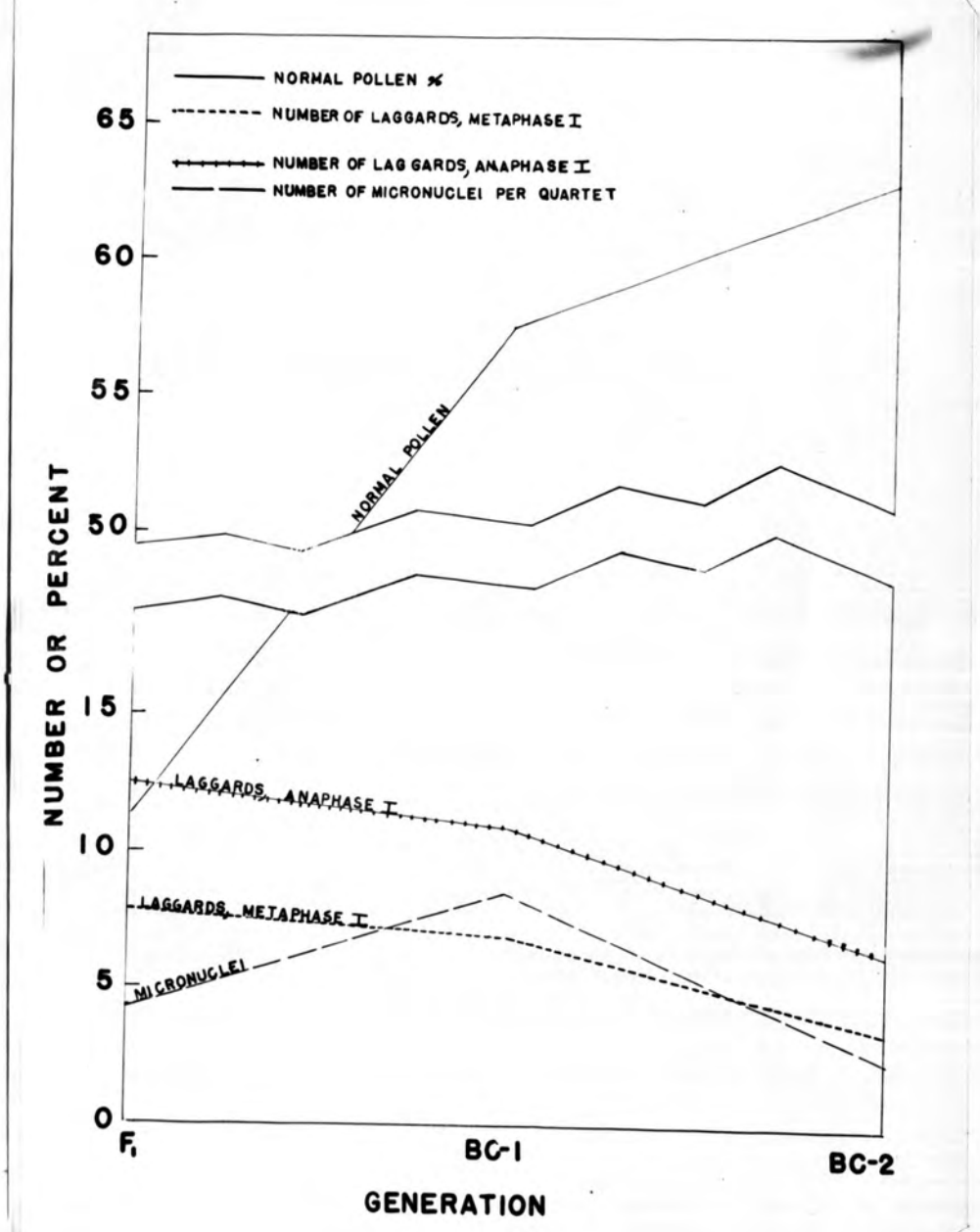


Fig. 8. The average percentage normal pollen, number of micronuclei per quartet, and number of laggards at metaphase I and anaphase I observed for 3 generations: F_1, BC-1, and BC-2.

in chromosome number in BC-1 and (2) the presence of two complete complements of T.vulgare chromosomes in BC-1.

The 63 (2N) chromosomes in BC-1 (as compared to 42 in F_1) are undoubtedly the result of an unreduced egg being fertilized when the backcross was made. The number of lagging chromosomes observed in anaphase I in both generations were approximately equal, but the total number of chromosomes had increased greatly in BC-1, and this may have interferred with the inclusion of these lagging chromosomes in the second division nuclei.

Also, two complete complements of T.vulgare chromosomes are assumed to be present in BC-1, and it is further assumed that the division of these chromosomes occurs normally and is completed quickly thereby preventing many of the lagging chromosomes from being included in the nuclei of the second division.

The type of univalents in each generation may also have some bearing on the number of micronuclei observed. In the F_1 the univalents are thought to be made up of half T.vulgare chromosomes and half A.trichophorum chromosomes, while in BC-1, two complete complements of wheat chromosomes are present and the univalents are assumed to be of A.trichophorum origin.

The data were analyzed to secure a statistical interpretation of the generation differences. The summaries of the analysis of variance conducted on these observations, represented in Table 4 as averages, are presented in Tables V and VI.

Table V: Summary of analysis of variance of normal pollen and number of micronuclei per quartet as calculated on the F_1's and two backcross generations.

Source of Variation	df	Pollen Fertility Percent mean square	No. Micronuclei per quartet mean square
TOTAL	14	———	———
Between Generations	2	2858.094**	57.138**
Within Generations	12	88.242	2.334

** Exceeds the 1% level

Table VI: Summary of analysis of variance of number of laggards at metaphase I and anaphase I as calculated on F_1's and two backcross generations.

Source	df	Mean Square
TOTAL	29	———
Between Generations	2	77.945**
Between Phases	1	105.657**
Error	26	1.933

** Exceeds 1% level.

Highly significant differences were obtained between generations for all observations: percentage normal pollen, number of micronuclei, and number of laggards at metaphase I and anaphase I.

Observed and Theoretical Backcross Affect

Theoretically, backcrossing should decrease chromosomal abnormalities by one-half for each generation. Because BC-1 was produced by the fertilization of an unreduced egg, this theoretical halving of chromosomal abnormalities was not true in the first backcross generation as compared to F_1. However, an inspection of the data indicated that the chromosomal abnormalities were approximately halved in BC-2. A Chi Square analysis was made to test

the closeness of fit of these data (BC-1 and BC-2) to this theoretical 2:1 ratio. The observed abnormalities are presented and compared with the theoretical values in Table VII.

Table VII : Observed average percentage normal pollen, number of micronuclei and number of laggards at metaphase I and anaphase I of BC-1 is compared with BC-2 on the theoretical 2:1 ratio expected by backcrossing.

	Normal Pollen %		Micronuclei per quartet		Laggards Metaphase I		Laggards Anaphase I	
	Obs.	Theo.	Obs.	Theo.	Obs.	Theo.	Obs.	Theo.
BC-1	57.6	40.0	8.47	7.23	6.97	6.89	11.07	11.61
BC-2	62.3	79.9	2.37	3.61	3.37	3.45	6.35	5.81
P	.01		.55		.80		.98	

A satisfactory fit of the data to the theoretical with the exception of percentage normal pollen is indicated by the P values obtained. The percentage normal pollen does not follow this trend as affected by backcrossing. This is possibly due to the result of environmental conditions when the pollen was collected, limitations on pollen observations, or to genetic and chromosomal abnormalities.

Pairing Relationship

The chromosome number, pairing relationship, and number of bridges at anaphase I of the parents, F_1, BC-1, and BC-2 plants observed are presented in Table VIII. Many more cells were examined than indicated in the table, but only those cells of which fairly accurate observations could be made were used in determining the range of pairing. The final conclusion of pairing relationship, as listed under "Best Observations", was reached by using the clearest and most distinct cells of this group.

The two parents, Minter and A. trichophorum #4, were quite regular in their meiotic division. Both had 21 bivalents and few abnormalities, Fig. 9 and 10. No bridges were noted in Minter wheat at anaphase I, but a total

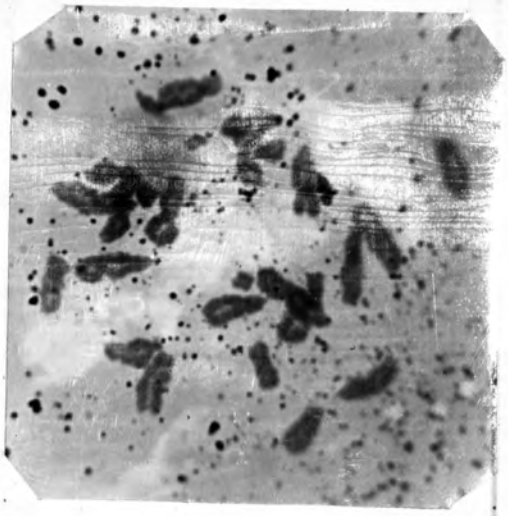


Fig. 9. T. vulgare, variety Minter. Diakinesis showing complete pairing of 21 bivalents. X980

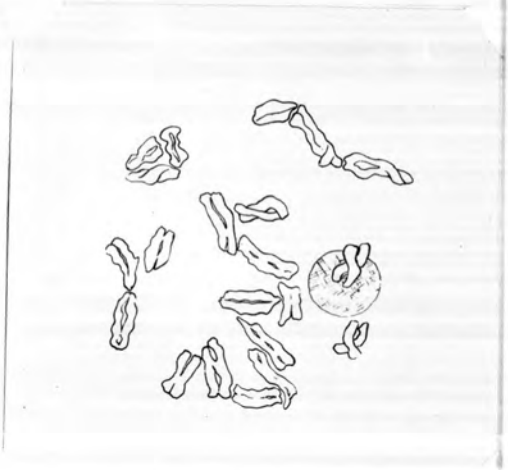


Fig. 10. A. trichophorum, selection #4. Diakinesis showing complete pairing of 21 bivalents. X980

of 12 bridges were observed in 100 anaphase I cells examined in A.trichophorum #4. Only one bridge occurred in each of these 12 cells.

Table VIII: Chromosome number, pairing relationship, and bridges at anaphase I as observed in 3 generations: F_1, BC-1, and BC-2.

	Chromosome No. 2N	No. cells observed	Bivalents Range	Best Observations Bivalents	Univalents	Bridges at Anaphase I Av.No./cell*
Parents						
T.vulgare	42	10	—	21	0	0
A.trichophorum #4	42	13	—	21	0	.12
F_1	42	33	1-11	11**	20	.36
Backcross						
Line 31 BC-1	63	5	18-24	21	21	.05
BC-2	46	6	18-20	19	8	.02
Line 35A BC-1	63	5	21-25	23	17	.18
BC-2	—		—	—	—	0
Line 35B BC-1	63	8	22-26	23	17	.12
BC-2	50	9	19-24	23	4	.10
Line 9 BC-1	63	12	17-25	19	25	.6
BC-2	50	9	19-22	22	6	0
Line 12A BC-1	63		—	—	—	.05
BC-2	—		—	—	—	.05
Line 12B BC-1	63		—	—	—	.11
BC-2	—		—	—	—	0

* Based on 100 observed cells
** See text for pairing relationship in F_1's.

Observations of metaphase I cells in the F_1 indicated that pairing was very erratic, varying considerably from cell to cell. All variations from 1 to 11 bivalents were observed. This indicated a partial homology between one or two genomes of the T.vulgare and A.trichophorum chromosomes. It seemed evident from the observations that this pairing which occurs between these chromosomes or parts of chromosomes is a loose relationship which

makes for the continuous falling apart of these pairs during late prophase and metaphase I. An example of this precocious separation in metaphase I is presented in Fig. 14 in which 3 bivalents appear to have separated while the other bivalents remain joined. Examples of variable pairing at metaphase I is presented in Fig. 11, 12, and 13 which show 2, 4, and 11 bivalents respectively. As the possibility exists that the bivalents at metaphase I do not separate at the same time, the number of bivalents noted would depend upon the stage of metaphase I separation observed, rather than on the pairing relationship alone. Observations of diakinesis and other prophase figures would have been valuable in the further explanation of this F_1 pairing, but these were not available. More bridges occurred at anaphase I in the F_1 than in any other generation.

The BC-1 plants have 63 chromosomes as shown in Fig. 15. If this resulted from the fertilization of an unreduced F_1 egg by the wheat pollen, the BC-1 plants would contain 21 A.trichophorum chromosomes and 42 T.vulgare chromosomes. This should result in 21 bivalents plus some additional associations with the A.trichophorum chromosomes. Best observations revealed 21 to 23 bivalents with the remainder being mostly univalents. A few multivalent associations were observed. Bridges in anaphase I occurred in all plants observed.

Two BC-2 plants had 50 chromosomes and one plant had 46. Fig. 20, 21, and 22 show diakinesis and metaphase I figures. A large increase in the number of bivalents over the number observed in BC-1 was not noted; however, there were fewer univalents than in the previous generation. Fewer bridges in anaphase I cells were also noted in this generation.

No observations of pairing relationship of the BC-1 selfed plants were made.

Abnormal Division of F_1

Evidence of non-reduction in the F_1 was sought to substantiate the appearance of an extra complement of chromosomes in BC-1. All six BC-1 plants investigated had 21 additional chromosomes; therefore, this may be an indication that only those eggs with the 2N number were viable. No pollen mother cells containing this double number of chromosomes were observed, but many cells having a different number of chromosomes at each pole were noted. Cells were also observed undergoing an extremely uneven division in which the chromosomes are going to three poles was occasionally observed and is shown in Fig. 19. The probability of pollen cells containing all 42 chromosomes on the basis of random distribution of 42 chromosomes is so small that the occurrance of many cells of this type is extremely doubtful. Pollen cells containing a double complement of chromosomes may have been produced, but their appearance may have been such that detection by observation was impossible.

To determine the manner in which the chromosomes in these cells were distributed, counts of chromosomes at each pole of 200 anaphase I cells were made. These data were then compared with the distribution of chromosomes on a random basis. Observations were necessarily limited to those cells in the early stage of division, as late anaphase I cells contained too many chromosomes at the poles for accurate counting. The difference in the number of chromosomes at the poles in a cell determined the class in which that cell was placed. The number of observations in each class were then converted into the percentage of the total 200 cells observed.

The calculated random distribution of 21 and 42 chromosomes was obtained by the use of a mathematical table (5) derived from the integral of the formula of the normal curve. By converting the linear measurement of the bottom of the curve, which was divided into 21 or 42 classes, into area

under the curve, the percentage of the total area occupied by each class was obtained.

The comparison of the percentage of observed cells in each class with the percentage of cells in each class calculated on a random distribution of 21 or 42 chromosomes is presented in Table IX.

Table IX: Observed difference in the number of chromosomes at each pole at early anaphase I of F_1 as compared with the theoretical random distribution of 21 and 42 chromosomes.

CLASS Difference in number of chromosomes at each pole	CELLS OBSERVED		RANDOM DISTRIBUTION			
			21 chromosomes		42 chromosomes	
	No.	% of Total	% of total in each class		% of total in each class	
0	19	9.5	19.0		9.6	
1	38	19.0	17.2		9.4	
2	40	20.0	16.1	76.7%	9.2	44.5%
3	26	13.0	13.6		8.8	
4	22	11.0	10.8		7.6	
5 - 26	55	27.5				
5 - 21			23.3			
5 - 42					55.4	

As the first five classes contained nearly three-fourths of the observed cells, these were combined for convenience of comparison. The combined class 0-4 have 72.5% of the observed cells, 76.7% of the cells calculated on the basis of random distribution of 21 chromosomes, and 44.5% of the cells calculated on the basis of random distribution of 42 chromosomes. This indicates that the 42 chromosomes of F_1 are not distributed at random. Cytological observations of the F_1 indicated a maximum of 11 bivalents which for the most part were distributed in the normal manner. The distribution of the remaining 20 chromosomes compares favorably with the distribution of a like number of a random basis.

In as much as a double complement of chromosomes in the egg could not have occurred on the basis of the random distribution of 42 chromosomes or

by the normal division of 11 bivalents and the random distribution of the remaining chromosomes with the regularity indicated in this study, some other explanation is necessary. Hence, it is extremely probable that this p.m.c. division occurs differently than the similar division in the egg.

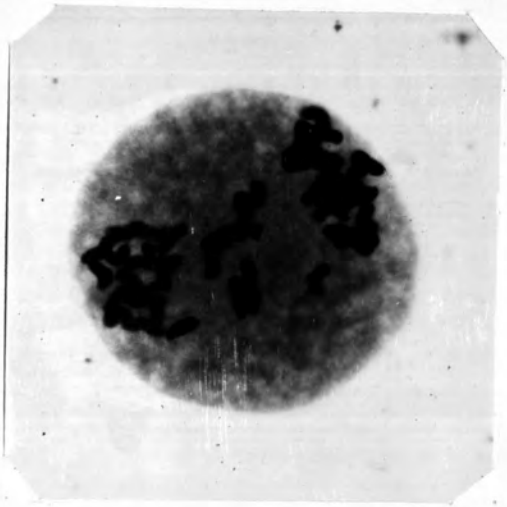


Fig. 11. F_1. Late metaphase I showing 2 bivalents. Most of the other chromosomes are at the poles. X980

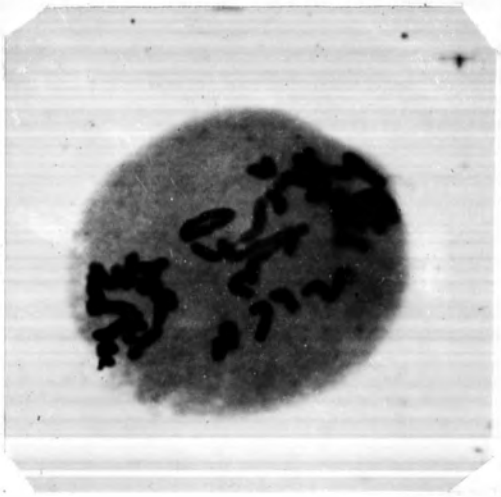


Fig. 12. F_1. Late metaphase I showing 4 bivalents and many chromosomes at the poles. X980.

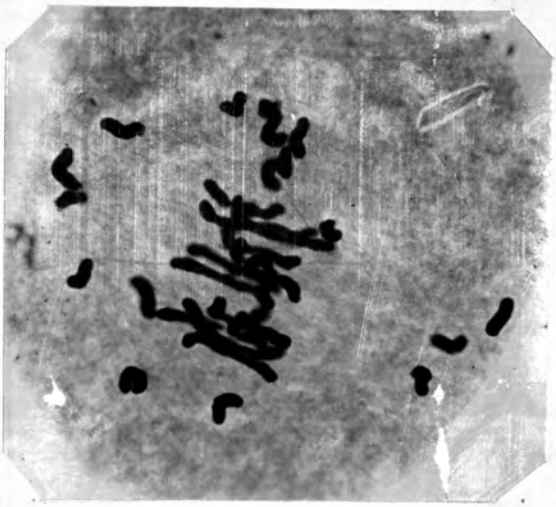


Fig. 13. F_1. Metaphase I showing maximum pairing observed--11 bivalents, 20 univalents. X980.

Fig. 14. F_1. Late metaphase I showing precocious separation of three bivalents. X980.

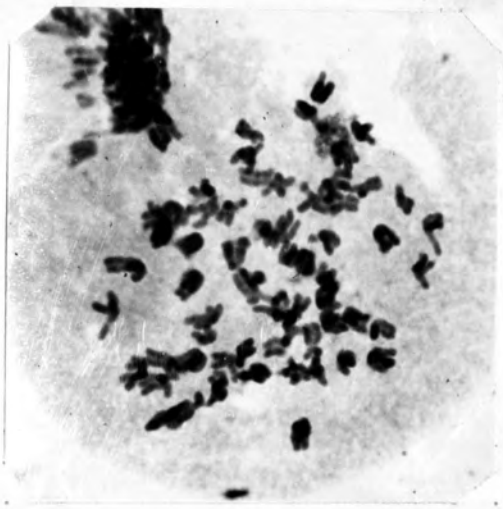


Fig. 15. BC-1. An anaphase I cell containing 63 chromosomes. X980

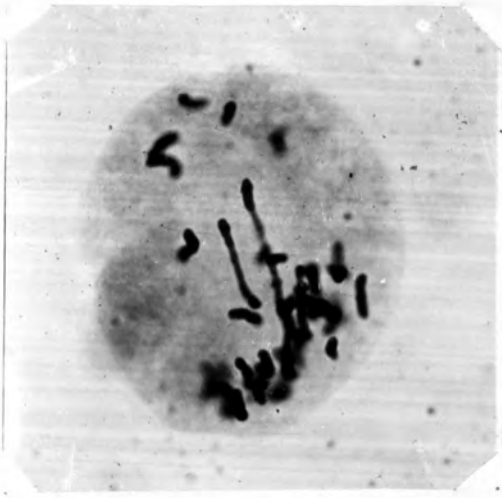


Fig. 16. F_1. Late metaphase showing very uneven grouping of chromosomes at the poles. X980.

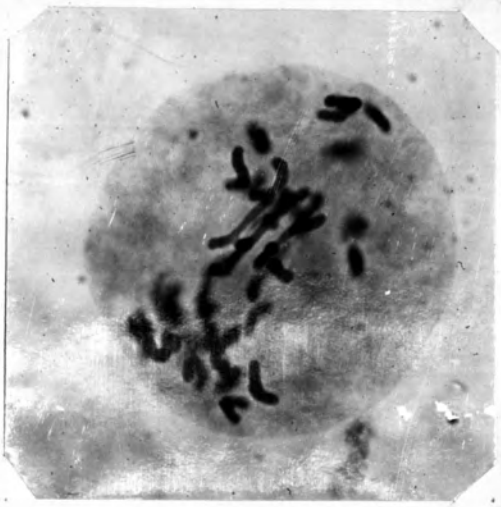


Fig. 17. F_1. Late metaphase I showing uneven division. X 980.

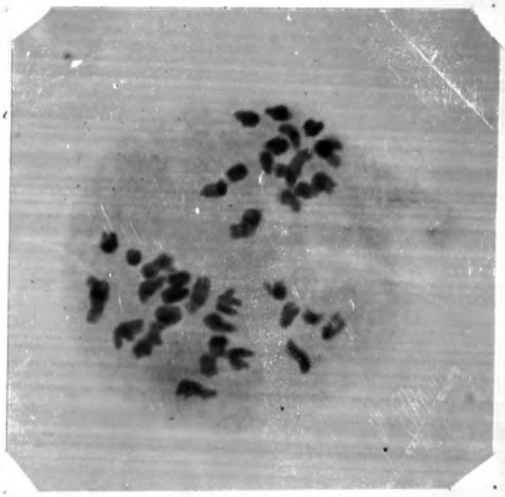


Fig. 18. F_1. Uneven anaphase I division. X980.

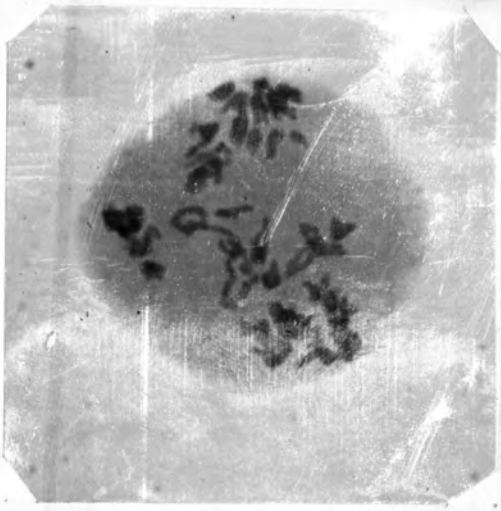


Fig. 19. F_1. Abnormal anaphase I division showing chromosomes going to 3 poles. X980.

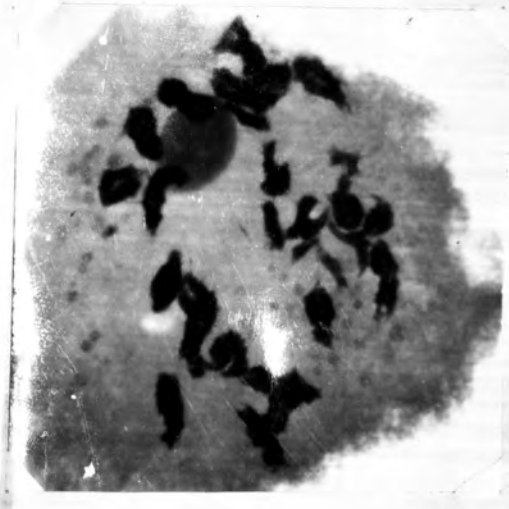


Fig. 20. BC-2. Diakinesis showing 22 univalents, and 6 univalents. X980.

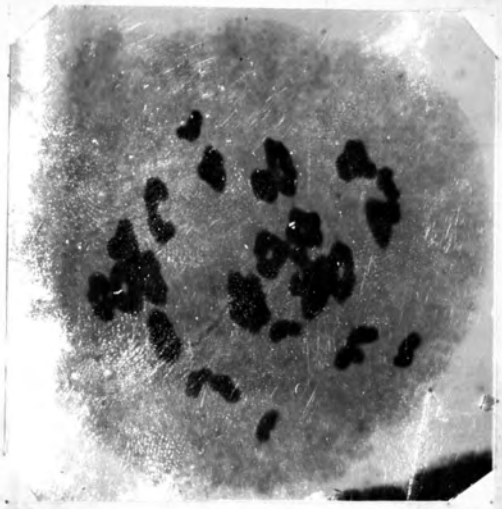


Fig. 21. BC-2. Metaphase I showing 19 bivalents and 12 univalents. X980.

Fig. 22. BC-2. Metaphase I showing 19 bivalents and 12 univalents. X980.

DISCUSSION

Similar Triticum-Agropyron crossing programs have been started in many sections of the country. It is desirable, even in these "wide" crossing programs, to use adapted parents possessing the quality characters desired. This program was initiated to supplement a breeding program organized around a group of "Sando" hybrids (T.vulgare x T.elongatum) obtained from S.P. Swanson. In these "wide" crosses the low cross fertility, low seed-set, and other abnormalities in subsequent generations result in slow progress. The perennial nature of these first generations is a distinct advantage by allowing observations of the same plants for several years. Also, a plant which has proven to be valuable will be available for future work.

The original plan of this project was a cytological study comparing the chromosome activities in three breeding methods, i.e., (1) Self-fertilization and selection, (2) Backcrossing using T.vulgare as the recurrent parent, and (3) Backcrossing onto an amphiploid derived from the F_1 using T.vulgare as the recurrent parent. No selfed-seed or chromosome doubling of the F_1 was obtained; therefore, two phases of the problem were dropped.

The backcross breeding system is used to add desirable genes and yet retain most of the characters of the recurrent parent. Plants used in ordinary backcross breeding programs usually have only allelic differences. In addition to this, "wide" crosses have extreme chromosome differences. A cytological investigation of several backcross generations show chromosome homologies, genome comparisons, and abnormalities. The differences and rates of change from generation to generation provide a more intelligent guide for the remainder of the breeding program. It also provides more precise information to evaluate phenotypic results.

Collection of material for cytological study was limited by the small number of plants available. Vegetative propogation and vigor of the F_1 plants provided an adequate number of these plants. In an attempt to keep the

observations as uniform as possible, only one of several sister plants of BC-1 and BC-2 was used in each backcross line studied. The plants, being perennial, produced shoots continuously into late summer. The collection of these spikes at the correct stage was made under varying weather and temperature conditions. This may have influenced the observations somewhat.

Previous descriptions of F_1's indicate a loose pairing relationship with a maximum of 11 bivalents. This may indicate homology with one genome of T.vulgare, presumedly the B genome (8), and possibly with another genome as well. At best, the F_1 pairing is loose, the division of bivalents is not normal, and many univalents are present.

The absence of pollen dehiscence in the F_1 is one of the reasons for their self-sterility. Observations indicate that some normal pollen is produced, but the amount is so small that dehiscence occurs rarely. Dehiscence was observed in only three plants.

The supposition is that BC-1, not a normal backcross, should have two complements of T.vulgare chromosomes and one complement of A.trichophorum chromosomes. Thus, it should have 21 bivalents. Observations agree well with this; however, some cells were observed having fewer than this number. Little change in the number of bivalents in BC-2 compared with BC-1 was noted. This could be expected when it is considered that the two complements of T.vulgare chromosomes in BC-1 would pair and separate normally, while the remaining chromosomes, for the most part unpaired, may tend to be distributed on a random basis. Thus, the next backcross, which would add a complement of T.vulgare chromosomes, should result in 21 paired T.vulgare chromosomes, plus some additional pairing due to the A.trichophorum chromosomes. A few univalents should also be present.

The Agropyron chromosomes in the BC-1, although unpaired for the most part, are important. During gamete formation, chromosome association occurs

as well as inclusions of these unpaired chromosomes to transmit the Agropyron characters. These BC-1 plants, having many characters in common with the Agropyron parent, are perennial and as such can be grown and kept for the future. Progeny studies may indicate the relative merit of individual plants. A backcrossing program with forage possibilities in mind, using the Agropyron as the recurrent parent, may be feasible starting with either the F_1 or BC-1.

One of the most interesting features of this study was the occurrence of an additional complement of chromosomes in the BC-1 plants. Similar occurrences have been reported. Love and Suneson (7) obtained from a T.durum x A.trichophorum cross (2N=35) derivatives having 35, 56, and 70 chromosomes. The 35 chromosome plant was sterile. From a T.macha x A.trichophorum F_1 (2N=42), a derivative was observed having 70 chromosomes. This plant was fairly fertile. Various combinations of reduced and unreduced gametes were discussed explaining this phenomenon. Khisnjak's work as reported by Smith (15) noted that a T.vulgare x A.intermedium hybrid undoubtedly formed an unreduced egg, as the backcross resulted in a triple hybrid (a plant of 3N chromosome number). A T.durum x A.intermedium cross produced an amphiploid, and a T.durum x A.intermedium F_1 backcrossed with T.vulgare resulted in a triple hybrid. Another example of this was noted when wheat backcrosses of A.glaucum wheat hybrids were examined cytologically by Peto (2) revealing triple hybrids.

This occurrance of unreduced gametes, free in nature, is one of the many variations attributed to the Agropyrons. This feature may account for some of the variations exhibited with the species, and perhaps species of Agropyron have arisen from unreduced gametes. In any event, these partially fertile plants containing the extra complement of chromosomes should prove valuable in a breeding program.

The production of fertile amphiploids from self-sterile F_1's by colchicine or some other agent is one method of obtaining the continuation of this valuable germ plasm. An amphiploid would offer several advantages.

(1) This would be a fertile, comparatively stable plant having one-half of its chromosomes from each parent. If not valuable in itself, it would have value in a breeding program.

(2) Backcrossing this amphiploid to wheat, should result in a plant with two complements of T.vulgare chromosomes and one complement of Agropyron chromosomes. This would be one method of adding Agropyron genes to the wheat.

(3) Having a large number of chromosomes (2N=84), the amphiploid would provide a means for frequent exchange of chromatic material. Induced chromosome breaking by X-ray or other means might be effective for transferring genes.

The BC-1 plants produced in this study have some of the advantages offered by the amphiploids. As stated, an amphiploid backcrossed to wheat, would result in a plant with two complements of T.vulgare chromosomes and one complement of Agropyron chromosomes. Evidence indicates that this is the situation in BC-1. Thus, this goal was reached in this study even though attempts at chromosome doubling by colchicine failed.

When considering this project, several calculations were made regarding the effect of backcrossing. Selection pressure acting on the chromosomes going into a gamete was disregarded and the calculations were based on the random distribution of chromosomes. It was thought that the gametes from a F_1 would tend to have the mean number of both T.vulgare and A.trichophorum chromosomes, or 10 or 11 of each. The BC-1 plant would then contain less than 21 but more than 10 homologous paired T.vulgare chromosomes and about 10 Agropyron chromosomes, mostly unpaired univalents. Again figuring that the Agropyron chromosomes would be halved, the second backcross would have near

21 paired chromosomes of T.vulgare and about 5 Agropyron chromosomes. Additional selection or backcrossing in future generations would decrease the number of Agropyron chromosomes toward 0.

Actually, the number of chromosomes increased in the BC-1 and these plants cannot be compared on this basis with a normal backcross. The two complements of T.vulgare and one complement of A.trichophorum chromosomes present in BC-1 would be expected to result in 21 bivalents in the next backcross and half or about 10 A.trichophorum chromosomes. Actually, the second backcross plants do contain about the same number of bivalents as the BC-1, 21, but the univalents (presumably A.trichophorum chromosomes) decreased more than half from an average of 20 to 6.

Even though the chromosome number increased in BC-1, the BC-2 plants are similar to the predicted BC-2 plants, having approximately 21 bivalents and 6 univalents. In both cases the next backcross or selection should decrease the univalents toward 0.

The immediate aim of the breeding program is to increase the population within each generation. By growing all F_1, BC-1, BC-1 Selfs, BC-2, BC-2 Self plants in the field and observing them for winterhardiness, drought resistance, disease resistance, and other characters, the desired selections can be made. Some of these parent plants may not be valuable in themselves, but progeny observations may indicate their worth in the breeding program. With this information, new breeding programs can be started and these superior lines employed.

SUMMARY

1. Although exhibiting low cross-fertility, two Agropyron species A.trichophorum and Ree Wheatgrass were successfully crossed with T.vulgare, var. Minter. Individual Agropyron plants differed in their ability to cross with wheat.

2. All F_1 plants were self-sterile. Only those plants having A.trichophorum #4 in their parentage were backcross fertile with the wheat parent. Individual F_1 plants in this group also differed in their backcross fertility.

3. A pollen study to determine the percentage of normal pollen was conducted on F_1 plants grouped according to their Agropyron parent. The F_1 plants having A.trichophorum #4 in their parentage had the highest average percentage of normal pollen of all groups.

4. Cytological observations were made of three generations, F_1, BC-1, and BC-2, within six backcross lines with the following results: the average percentage of normal pollen increased with each generation; the number of micronuclei per quartet increased in BC-1 but decreased below the F_1 in BC-2; the number of laggards at metaphase I and anaphase I decreased in each backcross generation.

5. The 2N chromosome number and pairing relationship of the plants used were determined as presented in the following table. The pairing of BC-1 and BC-2 are approximate averages of the several plants observed.

Parents or Generation	2N chromosome No.	Bivalents	Univalents
T.vulgare, var. Minter	42	21	0
A.trichophorum #4	42	21	0
F_1	42	11	20
BC-1	63	21	21
BC-2	near 50	21	6

6. BC-1 plants containing 63 chromosomes were evidently produced by an unreduced F_1 egg being fertilized by T.vulgare pollen when the backcross was made. This being the case, these plants are composed of two complements of T.vulgare chromosomes and one complement of A.trichophorum chromosomes. These plants have the same make-up as expected by backcrossing T.vulgare onto an amphiploid.

7. Pollen mother cells of F_1 were studied to determine the distribution of the chromosomes and the chances of an unreduced cell being produced. By comparing the observed chromosome distribution with the theoretical, the following conclusion was reached: eleven pairs of chromosomes were distribut in the normal manner, and the 20 univalents were distributed on a random basis. This would hardly account for the regularity that 2N eggs were produced; therefore, other factors must be involved. Evidently only F_1 eggs of 2N number were viable as all 6 BC-1 plants observed possessed 63 chromosomes. However, it is possible that 2N pollen cells were not observabl as such, or that the comparative divisions in the egg and p.m.c. differ.

8. F_1 plants are generally intermediate phenotypically to the Agropyron and the wheat with many of the characters dominately Agropyron. After two backcrosses to wheat, pubescence, habit, and perennial growth are Agropyron characters exhibited. In spike type, awn type, kernel size and shape, and stage of pollen mother cell division, the plants resemble the recurrent wheat parent. Self and cross fertility increased with each backcross generation. Perennial habit is exhibited in all generations grown to date.

9. F_1 plants varied in rust reaction with some highly resistant plants. No accurate observations of rust was made in BC-1 and BC-2.

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