PRELIMINARY STUDIES OF *TRITICUM* SPP. X *AGROPYRON ELONGATUM* HYBRID DERIVATIVES

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INTRODUCTION

One of the principal needs of the wheat growers in Oklahoma and surrounding states is an adapted variety with leaf rust resistance combined with the high yield and the good quality which are at present available. All of the rust-resistant varieties which are grown now have the type of resistance which is effective only in years when the amounts of inoculum are low. In years with great amounts and wide-spread distribution of inoculum the losses in these varieties may be great. Varieties with greater resistance are needed.

Intra- and inter-specific hybridization in *Triticum* has been the chief source of resistance in the past. More recently, intergeneric hybrids of *Triticum* with *Agropyron*, *Secale*, and *Aegilops* have gained prominence for both disease resistance and other desirable characters. Upon receipt of hybrids involving *Triticum* and *Agropyron elongatum* (Host) Beauv. (sometimes called tall wheatgrass) more complete studies of various selections were initiated. This paper is a report of some of these studies.

REVIEW OF LITERATURE

General Reports of *Triticum*-*Agropyron* Hybrids

Natural hybrid plants of *Triticum* spp. X *Agropyron glaucum* Roem. and Schult. were discovered in the Caucasus Region of the U. S. S. R. by N. V. Cicin in 1930, according to Verushkine and Shechurdine (44)/1. The following year Cicin successfully crossed A. glaucum, A. elongatum, and A. trichophorum with Triticum vulgare Vill. and with T. durum Desf. Cicin and other plant breeders in the Soviet States worked intensively and soon Canadian plant breeders followed their example (3).

The Triticum spp. X A. elongatum hybrids were observed to resemble their wheatgrass parent in the early generations. This "dominance" of Agropyron is emphasized by Verushkine and Shechurdine (44). Armstrong (3), Johnson (16), and White (45) have stated that a good amount of this "dominance" is partial but that practically all characters are closer to Agropyron than Triticum in their nature. Armstrong (3) pointed out that this predominance of wheatgrass type is not necessarily due to dominance in the usual genetic sense but may be due to "replication" of genes of A. elongatum ($2n = 70$) over T. vulgare ($2n = 42$) and T. durum ($2n = 28$). Cicin (10, 11) and Verushkin (42) stated that Agropyron characters predominate in the F_1 generation of Triticum-Agropyron hybrids.

A very few characters were reported which indicate at least partial Triticum dominance. Cicin (11), Johnson (16), Lapin (19), and White (45) have reported that the spring habit of growth of spring wheat varieties is dominant to the winter habit of growth of A. elongatum. All plants of Triticum spp. (winter type) X A. elongatum F_1 were true winter types.

/1 Numbers in parentheses refer to "Literature Cited", p.

White (45) stated that the free-threshing character of T. vulgare is partially dominant over the adherence of the lemma and palea in A. elongatum. This character of glume adherence was classified nearer the Agropyron type by Armstrong (3) and Johnson (16). Johnson (16) noted that the purple auricle of T. vulgare var. Kharkov was dominant to the white auricle of A. elongatum.

Head characters of the early and later generations resemble Agropyron more than Triticum, according to Cicin (10, 11) and Verushkin (42, 44). Armstrong (3) and Johnson (16) confirmed these observations. Both the latter authors stated that seeds produced on F_1 plants resembled wheat more than Agropyron.

Fertility

Armstrong (3) observed only one fertile F_1 plant in the greenhouse. Johnson (16), studying the same plants after transplanting them to the field, found that some plants of each cross were fertile and set some seed. Both writers mentioned above, along with White (45), observed that in the sterile plants the anthers were non-dehiscent. Johnson, et al (18) noted moderately fertile lines in F_3 generations. White (45) stated that fertility increased with each generation of backcross to wheat.

Johnson (16) inspected the pollen of Triticum-Agropyron hybrids with Belling's iron-acetocarmine (28) as a stain and classed the pollen grains which were obviously abortive "bad" pollen and all other spores "good" pollen. A significant correlation with seed-set was observed. Anthony and Harlan (2), Johnson (17), and Bair and Loomis (5) germinated pollen with varying degrees of success. Blakeslee (6) and Blakeslee and Cartledge (7) studied Datura pollen by inspection. Nissen (22) studied pollen of Poa pratensis both by inspection and by germination. He stated that pollen which was squeezed from a ripe anther was better in appearance but lower in germination than pollen which was shed through anther dehiscence.

Seed-set of Triticum-Agropyron hybrids was studied by Armstrong (3). His data were recorded both as the percent fertile of the fully-developed florets and as "percent fertile spikelets" (the number of seeds per plant divided by the number of spikelets per plant). Sax (29) recorded seed-set data as seeds per spikelet in interspecific wheat hybrids. McFadden and Sears (20), in Triticum-Aegilops hybrids, removed all except the first two florets of each spikelet and reported their data as "percent fertile primary florets". The first two florets of the spikelet were termed "primary florets" by these two co-workers. McFadden and Sears also removed such spikelets at the apex and base of the spike as were normally abortive.

Smith (31) and Pomogaeva (25) observed that A. elongatum was cross-pollinated to a great extent but that self-sterility is not complete. Pomogaeva (25) further stated that Triticum spp. X A. elongatum hybrids tended towards selfing.

Seed Shriveling

Armstrong (3) and Johnson (16) mentioned some wrinkling of the crossed seeds (F_0) of Triticum-Agropyron hybrids but that the seeds resembled the Triticum (female) parent in size and shape. In interspecific wheat hybrids, Sax (29) and Thompson (35) noted severe shriveling which correlated with chromosomal aberrations.

Wheat Genetics

The resistance to leaf rust, caused by Puccinia rubigovera tritici (Erikss.) Carleton, is governed in most cases by single genes if pure strains of wheat and a single rust race is used for the test of resistance, according to Chester (9). Chester lists 20 crosses between varieties of T. vulgare with monohybrid ratios with dominance of resistance, 20 crosses with monohybrid ratios with resistance recessive, nine cases of monohybrid ratios with the F_1 generation intermediate, and five crosses with dihybrid ratios. It was pointed out by this author that the inheritance of leaf rust resistance appeared to be exceedingly complex in field studies where the plants were exposed to mixtures of inoculum consisting of several races of rust.

There are two main factors involved in most hybrids between true awnless and fully awned varieties of T. vulgare. Quisenberry and Clark (26) crossed two awnletted types of T. vulgare and observed segregates which varied from fully awned to true awnless. The segregation indicated that two alleles were responsible for the genetical difference between the two varieties and that numerous modifying factors also were involved. Clark (12) crossed Kota (awned) and Hard Federation (awnless) and observed a 2-factor ratio in the F_2 generation. None of the F_2 lines bred true in the F_3 population and modifying factors were assumed. Gaines (13) reported a monohybrid ratio in the cross fully awned T. vulgare (Turkey X Bluestem) X true awnless T. compactum Host var. White Club. From his illustrations, it is evident that White Club is a true awnless type. Gaines also stated that the club type segregates developed shorter awns than the fusiform types.

Boshnakian (8) made extensive studies of clavate-headedness. He demonstrated that clavateness and head density are two different characters and are governed by different genes. He reported that plants receiving more nutrients, especially nitrogen, tended to produce heads which were more clavate while head density was less variable. Extreme applications of nitrogen to potted plants of T. compactum in the greenhouse produced vulgare-type heads on the first tillers and typical club heads on their later tillers. According to Boshnakian, clavate heads tend towards a greater average density. The inheritance of clavate-headedness was stated to be complex with the F_1 intermediate. Stewart (33) reported a similar inheritance, with low correlation in clavateness between F_2 and F_3 populations, but clavateness correlated with head density.

The inheritance of seed color (red vs. white seeds) is governed by three factors with a single dominant gene for red producing red seeds in spite of the five recessive genes which may be present at the other loci, according to Nilsson-Ehle (21). The F_2 population (red X white varieties) varied from white to dark red with blending according to the number of dominant genes present. Only one white seed-producing plant per 63 red-seeded plants were observed in the F_2 population, and all the white-seeded plants bred true. Ratios of 15:1 and 3:1 were observed in other red- X white-seeded hybrids.

Disease Resistance

Johnson (16) reported that the first generation of Triticum spp. X A. elongatum hybrids was completely free of leaf rust and stem rust of wheat in the field. White (45) stated that later generations developed segregates which were susceptible to these two diseases only if backcrossed to wheat.

Armstrong (3) and Johnson (16) stated that Triticum X A. elongatum F_1 plants were free of ergot (caused by Claviceps spp.) as was the A. elongatum parent. White (45), on the other hand, observed all Triticum-Agropyron derivatives to be susceptible to ergot in the first generation. In later generations, the ergot susceptibility seemed to be lost in certain lines. The occurrence of ergot was negatively correlated with anther dehiscence in the plants and the consequent length of the period during which the florets were open.

Lapin (19) reported that Triticum-A. elongatum hybrids were quite disease-resistant as well as being tolerant of salts and drouth. Verushkin (43) observed similar disease-resistance and drouth tolerance, but he mentioned no salt tolerance.

Chromosomes Studies

Peto (23) reported the chromosome number of A. elongatum to be 70 (2n), having multivalent associations of 3, 4, 5, 6, and 8 chromosomes. The F_1 of three T. vulgare (n = 21) X A. elongatum (n = 35) hybrids had 56 chromosomes (2n) with 13.0-19.5 univalents, 9.5-11.7 bivalents, 3.0-3.4 trivalents, 1.1-1.7 tetravalents, 0.4-0.8 pentavalents, 0.0-0.1 hexavalents, and 0.0-0.1 octavalents at the meiotic metaphase. Chromosome numbers ranged from 54-59 (2n) in the F_2 and Peto (24) assumed that the plants would stabilize at 42 and 70 chromosomes (2n).

Vakar (36, 37, 38, and 39) also reported 56 chromosomes in the first generation hybrids. He found (36, 38, and 39) 14-28 bivalents and stated that the self-fertile types had 28 bivalents (38) and that meiosis resembled that of wheat species hybrids (38).

Hizhnjak (14) reported 19-23 bivalents in the F_1 hybrids. Sapegin (27) used a type of A. elongatum with 56 chromosomes (2n) and produced F_1 plants with 49 chromosomes having 21 bivalents and 7 univalents.

Multinucleate pollen grains were noted by all of the above-mentioned authors (14, 23, 27, and 38). Vakar (38) reported that in some plants the second meiotic division took place in the pollen grains, producing "dyadic pollen".

Vakar (38) also reported that the F_1-F_5 generations were constant at 56 chromosomes. Armstrong and Stevenson (4) found 49-58 chromosomes in F_5 plants and stated that most of these were wheat chormosomes or at least partially homologous with wheat chromosomes.

Chemical Composition

Armstrong and Stevenson (4) reported that the protein content of T. vulgare X A. elongatum F_5 was slightly higher than T. vulgare in the forage and considerably higher in the seeds. The seeds were stated to be of good quality for feed but not for flour.

Shibaev (30) studied the milling and baking quality of A. glaucum, and reported as gluten 25.0% for A. elongatum compared with 16.0% and 17.5% for two wheat varieties. Triticum-Agropyron hybrids contained 20.8% "gluten" in intermediate types and 15.5%-16.0% in wheat-like derivatives. The milling and baking quality of A. glaucum was better than rye but inferior to wheat.

Verushkin (43) quoted Rauschenbach that Agropyron seeds are similar chemically to wheat, and also Shibaev that the seeds of Agropyron species are about equal to wheat in milling and baking tests.

MATERIALS AND METHODS

Materials Studied

Early in 1947 several Triticum spp. X A. elongatum hybrid derivatives were received from the Kansas station. Such of these hybrids as were studied, along with their backcross derivatives, are listed below. The numbers by which they are listed will be used throughout the remainder of this paper when referring to them.

Hybrid 1. (T. vulgare var. Chinese X Secale cereale) X A. elongatum) X T. vulgare var. Forward. 1946 Kansas plot number 411. A summary of the characters of this and other hybrids and the male backcross parents is found in Table 1.

Hybrid 2. Hybrid 1 X _T. vulgare_ var. Kawvale-Marquillo X Kawvale-Tenmarq C.I. 12128[2].

Hybrid 3. Hybrid 1 X _T. vulgare_ var. Tenmarq C.I. 6936.

Hybrid 4. _Triticum_ spp. X _A. elongatum_ backcrossed to _Triticum_ spp. an unknown number of times. 1946 Kansas plot number 4708.

Hybrid 5. Hybrid 4 X _T. vulgare_ var. Pawnee C.I. 11669.

The male backcross parents are listed below.

1. _T. vulgare_ var. Kawvale-Marquillo X Kawvale-Tenmarq C.I. 12128.

2. _T. vulgare_ var. Tenmarq C.I. 6936.

3. _T. vulgare_ var. Pawnee C.I. 11669.

The selections received from Kansas were planted in February, 1947, and those selections which matured seed were harvested. The 1947 seed was planted the following fall and for those selections which did not mature seed, the 1946 Kansas sources were used. In 1948, two successful backcrosses to _T. vulgare_ types in one selection (Hybrid 1) and one successful backcross to a vulgare-type with another (Hybrid 4) were produced. The crossed seeds (F_0) were space-planted in the field in the fall of 1948 and the bulk composites of the non-backcrossed material were replanted (in bulk) for further observation. The F_1 plants were harvested individually

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/2 C.I. numbers are the accession numbers of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture.

Table 1. Summary of the characters of the hybrids and the backcross parents studied.

Selection	Winter hardi-ness/1	Awn type/2	Head clav-ate-ness/3	Head den-sity/4	Leaf rust reac-tion/5	Habit/6	Dates headed/7
Hybrid 1	G	A-TA	F	L	CS	W	5-7
Hybrid 2	G	A	F	L	CS	W	5-6
Hybrid 3	G	A-TA	F	L	CS	W	5-9
Hybrid 4	P-F	4A-CA	F-C	VL-SD	0-0;	F	5-13
Hybrid 5 F_1	G	TA	F	SL	0-0;	-	5-5
Hybrid 5 F_2	P-G	A-CA	F-C	L-SD	0;-CS	-	5-5
C.I. 12128	G	A	F	L	R	W	---
Tenmarq	G	A	F	L	CS	W	---
Pawnee	G	A	F	L	CS	W	5-7

/1 Winterhardiness: P = poor, F = fair, and G = good.

/2 Awns: A = awned, 4A = four-awned, TA = tip awned, and CA = completely awnless.

/3 Clavateness: F = fusiform, and C = clavate.

/4 Density: VL = very lax, L = lax, SL = semi-lax, and SD = semi-dense.

/5 Rust reactions (field): CS = completely susceptible, R = resistant, 0; = zero-fleck, and 0 = zero (immune).

/6 Habit: W = winter habit, F = facultative winter habit.

/7 Dates headed: The first number refers to the month, the second to the day of the month.

in 1949 and space-planted as F_2 plant selections in the fall. In addition, 105 head selections were made from the bulk-planted material of Hybrid 4 and seed from each head space-planted in a single row. Also from Hybrid 4, some of the bulked seed of 1949 was planted in a small field plot at the rate of 1/2 bu. per A., using a modified International Harvester Co. grain drill in 14-inch row-spacing. Plant selections were made of all space-planted material and harvested individually in 1950. The special increase plot was harvested with a standard International Harvester Co. grain binder.

Field Methods

The bulked material was planted using a manually-operated 1-row Columbia drill. The rows were 10 feet long and 1 foot apart for all nursery material except for the F_1 plants, which were planted in 3-foot rows in 1949. The seeds of the space-planted material (all plant and head selections and the F_0 seeds) were spaced approximately 3 inches apart within the row, with 10 seeds maximum per 3-foot row and 35 seeds per 10-foot row.

Emergence notes taken were by estimation of the percent stand for bulk-planted material and by actual plant counts of space-planted material. The spring stand was then estimated similarly for the bulked material and counted for space-planted selections. The percent survival was then computed as the percent spring stand divided by the percent fall stand, or the number of plants in the spring divided by the number of plants in the fall, for each of the two methods of planting respectively.

The maturity data were estimations of the dates on which 75% of the heads of the plots were fully emerged from the leaf sheath or boot (heading dates) and the dates on which 75% of the heads of the plots were fully ripe (ripening dates).

In the bulk plantings each plot (selection) was harvested by sickle in its entirety and the resultant bundle protected by covering the heads with a paper sack and the removal of the bundle to shelter. The space-planted material was selected for promising plants, removing all the mature heads of each and keeping them separate as reselections. These heads were placed in legal-size envelopes, a single selection per envelope, marked with selection numbers, and moved to shelter.

Fertility and Seed Shriveling

Fertility was studied by observing the pollen and the actual seed-set of 41 plants of the hybrids and of Pawnee. Pollen germination attempts on agar (0.75% aqueous) and sucrose (9-16% aqueous) were unsuccessful. The pollen grains were therefore inspected similar to the methods used by Johnson (16) and Thompson (35). Heads which had ripe (bright yellow) anthers were selected in the field, wrapped in dampened paper towels, removed to the laboratory, and placed in beakers with their stems in tap water until the pollen could be observed. The pollen of all heads was observed the day it was collected. Anthers which presented a bright yellow color were selected from each head, squeezed gently between forceps into a few drops of Belling's iron-acetocarmine (28) on a slide and covered by a coverslip.

The slide was examined under a microscope equipped with a mechanical stage, moving straight across the slide and counting fields until the desired sample size of pollen grains was counted (usually 300 pollen grains or more). In all cases the coverslip was traversed at least once. The pollen grains were classed as follows: class I, turgid pollen grains 96%-100% full of dense cytoplasm; class II, pollen grains 51%-95% full of cytoplasm; and class III, pollen grains which were essentially empty. All these percentages were estimations.

The seed-set data were collected in a manner similar to that of McFadden and Sears (20) as previously described. All spikes of each plant which matured normally were studied except for the head selections made in 1949 and the heads of _T. vulgare_ var. Triumph C.I. 12132 which were used for a check with these head selections. The wheat check for the seed-set studies on the space-planted material in 1949 was also Triumph (space-planted in this case), while space-planted Pawnee was used in 1950. The Triumph heads used for the check of the head selections of Hybrid 4 in 1949 were random selections from a bundle produced in the 1949 Stillwater pure seed increase plots. Nineteen plants of the space-planted Triumph were used as a check in 1949 and five plants of Pawnee were used as a check in 1950.

The system of classification of seed shriveling was similar to that followed by Thompson (35) except that the classes of small plump and small wrinkled seeds were disregarded due to the small numbers of these classes which were noted. The remaining classes (Fig. 1) were large plump, large wrinkled, and shriveled seeds.

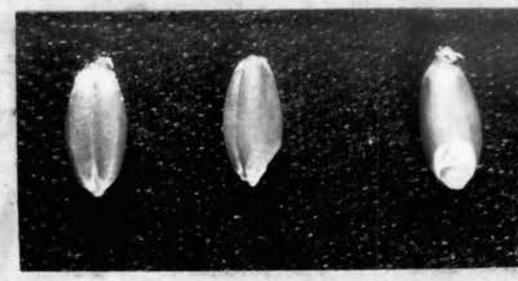
Genetical Studies

Genetical studies were made of several characters in Hybrid 5. The F_1 seeds of six plants of this hybrid were selected for the most plump types in the fall of 1949. From these seeds the F_2 population of 1,449 plants was produced and later studied. Due to poor head and seed production of the spring-sown parental materials, seed from the actual parent plants of this hybrid were not saved for observation of their genetic behavior.

The heads of Hybrid 4 were placed in three awn classes: completely awnless, tip awned, and 4-awned (awn class #4 of Quisenberry and Clark (26). In the F_2 plants of Hybrid 5 the awns were classed completely awnless, tip awned, and awned (fully awned). See figure 2 for the latter classification group. All plants of Hybrids 4 and 5 which produced heads were classified for awnedness in 1949 and 1950.

The clavateness of the heads was classed (by estimation) clavate, intermediate, and fusiform (see Fig. 3) for each plant of Hybrids 4 and 5 in 1950.

The seeds of the F_2 population of Hybrid 5 were classified, by estimation, dark red, red, light red, golden, and white. Only such plants as were selected for further observation were studied for seed color since the segregation was not noticed until the remainder of the F_2 population was harvested and threshed in bulk. The first three classes were



a. Pawnee (ck.).

b. Plump seed.

c. Wrinkled seed.

d. Shriveled seed

Figure 1. Wrinkling and shriveling of the seeds of Hybrid 4 (b to d). 2x.

Figure 2. Awn type segregations in Hybrid 5 F_2. Heads were classed (from left to right) as follows: 1 and 2, awned; 3 and 4, tip awned; 5 and 6, awnless.

Figure 3. Head types in Hybrid 4, Hybrid 5 F_1, and Pawnee. Hybrid 4 (heads 1-3) classed fusiform, intermediate, and clavate respectively; Hybrid 5 F_1 fusiform, and Pawnee, fusiform (heads 4 and 5).

rather difficult to separate definitely so they were grouped into a single "red" class for statistical analysis.

In the studies of leaf rust of wheat, the percent infection was determined for each F_2 plant of Hybrid 5 according to the modified Cobb scale (9). A completely susceptible type of pustule was noted on all plants (except 12) producing these lesions, making the classification of resistant and susceptible types quite simple. The 12 plants were infected up to 10% but only pustules of about a 1-resistant type were produced. These plants were classed resistant for statistical handling of the resultant data, in which only two classes were used: resistant and susceptible.

The heights of the plants of Hybrid 5 F_2 were measured from the ground line to the apex of the tallest head, excluding the awns from the measurement.

The winterhardiness was estimated in two ways: the percent survival (computed as described on p. 12) and by estimating the percent leaf injury of each plant early in the spring of 1949. In the latter method, the plants were placed in the following classes: those plants with 0%-9%, 10%-49%, 50%-99%, and 100% of their leaves killed and yellowed by winter conditions.

Cyto-morphological Studies

Stem pieces of one plant of Hybrid 1, two plants of Hybrid 4, and one plant of Pawnee were collected after the spikes had formed fully (but had not yet ripened), including the first node below the head. These pieces were killed and fixed in formalin-acetic acid-alcohol (FAA) reagent (31).

The microscope slides were prepared from paraffin sections./3 Each stem piece was sectioned approximately 3 cm. above the first node below the spike.

Material for studying pollen mother-cells was collected, removing the young spikes before the sheath (boot) had started to swell appreciably. Anthers of each spike were studied with iron-aceto-carmine smears to make certain that pollen mother-cells were approximately in the proper stage of development. These spikes were immediately placed in Bouin's killing and fixing fluid (29) and left at least 24 hours. They were then transferred to 50% ethyl-n-butyl alcohol solution (29) and then transferred to 70% solution after 8 hours. Repeated changes of the 70% solution were made until the material was relatively free of picric acid. The n-butyl alcohol technique of dehydration was then followed, using 48° - 50° C. melting point paraffin for the infiltration.

For embedding, approximately 15 grams of beeswax was added to 250 grams (two 1/4-pound blocks) of paraffin. The florets were then sectioned longitudinally at 40 microns and fixed on microscope slides with Szombathy's fixative. Two techniques of staining were tried: safranin O counterstained with fast green FCF (29) and the Cajal-Brozhek technique (15) using basic fuchsin (1 cc. saturated aqueous solution per 250 cc. distilled water) and picro-indigo-carmine (a stock

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/3 The slides were prepared by P. E. Holloway, formerly laboratory technician at this station.

solution of 1 part saturated aqueous picric acid and 2 parts saturated aqueous indigo-carmine, diluted 1:40 in distilled water). The merits of these staining techniques are discussed on subsequent pages of this paper.

Milling and Baking Tests

In 1950, an increase plot of Hybrid 4 was grown and a 5-pound sample sent to the Regional Milling and Baking Laboratory at Manhattan, Kansas. At the same time, a composite sample including seed from all six lines of Hybrid 5 F_2 was prepared and sent with the shipment. A plot of T. vulgare var. Comanche C.I. 11673 was grown and the seed used as a check to compare with the milling and baking tests of Hybrids 4 and 5.

Statistical Methods

All methods used in statistical analyses of data reported in this paper were taken from Snedecor (32).

EXPERIMENTAL RESULTS

Field Notes

The field notes on Hybrid 5 are summarized in Table 2. Each F_2 line and the 5 F_1 plants were earlier than Pawnee in 1950. However, both rows of Pawnee had a space of 2 feet or more on one side of the rows and for their entire lengths due to the winter-killing in Hybrid 4. The Pawnee plants were doubtless comparably later.

The heights of the F_2 lines of Hybrid 5 are not altogether comparable to each other. A gradient in fertility was noted

Table 2. Summary of field observations on the F_1 and F_2 generations of (Triticum spp. X A. elongatum)X Pawnee (Hybrid no. 5) 1949, 1950.

Selection	Reaction to leaf rust of wheat: No. plants resis-tant	No. plants suscep-tible	Total	Inheritance of head type: No. plants fusi-form	No. plants inter-mediate	No. plants cla-vate	Total
Hybrid no. 5 F_2							
'48X15-1	19	33	52	36	12	4	52
'48X15-2	201	161	362	260	81	21	362
'48X15-3	179	146	325	271	54	6	331
'48X15-4	57	118	175	183	0	0	183
'48X15-5	102	91	193	139	47	10	196
'48X15-6	176	143	319	211	93	21	325
Total	734	692	1,426	1,100	287	62	1,449
Hybrid no. 5 F_1							
1949	6	0	6	---	---	---	---
1950	5	0	5	0	5	0	5
Pawnee (P)	0	55	55	55	0	0	55

Selection	Inheritance of awn type: No. plants awn-less	No. plants inter-med-iate	No. plants awned	Total	Plant height: Mean plant height(in.)	No. plants	Maturity: Mean date ripe	No. plants
Hybrid no. 5 F_2								
'48X15-1	7	34	11	52	24.1	52	6-11	52
'48X15-2	71	201	90	362	23.7	360	6-9	359
'48X15-3	58	208	65	331	20.1	331	6-9	329
'48X15-4	67	84	32	183	21.1	183	6-6	183
'48X15-5	39	114	43	196	18.9	195	6-8	194
'48X15-6	75	174	76	325	18.6	325	6-8	319
Total or mean	317	815	317	1,449	20.8	1,446	6-9	1,436
Hybrid no. 5 F_1								
1949	0	6	0	6	---	---	5-6*	6
1950	0	5	0	5	---	---	6-13	5
Pawnee (P)	0	0	55	55	---	---	6-12	55

Table 2 (Continued).

Selection	No. plants 100% leaf injury	No. plants 50-99% leaf injury	No. plants 10-49% leaf injury	No. plants 0-9% leaf injury	Total	Pct. winter survival
	Inheritance of winterhardiness					
Hybrid no. 5 F_2						
'48X15-1	3	14	28	14	59	93.3
'48X15-2	6	88	211	66	371	91.4
'48X15-3	8	73	228	42	351	93.5
'48X15-4	0	37	120	20	177	95.8**
'48X15-5	8	52	122	22	204	91.1
'48X15-6	13	90	205	42	350	89.5
Total or mean	38	354	914	206	1,512	92.4
Hybrid no. 5 F_1						
1949	-	-	-	-	6	100.0
1950	0	0	5***	0	5	100.0
Pawnee (P)	1	0	5***	21	27	96.5

Selection	No. plants dark red seed	No. plants red seed	No. plants light red seed	No. plants golden seed	No. plants white seed	Total
	Inheritance of seed color****					
Hybrid no. 5 F_2						
'48X15-1	2	3	0	0	0	5
'48X15-2	14	46	34	17	3	114
'48X15-3	11	25	32	5	1	74
'48X15-4	5	19	12	2	1	39
'48X15-5	6	14	20	2	1	43
'48X15-6	20	24	12	4	0	60
Total	58	131	110	30	6	335
Hybrid no. 5 F_1						
1949	-	-	-	-	-	-
1950	0	2	3	0	0	5
Pawnee(P)	-	-	-	-	-	-

*Date headed in 1949. Pawnee headed 5-8 in 1949.
**Computed after correction of total to 183 (number mature plants).
***Extent of leaf injury about 20%.
****Seed color data only on resistant plants harvested for further observation.

from the north end to the south end of the range in which the population was growing (line 1 to line 6). The increase in height for line 4 is likely significant, however, since the gradient was noted within this plot as well as all the plots as a group. The possible relationship of the plant height to the clavateness of the heads will be discussed later.

In the fall of 1949, a few plants of Hybrid 4 were infected with leaf rust. The pustules were small and in only a few cases the secondary rings of pustules were formed. Most of these plants were subsequently winter-killed but the surviving plants (3 of 12) were approximately as resistant in the mature-plant stage as the remainder of the population.

During the latter stages of maturation, nearly all plants of Hybrid 4 developed leaf rust pustules. The pustules were small but little or no necrosis was evident in the surrounding host tissue. The daily maximum temperatures ranged from 84° - 95° F. during the same period. Certain plants which were noted and harvested individually, presented resistant reactions (2R) to the disease during this period. The entire population was exceedingly late in maturity and frequently plants with many of their leaves and all of their spikes still green "ripened" in 4-5 days. Normal ripening, in the absence of the high temperatures which occurred at this time, would have required 7-10 days.

The plants of Hybrids 4 and 5 were noted to be susceptible to attack by the green bug (*Toxoptera graminum* Rond.) in the fall of 1949 and to *Septoria* leaf spot (probably caused by *S. tritici* Rob. in Desm.) in 1950 and 1951. Hybrids 4 and 5 differed little from most adapted wheat varieties for susceptibility to greenbugs. Both hybrids were quite susceptible to *Septoria*.

Fertility and Seed Shriveling

The appearance of the pollen of Hybrids 1, 2, and 3 was distinctly different from that of Hybrids 4 and 5 and of Pawnee. The amounts of "class II" pollen accounted for much of this difference. The average percentages of "class II" pollen, shown in Table 3, were: Hybrid 1, 23.9%; Hybrid 2, 47.7%; Hybrid 3, 86.5%. Similar averages for Hybrid 4, Hybrid 5 F_1, and Pawnee were 20.7%, 7.3%, and 0.5% respectively. The better pollen grains (class I) were less turgid in Hybrids 1, 2, and 3 than in the latter two hybrids and Pawnee. The average percentages of bad pollen (class III) were: Hybrid 1, 21.6; Hybrid 2, 18.0; Hybrid 3, 3.4; Hybrid 4, 2.9; Hybrid 5 F_1, 3.3; and Pawnee, 4.0. The detailed data are itemized in the appendix, Table 1.

In the main, the appearance of the pollen of Hybrid 4 and of Hybrid 5 F_1 was good, the pollen grains being large and plump, and the cytoplasm appearing to be rather dense. In Hybrids 1, 2, and 3 the pollen, even in class I, was less plump than in Hybrids 4 and 5 and in Pawnee, the cytoplasm being considerably less dense in the former three hybrids. It was noted that there were large number of pollen grains which were intermediate between classes I and II but that the bounds of class III (bad pollen) were reasonable distinct.

Table 3. Summary of fertility and seed shriveling. 1949, 1950.

Variety or selection	Year	Pollen Pct. class II	Pollen Pct. class III	Pct. fertile florets	Pct. wrinkled seeds
Hybrid 1	1949	-	-	89.5	--
	1950	23.9	21.6	67.5	3.5
Hybrid 2	1949	-	-	96.4	-
	1950	47.7	18.0	92.5	0.8
Hybrid 3	1949	-	-	85.7	-
	1950	86.5	3.4	89.5	1.0
Hybrid 4	1949	-	-	95.0	-
	1950	20.7	2.9	88.7	44.4
Hybrid 5 F_1	1949	-	-	88.3	-
	1950	7.3	3.3	88.7	23.2
Hybrid 5 F_2	1950	-	-	84.1	16.6
Pawnee (ck.)	1950	0.5	4.0	90.3	0.8
Triumph (ck.)	1949				
Space-planted		-	-	97.6	-
1/2 Bu./A.		-	-	94.8	-
Ave.		-	-	96.2	-

In heads which developed normally, the seed-set of the "primary" florets was quite uniform. The development of "secondary" and of "tertiary" florets appears to depend mainly upon the nutrition of the plants as affected by soil fertility and the spacing of the plants and upon their vigor.

The seed-set data are found in Table 3. The averages of the percent fertile primary florets were: Hybrid 1, 67.5; Hybrid 2, 92.5; Hybrid 3, 89.5; Hybrid 4, 88.7; Hybrid 5 F_2, 84.1; and Pawnee, 90.3, in 1950. In 1949, the averages of the percent fertile primary florets were somewhat higher for Triumph than for Pawnee in 1950, the average for plants spaced 3 inches apart being 97.6 and the average for plants seeded at the rate of 0.5 bushels per acre being 94.8. These data are itemized in Appendix Table 1.

There was considerably more wrinkling of the seeds of Hybrid 4 than in any of the other selections in 1950. Although a systematic study of this character was not made in 1949, this condition was not observed. In 1950, the average percentages of seeds of the "wrinkled" class (Table 3) were: Hybrid 1, 3.5; Hybrid 2, 0.8; Hybrid 3, 1.0; Hybrid 4, 44.4; Hybrid 5 F_1, 23.2; Hybrid 5 F_2, 16.6; and Pawnee, 0.8. Similar percentages of "shriveled" seeds were: Hybrids 1, 2, and 3, 0.0; Hybrid 4, 1.2; Hybrid 5 F_1, 0.4; Hybrid 5 F_2, 0.6; and Pawnee, 0.2. These data are itemized in Appendix Table 1.

The appearance of the wrinkled and shriveled seeds may be seen in figure 1. Usually the embryos of the hybrid seeds are not severely affected and the shriveled seeds germinate fairly well. It may be noted in figure 1 that, with slight wrinkling, the shrinkage is found in isolated depressions which are somewhat more numerous on the backs of the kernels. If the pericarp is actually wrinkled in any direction, the wrinkles will lie at right angles to the crease on the backs of the kernels. As the wrinkling becomes more severe, the crease may become more open at the germ end of the kernel, producing a shallow furrow on the side of the kernel which is parallel with the crease (see Fig. 1d, side view).

The effects of seed wrinkling upon plant emergence is, apparently, slight. In the fall of 1950, seeds of the plump and wrinkled classes which were produced by the same plants were planted in paired rows for comparison. Nine such comparisons were made. In an analysis of variance upon emergence (Table 4) no statistically significant differences were observed. In the numbers of plants which emerged and died subsequently (before winterkilling could be construed to have caused the deaths), an F value of 4.08 was obtained for plump versus wrinkled seeds. The tabulated F (5% level of significance) was 5.32. Statistical significance was approached here but more plants from plump seeds died than in those produced from wrinkled seeds.

The percent bad pollen (class III) correlated negatively with the percent fertile primary florets in 1950 (r = -0.643, d.f. = 38; tabulated r0.01 = 0.418, d.f. = 35). This fact indicates that the same factors which affected the pollen development affected fertility of the florets. Upon further study of the data, it becomes apparent that the effects of these factors upon general seed-set are appreciably smaller than the effects upon the pollen.

In other correlation studies, an r value of 0.077 (d.f. = 66) between the percent fertile primary florets and the percent wrinkled seeds was obtained, while the tabulated r0.05 = 0.232 (d.f. = 70). The results were similar in comparing the percent fertile primary florets to the percent shriveled seeds (r = -0.036, d.f. = 66). The correlation coefficient of the percent wrinkled seeds to the date ripe (on Hybrid 5 F_2 only) was 0.373 (d.f. = 26), while the tabulated r0.05 = 0.374 (d.f. = 26). Statistical significance is closely approached in this case and it is assumed that the extremely

Table 4. Analyses of variance upon plant emergence and seedling death with plump and wrinkled seed classes in Hybrid 4. 1950.

Plant Emergence				
Source of variation	d.f.	Sum of squares	Mean square	F
Lines	8	163.73	20.46	-
Plump vs. Wrinkled	1	0.40	0.40	-
Error	8	401.83	50.23	
Total	17	565.96	---	

Pct. Dead Plants 10-23-50				
Source of variation	d.f.	Sum of squares	Mean square	F
Lines	8	183.72	22.97	1.39
Plump vs. Wrinkled	1	67.28	67.28	4.08
Error	8	132.06	16.51	
Total	17	383.06	---	

high temperatures during the ripening period in 1950 were responsible for this correlation. Daily maximum temperatures varied from 84°-95° F. during the latter 4-5 days of the ripening period of these plants.

Genetical Studies

All the genetical data are summarized in Table 2. The apparent discrepancies in the numbers of F_2 plants studied are due to an inability to make the respective observations upon certain plants. For instance, the natural infection of leaf rust in the field became general so late that by the time rust reactions could be estimated, all the leaves were dead on several very early plants. The actual population of F_2 plants was 1,449 at maturity.

The Chi-square test for independence (32) upon the awn type data is found in Appendix Table 2. F_2 lines 3 and 4 differed from the average ratio (total data). The X^2 values were, for line 3, 6.172 (d.f. = 2, P = between 2% and 5%) and for line 4, 23.296 (d.f. = 2, P = less than 1%). On the basis of this test, the awnedness data in line 4 were excluded from tests of genetical ratios of the lines. Line 3 data were included in spite of the fact that they differed significantly from the average for this hybrid, since line 3 appeared to be more similar to the other four lines than to line 4.

The Chi-square tests for goodness of fit to a ratio of 3 completely awnless : 9 tip awned : 4 awned in the inheritance of awnedness are found in Appendix Table 3. If the plants had been classed according to genotype, better fits might be expected. Quisenberry and Clark (26) and Clark (12) reported that there is considerable difficulty involved in the classification of awns in the F_2 generation. In both cases reclassification of the F_2 plants on the basis of the genetical behavior of the F_3 population was necessary. The Chi-square value of 4.307 (d.f. = 2) from the total is non-significant statistically (P = 10-20%).

The inheritance of clavate-headedness is confused by the fact that the Hybrid 4 parent was, apparently, heterozygous for this character. It is also quite difficult to estimate by visual observation the degree of clavateness of a wheat head. It would have been quite desirable to have used Boshnakian's coefficient of squareheadedness (8), especially since clavateness is so easily confused with head density (Fig. 2).

In figure 2, the Boshnakian coefficients of squareheadedness (clavate-headedness) are (left to right) 1.00 (classed fusiform), 1.50 (fusiform), 1.25 (fusiform), 1.40 (intermediate), 2.00 (intermediate), and 1.40 (fusiform). The classifications of the head types given (other than the coefficients of squareheadedness) above are the classifications given in the original data by visual observation and estimation of the degree of clavateness. The range of the coefficients for the "fusiform" types is 1.00-1.50; similarly, the range for the "intermediate" types is 1.40-2.00. In figure 3, the coefficients of squareheadedness are (left to right) 1.40 (classed fusiform), 1.60 (intermediate), 2.00 (clavate), 1.40 (fusiform), and 1.00 (fusiform). The correlation in figure 3 is better between the estimation and the actual measurement of this character. It is notable that these plants were more thinly spaced than the plants of Hybrid 5 F_2 and that the character had a better chance to develop. The low correlation between the F_2 classification and the corresponding coefficients is thought to be due to the closer spacing of the plants and the confusion of clavateness with head density. The average internode lengths in figure 2 are, left to right, 3.6 mm., 4.1 mm., 3.8 mm., 2.7 mm., and 4.0 mm. Similar figures for the heads in figure 3 are, left to right, 4.3 mm., 3.7 mm., 4.0 mm., 4.1 mm., and 4.9 mm.

The classifications of the reactions of the F_2 plants to leaf rust of wheat were easily made. No plants which were intermediate in their rust reaction were noted in the field, except a very few (12 in all) which were infected up to 10% but which presented about a 1R-2R type pustule. All other plants with any pustulation presented susceptible type pustules (3S to 4S). The remaining resistant plants had readings of zero to zero-fleck.

From Appendix Table 4, it may be seen that F_2 lines 1 and 4 had decidedly different ratios for the inheritance of reaction to leaf rust when compared to the other 4 lines. On the strength of this Chi-square test for independence, these two F_2 lines were not included in estimates of the ratio for the inheritance of the resistance in this hybrid.

The Chi-square tests for goodness of fit in lines 2, 3, 5, and 6 to a 9 resistant to 7 susceptible ratio are found in Appendix Table 5. The lowest P values lie between 30% and 50%. While the fit is not noticeably bad at first glance, all the deviations from the expected in the resistant class are negative for all lines, while the corresponding deviations in the susceptible class are positive. For this reason, the goodness of fit is not bettered by the analysis of the total data. Line 4 yields a fair fit to a 4-factor complementary gene ratio (81:175; $X^2 = 0.077$, P = 80-%) but the numbers are rather small to consider such a ratio.

At Stillwater in 1950, the following leaf rust race groups are known to have been present: groups 2, 5, 6, 9, and 21. /4 The urediospores from pustules on the leaves of Hybrid 4 and Hybrid 5 F_2 were inviable so no knowledge of the race groups present on these plants is available. Race groups 5 and 6 were the ones most-frequently isolated from pustules in the nurseries adjacent to the hybrid nursery.

Several plants of Hybrid 4 were tested in the greenhouse during the winter 1950-51 for their reaction to representatives of six race groups. /4 The race groups and the reactions of the plants follow: group 2 (race 15), zero-fleck reaction; group 5, 2R; group 6 (race 105), zero-fleck reaction; group 6 (race 126), zero-fleck reaction; group 9, zero-fleck reaction; group 12 (race 58), zero-fleck reaction; and group 21 (race 54), zero-fleck reaction. These tests were made on the seedling stage of the plants.

Plant height was not analyzed statistically for genetic ratio but it may be stated that the plants of line 4 averaged taller than the other F_2 lines when the apparent soil gradient is considered. The possible significance of this observation will be discussed later.

Little can be stated about the inheritance of winterhardiness except that the Pawnee type of winterhardiness is dominant to the lower tolerance to winter conditions of

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/4 The identification of these race groups and the tests of the reaction of Hybrid 4 to leaf rust were made by Dr. Harry C. Young, Jr., and D. F. Wadsworth, cereals pathologists at this station.

Hybrid 4. The F_1 plants were as winterhardy as Pawnee or nearly so. The effects of the genes for winterhardiness appear to be cumulative.

Leaf rust resistance was associated with clavate-headedness in the F_2 population of Hybrid 5 (Appendix Table 6). P values of 10-20% for line 1, 10-20% for line 2, 1-% for line 3, 1-% for line 5, 1-% for line 6, and 1-% for the total data were recorded. The X^2 value for independence (total of individual X^2 values except those from the total data) was 75.456 (d.f. = 15, P = 1-%). The assumption was that if clavateness was associated with resistance in this hybrid, then the ratios of resistant to susceptible plants of each head type classification should differ. These data indicate that such was the condition.

Clavate-headedness was associated with short plant height in Hybrid 5 F_2. The average height in inches of the fusiform plants was 21.6, and for intermediate and clavate-headed plants, the heights were 19.9 and 19.5 respectively. Furthermore, line 4 was appreciably taller than the other F_2 lines and produced no clavate heads (according to the method of classification in 1950).

An association between clavate-headedness and awn type was not observable from the F_2 data. A test for association similar to that presented in Appendix Table 6 yielded a non-significant value of Chi-square for independence. Similarly, no association between resistance to leaf rust and awn type was observable.

Leaf rust resistance is probably not associated with seed color in this hybrid or the fit to the 3-factor ratio should be less apparent. The number of plants is quite small to estimate a 3-factor ratio but the fit in the total data is quite good. In a Chi-square test for independence (Appendix Table 7), line 6 differed from the average ratio (from the total data), the difference being statistically significant beyond the 1% point (X^2 = 13.328, d.f. = 4, P = 1-%). Upon grouping the first three classes and testing for a 57 red : 6 "golden" : 1 white ratio (Appendix Table 8), P = 30-50% for line 6 and 90-95% for the total data. The P value was reduced for line 2 by this grouping but it is still greater than 5%. A considerable error in classification was inevitable in these studies.

Although no statistical test was made, apparently the Hybrid 4 type of leaf rust resistance is associated with low winterhardiness. At any rate, most of the plants which were injured most severely by winter conditions were rust-resistant. Most of these plants were late, also, due, in part, to the fact that the winter injury was so severe that they were barely able to mature seed. This fact may account, at least in part, for the apparent association between rust resistance and late maturity.

Cyto-morphological Studies

Stem sections of only one plant of each of two selections from Hybrid 4, one selection from Hybrid 1, and of Pawnee were prepared, so no conclusions may be drawn. However, certain differences seem, at this juncture, to be quite definite (Figs. 4-7). A considerably larger quantity of mechanical tissue is present in the stems of Hybrid 4, and to a lesser extent in Hybrid 1, than is seen in Pawnee. The numbers of vascular bundles in the stem are also greater in both hybrids, especially the former. The latter condition may be associated, to a considerable extent, with the greater stem diameter of the hybrids as compared to Pawnee. A distinct band of parenchyma tissue is evident between the inner and outer series of vascular bundles in Hybrid 4. This band is considerably less evident in Hybrid 1. Both types of hybrids seem to have a greater amount of lignin-like substance on the outer surface of the epidermis than Pawnee. Another local wheat variety, Red Chief C.I. 12109, produces this character, however.

In general, Hybrid 1 is fairly similar to Pawnee in its stem morphology while Hybrid 4 is quite different from Pawnee. The large stem diameter is characteristic of several wheat varieties which are not adapted to this area, especially club wheat (*T. compactum*) varieties. The mechanical tissue increase in Hybrid 4 over Pawnee may well have been inherited from its *Agropyron* ancestor.

For paraffin sections of wheat florets for pollen mother-cells, the staining is exceedingly critical due to the thickness at which the material must be cut (40 microns). The size of wheat pollen mother-cells is approximately 30 microns so this thickness must be exceeded to assure having at least some nuclei which are still entire.

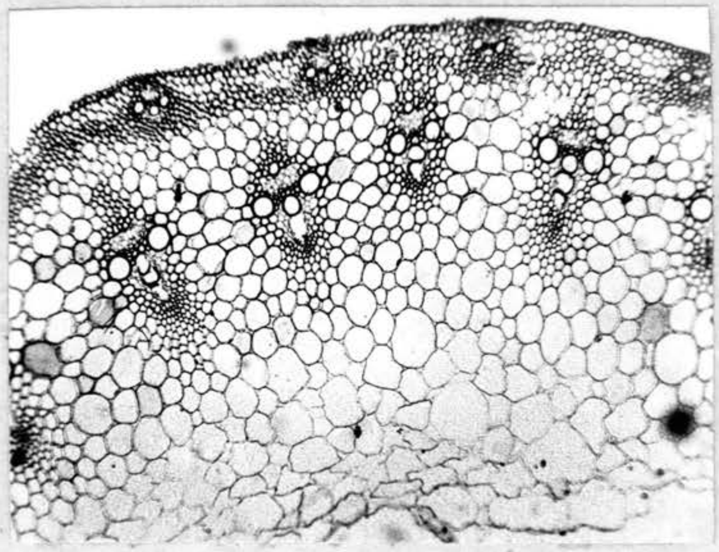

Figure 4. Photomicrograph of a stem cross section from Hybrid 4 (Stw. 493857-2H1).

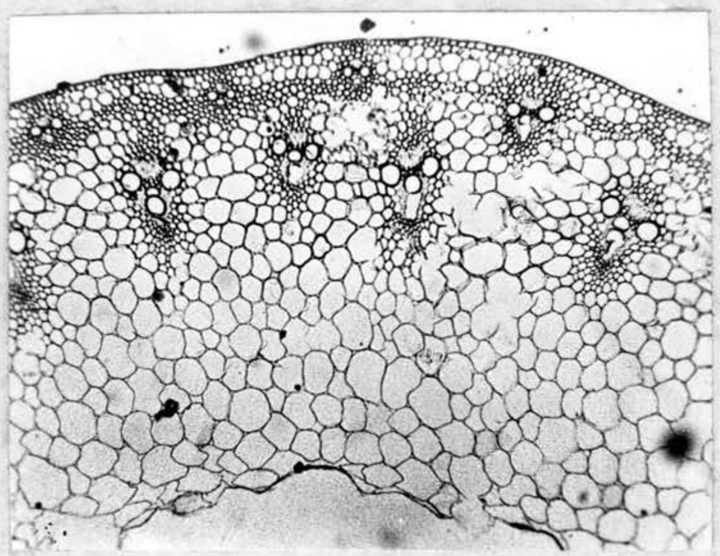

Figure 5. Stem cross section from Hybrid 4 (Stw. 493857-3).

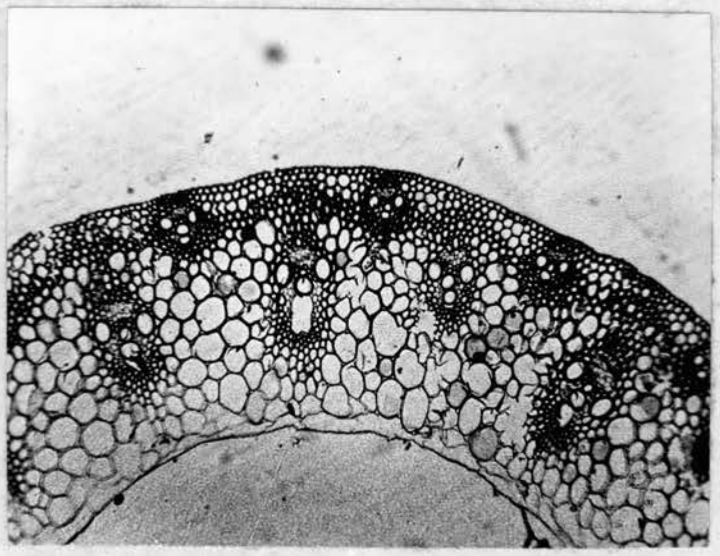

Figure 6. Stem cross section from Hybrid 1 (Stw. 493856-1).

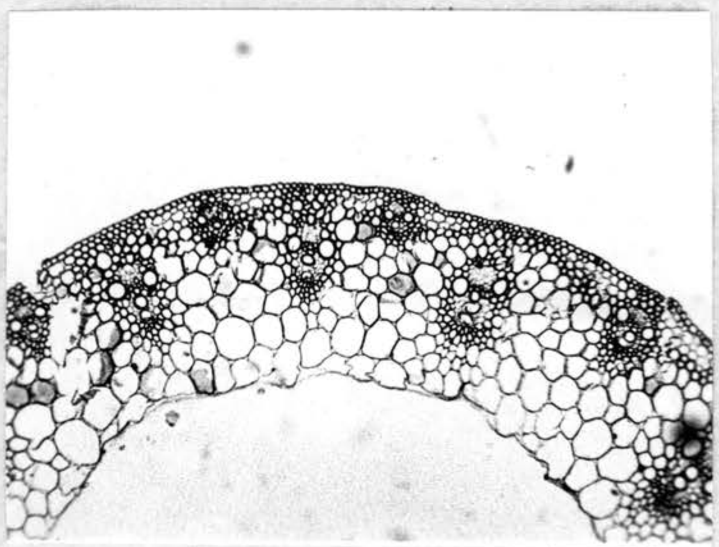

Figure 7. Stem cross section from Pawnee wheat (C.I. 11669).

Bouin's killing and fixing fluid (28) is quite satisfactory for pollen mother-cells except for the difficulty encountered in removing the picric acid. The picric acid causes some difficulty in staining the material. Nawaschin's reagent (28) is less convenient to use since it must be freshly prepared for each collection. Better staining results are obtained following Nawaschin's, however. The safranin O-fast green FCF technique is unsatisfactory for wheat chromosomes as followed by the author when Bouin's fluid is used as the killing and fixing reagent. Its performance following Nawaschin's in wheat material is unknown but on Indian grass (Sorghastrum nutans (L.) Nash) fair staining results may be obtained. In wheat too much safranin is retained by the chromosome matrix of material killed and fixed in Bouin's.

The Cajal-Brozhek technique (15) was modified considerably and proved to be quite satisfactory for staining following either Nawaschin's or Bouin's. Somewhat better results are obtained with material killed and fixed in Nawaschin's. Also, the concentration of the basic fuchsin had to be modified considerably, depending on the killing-fixing reagent used. Following Nawaschin's, the stock solution of basic fuchsin (saturated aqueous) must be diluted at the rate of 1 drop to 40 cc. distilled water. Following Bouin's, 1 cc. stock solution per 250 cc. distilled water was used.

None of the multinucleate tetrad cells mentioned by Peto (23) and Vakar (38) were noted. The results of the pollen studies indicated that the pollen development and meiosis were fairly regular. Lagging chromosomes are frequent both in the hybrids and Pawnee but these chromosomes are not usually lost. Sufficient progress towards the poles of the spindle is made to escape entrapment in the cell plate and to allow inclusion in the daughter nuclei.

Milling and Baking Tests

The percent ash (Table 5) for Hybrid 4 was (in 1950) 1.74%, while that of Hybrid 5 F_2 (1.59%) more nearly approached the ash content of Comanche (1.49%). The protein content of Hybrid 4 was also higher than the Comanche check, the analysis being 16.5%, while Hybrid 5 F_2 and Comanche contained 13.9% and 13.4% respectively. In the flour, the higher percentage of protein of Hybrid 4 is also apparent, the percent protein being 15.0 for Hybrid 4, 12.4 for Hybrid 5 F_2, and 12.2 for Comanche. The water absorption was unsatisfactory for Hybrids 4 and 5 F_2 being 57.4% and 54.6% respectively, while Comanche absorbed 62.7% of its dry weight of water. The loaf volume was quite good for both hybrids, Hybrid 4 being 1160 cc., Hybrid 5 F_2 925 cc., and Comanche 895 cc. Hybrid 4 was rated unsatisfactory in milling and baking for hard wheat due to its softness, while Hybrid 5 F_2 was of questionable quality for hard wheat. The Test weights (in pounds per bushel) were: Hybrid 4, 52.4; Hybrid 5 F_2, 59.1; and for Comanche, 60.2.

DISCUSSION

Fertility and Seed Shriveling

The fertility of Hybrids 2, 3, 4, and 5 is good although

Table 5. Milling and baking data for Hybrid 4 and Hybrid 5 F_2. 1950.

Variety or selection	Seed*: Wt./bu. (lbs.)	Seed*: Pct. ash	Seed*: Pct. protein	Seed*: Pct. flour yield	Flour*: Pct. ash	Flour*: Pct. protein
Hybrid 4	52.4	1.74	16.5	64.0	0.45	15.0
Hybrid 5 F_2	59.1	1.59	13.9	69.4	0.49	12.4
Comanche (ck.)	60.2	1.49	13.4	71.7	0.41	12.2

Variety or selection	Bread and baking data: Pct. H_2O absorption	Mixing time (min.)	Loaf volume (cc.): as received	Loaf volume (cc.): Corrected 13% protein
Hybrid 4	57.4**	2 3/8	1160	1008
Hybrid 5 F_2	54.6**	2 1/8	925	968
Comanche (ck.)	62.7	4 1/2	895	950

*Computed on a 14% moisture basis.

**Unsatisfactory for hard red winter wheat.

not excellent. If fertility alone were limiting seed yields, the yields of these hybrids should compare favorable with varieties of T. vulgare. Hybrid 1 has fair to good fertility and the seed-set of its backcross derivatives is improved. An important note is that the correlation coefficient in the comparison of the seed-set in 1949 with the derivatives of the plants studied when grown in 1950 was quite low. The value of $r = 0.199$ (d.f. = 17) was obtained; the tabulated value of $r0.05$ is 0.456 (d.f. = 17).

While very few comparisons could be made, these data indicate that environment is affecting the seed-set to a greater extent than the chromosome or genetic constitution of the plants.

The significance of the "class II" pollen is uncertain at this time. Apparently, however, these pollen grains which are only partially filled with cytoplasm are germinable and capable of effecting fertilization. There is little doubt that the "class III" pollen was inviable since the greater percentage of the pollen grains were completely empty and the remainder were so small and contained so few granules of cytoplasm that inviability can be assumed.

The correlation of the percent bad pollen with the percent fertile primary florets is to be expected. The indication is that the same factors which affected seed-set as a whole also affected the pollen, but that they affected the former to a lesser extent in most cases.

The observation of Nissen (22) that the appearance of pollen which is squeezed from relatively ripe anthers is better than that which is shed through normal anther dehiscence, was confirmed in this study. Whether or not the same observation would be valid if one observed pollen immediately following dehiscence is questionable, however.

The low correlations between the percent fertile primary florets and the percent wrinkled or shriveled seeds indicate that extreme chromosomal aberrations are not involved in seed shriveling. Since Hybrid 4, in which the most severe seed shriveling is found, was produced originally in California, it is thought that this shriveling is a manifestation of poor adaptation to Oklahoma growing conditions. If such is the case, one should expect the seed quality to be improved markedly by crossing this selection with an adapted wheat variety; that was exactly what was observed.

It was noted that the embryos appeared to be normal in all but the most strongly shriveled seeds. This observation was confirmed insofar as the studies extended in that the emergence was no lower in plants produced from wrinkled seeds than from plump seeds of approximately the same size. Furthermore, a smaller percentage of the plants from wrinkled seeds died after emergence than did those from plump seeds. No particular significance is attributed to this latter observation except that it indicates that the ability of the wrinkled seeds to produce plants capable of survival is not poorer than the ability of the plump seeds. It may well be pointed out that the conditions of soil tilth and moisture at the time the hybrids were seeded in October, 1950 were very near the optimum for wheat germination. No differences in vigor of the seedlings were observable except in the plants produced by strongly shriveled seeds.

Genetical Studies

The reason for the different ratios in the inheritance of leaf rust resistance in F_2 lines 1 and 4 of Hybrid 5 is uncertain at this time. Several possibilities may be suggested, however. There seems to be a relationship between the clavateness of the spikes and the resistance to leaf rust in this hybrid population. Conclusions pertaining to the nature of this association could not be derived from this study. This fact is especially true when one considers that the data are unreliable due to the method of estimation of the degree of the development of clavateness. The indicated association, even with the erroneous method of collecting data, cannot be ignored.

Assuming the relationship between clavateness and leaf rust resistance to be direct, then some factor involved in the production of this head type must influence resistance. Boshnakian (8) stated that the factors which influence the production of clavate heads are the tightness of the leaf sheath, the growth pressure of the plant stem as influenced by the genetics, the nutrition, the vigor of the plant, and the attitude of the spikelets on the rachis (i.e., the angle formed between the spikelet and the rachis). The influence of vigor and nutrition cannot be ignored, although better nutrition might tend towards a more succulent growth and more ease of infection by the pathogen. The direct effect of the attitudes of the spikelets can hardly be assumed to affect resistance. The most likely factor is the tightness of the leaf sheath. One cause of the tightness might be the amount of mechanical tissue present in the leaf sheath and the resultant inflexibility of this organ. If such be the case then the resistance should be due, in part at least, to the inability of the pathogen to form a pustule. Further observations along these lines may be desirable. It was noted that pustules of stem rust were small and appeared to be restricted in size although no physiological resistance to this disease was observed.

A second explanation suggested is that the resistance is largely physiological and that the association with head type is due to genetical linkage. Since the inheritance of clavateness is thought to be complex, linkage of this sort could be easily visualized. There is an appreciably greater amount of mechanical tissue present in Hybrid 4, at least in the stems, than in Pawnee. From studies made at this station on other varieties it was seen that Pawnee is typical of adapted varieties in this respect. The source of the increased mechanical tissue may be assumed to be the *A. elongatum* ancestor of this selection. Therefore, the source of clavateness may have been derived from *Agropyron*, even though this parent species was not clavate-headed itself. Cicin (11) reported clavate head types were found in wheat-like derivatives of *Triticum*-*Agropyron* hybrids. Since the source of resistance is supposed to be, in this case, *A. elongatum*, a genetical linkage between these two characters is not difficult to visualize. This concept is even more tenable when it is considered that the resistant fusiform-headed types are, so far as could be observed, as resistant as the clavate-headed types. Thus, if genetical linkage is involved, it is not complete.

It is assumed that the inheritance of resistance is more complex than the apparent 9:7 ratio for the four F_2 lines with similar ratios would indicate. The fact that all deviations have the same sign is the principal factor in this assumption. The fact that both ratios obtained (9:7, 81:175) resemble inheritance with complementary genes is easily visualized if one genetical factor controls the resistance to a single race or group of races. Since dominance of the genes giving resistance was complete, one of each of the genes controlling resistance to the races present should have to be in the dominant condition to prevent a plant from presenting a susceptible reaction in the field.

The actual leaf rust races which were present on Hybrid 5 F_2 are not known. One might reasonably assume that groups 5 and 6 were the most abundant as these groups were more frequently isolated from field collections than the other race groups (2, 9, and 21). The possibility that one or more additional races may have been present on lines 1 and 4 than on the other F_2 lines should not be overlooked. The three rows of line 3 which were adjacent to line 4 had 15 resistant and 15 susceptible plants, 10 resistant and 16 susceptible, and 15 resistant and 15 susceptible respectively, moving successively farther away from line 4. Line 3 grew on the north side of line 4 and the wind was frequently in the south and may have received spores from line 4. There was little time for general secondary infection after the first pustules were observed on these hybrids. Not more than 1 to 2 generations of the rust organism could have evolved by the time the reactions were read. Further observations upon this character may help to clarify these difficulties.

The fact that Hybrid 4 is not completely immune to leaf rust race group 5 in the seedling stage may well account for the presence of leaf rust on certain plants of this hybrid in October, 1949. The fact that such fall-rusted plants which did survive the winter (3 plants of 12) appeared to be as resistant in the adult-plant stage as the other plants of this hybrid is considered to be significant and encouraging.

An explanation of the rust susceptibility of the plants of Hybrid 4 as they neared maturity in 1950 is not immediately forthcoming. The maximum temperatures during the latter 10 days of the ripening period ranged from 84^{o}-95^{o}F. That this temperature was injurious to these plants is evident from their appearance. At a stage in which ripening appeared to be fully 1 to 2 weeks away, the plants "ripened" in 4 to 5 days. The effects of the temperature on the susceptibility of these plants is suggested.

The greater average height of the plants in F_2 line 4 (Table 2) may be related to the head type, either clavateness or density. Boshnakian (8) reported that both head clavateness and density correlated with short height. The effect of head density is more apparent from his studies but one would expect such a relationship due to the simpler inheritance of head density.

The awn segregation must be studied in the F_3 generation if any conclusions, even tentative, may be drawn. The difficulty in classifying the genotypes without using the genetical behavior of the offspring of the F_2 plants is recognized by Quisenberry and Clark (26) and by Clark (12). These two workers have concluded that two principal factors are involved in cases of hybrids between true awnless and fully awned wheat varieties. Such is the assumption of the author for the hybrids studied.

The different ratio for line 4 presents some difficulties if it is not the result of erroneous classification of the awn character of each plant of this line. Observations of the F_3 population which is growing in the field at the time of this writing should help to clarify this situation. Clark (12) and Quisenberry and Clark (26) assumed that a number of modifying factors were involved in the inheritance of awnedness. Since the Hybrid 4 parent plant was, apparently, heterozygous for several of the modifying factors as well. The fact that line 4 produced no clavate heads (as classified in 1950) is not a suitable explanation since no association between clavateness and awn type was demonstrable. Likely the difficulty of classification coupled with the modifying factors will best account for the excess of plants classified completely awnless.

If the 3:9:4 ratio is assumed, one may logically place the following genotypes in the respective classes: completely awnless, 1 AABB and 2 AABb; tip awned, 1 AAbb, 2 AaBB, 4 AaBb, and 2 Aabb; awned, 1 aaBB, 2 aaBb, and 1 aabb. A further breakdown of the classes into the respective genotypes should be possible within limits. Such a reclassification was tried by the author on the two extreme awn classes (completely awnless and awned) of the plants harvested for further observation and selection.

Two fairly definite types were selected within the completely awnless class: one which was assumed to be homozygous awnless with the genotype AABB (head 6, Fig. 2), and one which was assumed to be heterozygous for the factor which had the lesser effect on the awn type of the two genes involved (head 5, Fig. 2). One-third of this class was placed in the first group and 2/3 in the latter group. This separation may help to confirm the segregation assumed.

The separation of those heads in the awned group was less successful. Only two groups were separable and these groups separated the awn type class on, approximately, a 1:1 basis. The two groups are illustrated in figure 2, heads 1 and 2. Head 1 has awns of practically the same length on all spikelets while head 2 has no awns on the basal spikelet and somewhat reduced awns on the spikelet immediately above it.

The excellent fit of those plants sampled for seed color to a 63:1 ratio is important in this study. Firstly, since only rust-resistant plants were sampled, it indicated independent inheritance of these two characters. Secondly, it indicates normal behavior in the three wheat chromosomes carrying the genes for color. The lack of association is a further indication that this type of leaf rust resistance is an <u>Agropyron</u> character and is not derived from <u>Triticum</u>. At any rate, the genes are on none of these three wheat chromosomes or the percentage of linkage is practically zero.

Milling and Baking Quality

As should be expected when considering the softness of the kernels of Hybrid 4, its milling and baking quality for bakers' flour is poor. The loaf volume is quite good but the water absorption is unsatisfactory. The protein content of the seeds is considerably greater than Comanche, which was used for the wheat check. Armstrong and Stevenson (4) reported similar results in F_5 plants of T. vulgare X A. elongatum in that the hybrid derivatives were markedly higher in protein content than the seeds of the wheat parent.

The F_2 population of the backcross of Hybrid 4 to Pawnee produced seed which was markedly improved in its milling and baking quality over its low quality parent (Hybrid 4). As might be expected, the protein content decreased to a percentage much nearer the average for hard red winter wheat seed. The loaf volume was still good but the water absorption was not improved; in fact, it was slightly less than in its Hybrid 4 parent.

SUMMARY

1. Two derivatives of hybrids involving Triticum spp. and Agropyron elongatum (Host) Beauv. and their backcrosses were studied for several characters.

2. Characters studied were fertility, seed wrinkling and shriveling, milling and baking quality, cyto-morphology of the stems, and genetical studies of the inheritance of resistance to leaf rust of wheat, awnedness, clavate-headedness,

and seed color.

3. The hybrid (*T. vulgare* var. Chinese X *Secale cereale*) X *A. elongatum*) X *T. vulgare* var. Forward proved to be susceptible to leaf rust under field conditions and was studied for only a part of these characters.

4. The hybrid *Triticum* spp. X *A. elongatum* backcrossed to wheat (Hybrid 4) proved to be quite resistant to leaf rust in the field, usually presenting a reaction of zero to zero-fleck.

5. A reaction of zero-fleck to representatives of race groups 2, 6,(2 races), 9, 12, and 21 was observed in the latter hybrid in the greenhouse in the seedling stage of growth. Race group 5 (race 5) produced a 2-resistant reaction.

6. Fertility of both hybrids and their backcross progeny ranged from fair to good as indicated by studies of the pollen and seed-set.

7. Fertility in the hybrid mentioned in item 3, above (Hybrid 1), was increased by backcrossing to wheat.

8. The significance of the quantities of partially filled pollen grains cannot be interpreted by the author at this time. Apparently these pollen grains were viable.

9. A significant negative correlation ($r = -0.643$) was obtained between the percent bad pollen and the percent fertile primary florets.

10. A considerable amount of wrinkling and shriveling of seeds was observed in the plants of Hybrid 4 (item 4, above). It is thought that the causes are genetic rather than due to chromosomal aberrations.

11. The milling and baking quality of Hybrid 4 was unsatisfactory but was improved markedly by backcrossing to Pawnee wheat.

12. A 2-factor genetical ratio was observed in the awn segregation of 5 of 6 F_2 lines of Hybrid 4 X Pawnee. The interpretation of the ratio for the remaining F_2 line awaits F_3 data.

13. Clavate-headedness is thought to be complex in its inheritance. A considerable amount of error was introduced into the studies of this character due to the manner of estimating the degree of its development.

14. A 3-factor genetic ratio for the inheritance of seed color was in the hybrid mentioned in item 12.

15. Two ratios for the inheritance of leaf rust resistance were obtained: 9 resistant : 7 susceptible and 81 resistant : 175 susceptible ratios. It is suggested that the inheritance is complex.

16. Leaf rust resistance of the Hybrid 4 type was dominant to the susceptibility of Pawnee.

17. Winterhardiness of the Pawnee type was dominant in a cross with Hybrid 4.

18. Leaf rust resistance was associated with clavate-headedness in the F_2 population studied.

19. The Cajal-Brozhek staining technique using basic fuchsin and picro-indigo-carmine was found to be satisfactory as a chromosome stain in pollen mother-cells of wheat in paraffin sections following either Bouin's or Nawaschin's

killing and fixing reagents.

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APPENDIX

TABLE OF CONTENTS

Table 1. Fertility and seed shriveling in Hybrids 1, 2, 3, 4, and 5. 1949-1950.

Selection	Sel'n. no.	Pollen studies*: No. pollen grains studied	Pollen studies*: Pct. class I	Pollen studies*: Pct. class II	Pollen studies*: Pct. class III	Seed-set**: No. florets	Seed-set**: Pct. seed-set	Seed shriveling**: No. seeds studied	Seed shriveling**: Pct. wrinkled seeds	Seed shriveling**: Pct. shriveled seeds
1. (Chinese-rye X *A. elongatum*) X Forward										
	493853-5-1	599	23.4	74.0	2.7	74	86.5	63	12.7	0.0
	493853-5-2	153	85.0	0.7	14.4	70	60.0	42	0.0	0.0
	493853-5-3	571	68.3	21.9	9.8	167	68.3	113	0.9	0.0
	493853-5-4	201	66.2	7.5	26.4	294	74.5	100	2.0	0.0
	493853-5-5	161	29.8	15.5	54.7	108	48.1	51	2.0	0.0
Mean			54.5	23.9	21.6		67.5		3.5	0.0
	493853-5	Parent plant grown in 1949			--	200	89.5	--	--	--
2. Hybrid No. 1 X C.I. 12128										
	'48X13-2-1	446	12.6	69.7	17.7	96	93.7	100	1.0	0.0
	'48X13-2-2	333	2.7	71.5	25.8	208	88.0	100	0.0	0.0
	'48X13-2-3	72	41.7	26.4	31.9	163	84.7	100	2.0	0.0
	'48X13-2-4	438	64.6	29.2	6.2	16	100.0	16	0.0	0.0
	'48X13-2-5	317	49.8	41.6	8.5	204	96.1	100	1.0	0.0
Mean			34.3	47.7	18.0		92.5		0.8	0.0
	'48X13-2	F_1 plant grown in 1949			--	248	96.4	--	--	--
3. Hybrid No. 1 X Tenmarq										
	'48X14-3-1	350	7.1	86.0	6.9	185	89.2	100	0.0	0.0
	'48X14-3-2	498	12.2	85.3	2.4	326	88.0	100	0.0	0.0
	'48X14-3-3	416	2.4	95.2	2.4	437	87.6	100	2.0	0.0
	'48X14-3-4	583	3.3	94.5	2.2	227	95.6	100	0.0	0.0
	'48X14-3-5	567	15.3	81.7	3.0	86	81.4	100	1.0	0.0
	'48X14-3-6	325	20.9	75.7	3.4	44	95.4	72	2.8	0.0
Mean			10.2	86.5	3.4		89.5		1.0	0.0
	'48X14-3	F_1 plant grown in 1949			--	14	85.7	--	--	--

Table 1 (Continued)

Selection	Sel'n. no.	Pollen studies* No. pollen grains studied	Pct. class I	Pct. class II	Pct. class III	Seed-set** No. florets	Pct. seed-set	Seed shriveling** No. seeds studied	Pct. wrinkled seeds	Pct. shriveled seeds
4. *Triticum* spp. X *A. elongatum*										
	493959-5-1	315	12.1	86.7	1.3	174	91.9	100	78.0	11.0
	493959-5-10	273	94.5	2.9	2.6	124	88.7	100	73.0	1.0
Mean			53.3	44.8	2.0		90.3		75.5	6.0
	493959-5	Parent plant grown in 1949				34	88.2			
	493959-12-1	624	93.4	5.4	1.1	254	92.1	100	57.0	0.0
	493959-12-2	139	95.0	0.7	4.3	204	96.1	100	57.0	2.0
	493959-12-3	269	99.6	0.0	0.4	105	86.7	87	94.2	0.0
Mean			96.0	2.0	1.9		91.6		69.4	0.7
	493959-12	Parent plant grown in 1949				30	100.0	-	-	-
	493959-33-1	247	98.4	0.4	1.2	174	97.1	100	61.0	0.0
	493959-33	Parent plant grown in 1949				36	97.2	-	-	-
	493959-42-1	253	84.2	5.9	9.9	406	69.7	100	42.0	0.0
	493959-42	Parent plant grown in 1949				24	95.8	-	-	-
	493959-47-1	318	95.6	0.6	3.8	634	89.0	100	9.0	0.0
	493959-47	Parent plant grown in 1949				34	91.2	-	-	-
	493959-60-1	256	90.6	2.0	7.4	488	86.3	100	27.0	2.0
	493959-60	Parent plant grown in 1949				32	90.6	-	-	-
	493959-76-1	249	96.0	0.0	4.0	668	86.2	100	14.0	0.0
	493959-76	Parent plant grown in 1949				22	100.0	-	-	-
	493959-77-1	435	97.0	1.6	1.4	281	83.6	100	31.0	1.0
	493959-77	Parent plant grown in 1949				24	95.8	-	-	-
	493959-84-1	105	90.5	1.9	7.6	717	87.3	100	32.0	0.0
	493959-84	Parent plant grown in 1949				32	100.0	-	-	-

Table 1 (Continued)

Selection	Sel'n no.	Pollen studies* No. pollen grains studied	Pct. class I	Pct. class II	Pct. class III	Seed-set** No. florets	Pct. seed-set	Seed shriveling** No. seeds studied	Pct. wrinkled seeds	Pct. shriveled seeds
4. *Triticum* spp. X *A. elongatum* (Cont'd)										
	493959-87-10	383	77.5	21.7	0.8	158	91.8	100	26.0	0.0
	493959-87-13	517	38.3	60.5	1.2	364	95.9	100	20.0	0.0
Mean			57.9	41.2	1.0		93.8		23.0	0.0
	493959-87		Parent plant grown in 1949			34	91.2	---	--	-
Mean Hybrid No. 4 1950			76.4	20.7	2.9		88.7		44.4	1.2
Mean Hybrid No. 4 1949			--	--	--		95.0		--	--
5. Hybrid No. 4 X Pawnee										
	'48X15-1-1	--	--	--	--	76	96.1	50	0.0	0.0
	'48X15-1-2	--	--	--	--	140	78.6	50	68.0	0.0
	'48X15-1-3	--	--	--	--	112	93.7	50	6.0	0.0
	'48X15-1-4	--	--	--	--	234	74.8	50	8.0	0.0
	'48X15-1-5	--	--	--	--	148	80.4	50	16.0	0.0
Mean							84.7		19.6	0.0
	'48X15-1		F_1 plant grown in 1949			106	77.4	--	--	--
	'48X15-2-6	--	--	--	--	201	85.6	50	26.0	0.0
	'48X15-2-49	--	--	--	--	174	96.5	50	50.0	2.0
	'48X15-2-73	--	--	--	--	348	82.5	50	2.0	0.0
	'48X15-2-80	--	--	--	--	251	93.2	50	8.0	0.0
	'48X15-2-91	--	--	--	--	112	86.6	50	36.0	0.0
Mean							88.9		24.4	0.4
	'48X15-2		F_1 plant grown in 1949			432	89.6	--	--	--
	'48X15-3-7	--	--	--	--	514	69.6	50	32.0	2.0
	'48X15-3-8	--	--	--	--	278	74.5	50	10.0	10.0
	'48X15-3-17	--	--	--	--	350	90.9	50	20.0	0.0

Table 1. (Continued)

Selection	Sel'n no.	Pollen studies* No. pollen grains studied	Pollen studies* Pct. class I	Pollen studies* Pct. class II	Pollen studies* Pct. class III	Seed-set** No. florets	Seed-set** Pct. seed-set	Seed shriveling** No. seeds studied	Seed shriveling** Pct. wrinkled seeds	Seed shriveling** Pct. shriveled seeds
5. Hybrid No. 4 X Pawnee (Cont'd)										
	'48X15-3-20	--	--	--	--	274	82.8	50	14.0	0.0
	'48X15-3-56	--	--	--	--	228	72.4	50	8.0	2.0
Mean							78.0		16.8	2.8
	'48X15-3	F_1 plant grown in 1949				470	84.7	--	--	--
	'48X15-4-9	--	--	--	--	106	89.6	50	0.0	0.0
	'48X15-4-14	--	--	--	--	114	86.0	50	0.0	0.0
	'48X15-4-24	--	--	--	--	140	80.7	50	4.0	0.0
	'48X15-4-31	--	--	--	--	177	89.3	50	0.0	2.0
Mean							86.4		1.0	0.5
	'48X15-4	F_1 plant grown in 1949				230	94.8	--	--	--
	'48X15-5-13	--	--	--	--	207	81.2	50	20.0	0.0
	'48X15-5-19	--	--	--	--	232	86.2	50	0.0	0.0
	'48X15-5-23	--	--	--	--	138	96.4	50	2.0	0.0
	'48X15-5-32	--	--	--	--	308	81.2	50	30.0	0.0
Mean							86.2		13.0	0.0
	'48X15-5	F_1 plant grown in 1949				286	88.1	--	--	--
	'48X15-6-11	--	--	--	--	422	80.6	50	14.0	0.0
	'48X15-6-25	--	--	--	--	440	80.4	50	6.0	0.0
	'48X15-6-32	--	--	--	--	138	75.4	50	32.0	0.0
	'48X15-6-51	--	--	--	--	190	82.6	50	38.0	0.0
	'48X15-6-54	--	--	--	--	176	86.9	50	16.0	0.0
Mean							81.2		21.2	0.0
	'48X15-6	F_1 plant grown in 1949				380	95.3	--	--	--

Table I. (Continued)

Selection	Sel'n no.	Pollen studies* No. pollen grains studied	Pct. class I	Pct. class II	Pct. class III	Seed-set** No. florets	Pct. seed-set	Seed shriveling** No. seeds studied	Pct. wrinkled seeds	Pct. shriveled seeds
5. Hybrid No. 4 X Pawnee (Cont'd)										
F_1 1950	'48X15-7	556	68.9	26.6	4.5	160	87.5	100	0.0	0.0
	'48X15-8	597	97.0	1.2	1.8	162	90.1	100	39.0	1.0
	'48X15-9	466	94.0	4.3	1.7	274	87.6	100	37.0	0.0
	'48X15-10	293	90.4	3.8	5.8	360	87.8	100	24.0	0.0
	'48X15-11	371	96.8	0.5	2.7	456	90.3	100	16.0	1.0
Mean F_1 1950			89.4	7.3	3.3		88.7		23.2	0.4
Mean F_1 1949			--	--	--		88.3		--	--
Mean F_2 1950			--	--	--		84.1		16.6	0.6
Mean Hybrid No. 5 1950			89.4	7.3	3.3		84.8		17.6	0.6
6. Pawnee wheat C.I. 11669 (ck.) grown in 1950										
	4370-8	485	92.6	1.2	6.2	56	96.4	53	0.0	0.0
	4370-13	481	97.3	0.6	2.1	156	87.2	100	3.0	1.0
	4370-14	534	95.3	0.9	3.7	176	90.9	100	1.0	0.0
	4370-18	258	94.6	0.0	5.4	58	82.8	48	0.0	0.0
	4370-19	207	97.6	0.0	2.4	122	94.3	100	0.0	0.0
Mean			95.5	0.5	4.0		90.3		0.8	0.2
7. Triumph wheat C.I. 12132 (ck.) grown in 1949, space planted										
	3808-1	--	--	--	--	96	97.9	--	--	--
	3808-2	--	--	--	--	182	96.2	--	--	--
	3808-3	--	--	--	--	394	96.7	--	--	--
	3808-4	--	--	--	--	154	98.7	--	--	--
	3808-5	--	--	--	--	260	96.9	--	--	--
	3808-6	--	--	--	--	438	98.6	--	--	--
	3808-7	--	--	--	--	150	100.0	--	--	--

Table 1 (Continued)

Selection	Sel'n no.	No. pollen grains studied	Pct. class I	Pct. class II	Pct. class III	Seed-set** No. florets	Seed-set** Pct. seed-set	Seed shriveling** No. seeds studied	Seed shriveling** Pct. wrinkled seeds	Seed shriveling** Pct. shriveled seeds
		Pollen studies*								
7. Triumph wheat (Space-planted) (Cont'd)										
	3808-8	--	--	--	--	256	96.5	--	--	--
	3808-9	--	--	--	--	130	96.9	--	--	--
Mean			--	--	--		97.6		--	--
	3810-1	--	--	--	--	192	97.4	--	--	--
	3810-2	--	--	--	--	282	97.2	--	--	--
	3810-3	--	--	--	--	236	98.7	--	--	--
	3810-4	--	--	--	--	126	97.6	--	--	--
	3810-5	--	--	--	--	196	99.0	--	--	--
	3810-6	--	--	--	--	98	95.9	--	--	--
	3810-7	--	--	--	--	404	98.8	--	--	--
	3810-8	--	--	--	--	114	97.4	--	--	--
	3810-9	--	--	--	--	414	95.7	--	--	--
Mean			--	--	--		97.5		--	--
Mean (Space-planted material)			--				97.6		--	--
Drilled at rate of 1/2 bu./A. in 14 inch rows***					--	1,668	94.8	--	--	--
Mean Triumph			--	--	--		96.2		--	--

* "Class I": turgid pollen grains.
"Class II": pollen grains 50-95% full of cytoplasm.
"Class III": pollen grains essentially empty.

** Data from first and second florets only.
*** Data from random heads from a bundle of Triumph pure seed increase ('49 Stw. 361).

Table 2. Chi-square test for independence upon _Triticum_ spp. - _A. elongatum_ X Pawnee F_2 awnedness data. 1950.

	F_2 line no.	No. awnless plants	No. interm. plants	No. awned plants	Total	X^2	Pct. of time expected
Observed	1	7	34	11	52	2.466	20-30%
Expected*		11.4	29.3	11.4			
Deviations		-4.4	4.7	-0.4			
Observed	2	71	201	90	362	2.355	30+
Expected*		79.2	203.6	79.2			
Deviations		-8.2	-2.6	10.8			
Observed	3	58	208	65	331	6.172	2-5
Expected*		72.4	186.2	72.4			
Deviations		-14.4	21.8	-7.4			
Observed	4	67	84	32	183	23.296	1-
Expected*		40.0	102.9	40.0			
Deviations		27.0	-18.9	-8.0			
Observed	5	39	114	43	196	0.479	80+
Expected*		42.9	110.3	42.9			
Deviations		-3.9	3.7	0.1			
Observed	6	75	174	76	325	0.976	50-70
Expected*		71.1	182.8	71.1			
Deviations		3.9	-8.8	4.9			
Totals		317	815	317	1,449	35.744	1-
Ratio (%)		21.88	56.25	21.88			

*Based on the ratio from the total data; no genetic ratio assumed.

Table 3. Chi-square test for goodness of fit to a 3 awnless : 9 tip awned : 4 awned genetic ratio in Hybrid No. 5 F_2. 1950.

	F_2 line no.	No. awnless plants	No. interm. plants	No. awned plants	Total	X^2	Pct. of time expected
Observed	1	7	34	11	52	1.854	30-50%
Expected		9.7	29.2	13.0	51.9		
Deviations		-2.7	4.7	-2.0	0.0		
Observed	2	71	201	90	362	0.180	90-95
Expected		67.9	203.6	90.5	362.0		
Deviations		3.1	-2.6	-0.5	0.0		
Observed	3	58	208	65	331	6.628	2-5
Expected		62.1	186.2	82.7	331.0		
Deviations		-4.1	21.8	-17.7	0.0		
Observed	5	39	114	43	196	1.001	50-70
Expected		36.7	110.2	49.0	195.9		
Deviations		2.2	3.7	-6.0	-0.1		
Observed	6	75	174	76	325	4.008	10-20
Expected		60.9	182.8	81.2	324.9		
Deviations		14.1	-8.8	-5.2	0.1		
Observed	Totals	250	731	285	1,266	4.307	10-20
Expected		237.4	712.1	316.5	1,266.0		
Deviations		12.6	18.9	-31.5	0.0		
Total X^2 (Independence)						13.671	10-20

Table 4. Chi-square test for independence upon leaf rust resistance data in Hybrid No. 5 F_2. 1950.

	F_2 line no.	No. resis. Plants	No. suscep. plants	Total	X^2	Pct. of time expected
Observed	1	19	33	52	4.68	2-5%
Expected*		26.8	25.2	52.0		
Deviations		-7.8	7.8			
Observed	2	201	161	362	2.39	10-20
Expected*		186.3	175.7			
Deviations		14.7	-14.7			
Observed	3	179	146	325	1.69	20-
Expected*		167.3	157.7			
Deviations		11.7	-11.7			
Observed	4	57	118	175	25.06	1-
Expected*		90.1	84.9			
Deviations		-33.1	33.1			
Observed	5	102	91	193	0.15	70
Expected*		99.3	93.7			
Deviations		2.7	-2.7			
Observed	6	176	143	319	1.75	20-
Expected*		164.2	154.8			
Deviations		11.8	-11.8			
Totals		734	692	1,426	35.72	1-
Ratio (Pct.)		51.47%	48.53%			

*Based on the percentages of resistant and susceptible plants in the total population. No genetic ratio assumed.

Table 5. Chi-square test for goodness of fit to a 9 resistant : 7 susceptible genetic ratio using 4 Hybrid No. 5 F_2 lines with similar ratios. 1950.

	F_2 line no.	No. resis. plants	No. suscep. plants	Total	X^2	Pct. of time expected
Observed	2	201	161	362	0.077	80%
Expected		203.6	158.4			
Deviations		-2.6	2.6			
Observed	3	179	146	325	0.181	50-70
Expected		182.8	142.2			
Deviations		-3.8	3.8			
Observed	5	102	91	193	0.906	30-50
Expected		108.6	84.4			
Deviations		-6.6	6.6			
Observed	6	176	143	319	0.151	70+
Expected		179.4	136.6			
Deviations		-3.4	3.4			
Observed	Totals	658	541	1,199	0.916	30-50
Expected		674.4	542.6			
Deviations		-16.4	16.4			

Table 6. Relationship of the inheritance of leaf rust resistance and head type. 1950.

Head type	F_2 line no.	Resistant			Susceptible			Total	X^2	Pct. of time expected
		Obs.	Exp.	Dev.	Obs.	Exp.	Dev.			
Fusiform	1	10	11.9	-1.9	26	24.1	1.9	36	0.435	50+
Intermediate		6	4.0	2.0	6	8.0	-2.0	12	1.585	20+
Clavate		3	1.3	1.7	1	2.7	-1.7	4	3.188	5-10
Sub-total		19			33			52	5.208	10-20
Ratio (%)			32.95%			67.05%		--		
Fusiform	2	137	145.1	-8.1	121	112.9	8.1	258	1.039	30+
Intermediate		51	45.6	5.4	30	35.4	-5.4	81	1.484	20-30
Clavate		16	11.8	4.2	5	9.2	-4.2	21	3.398	5-10
Sub-total		204			156			360	5.921	10-20
Ratio (%)			56.25%			43.75%		(9:7)		
Fusiform	3	132	149.6	-17.6	134	116.4	17.6	266	4.745	2-5
Intermediate		43	30.4	12.6	11	23.6	-12.6	54	11.993	1-
Clavate		4	2.8	1.2	1	2.2	-1.2	5	1.153	30-
Sub-total		179			146			325	17.891	1-
Ratio (%)			56.25%			43.75%		(9:7)		
Fusiform	5	60	76.5	-16.5	76	59.5	16.5	136	8.135	1-
Intermediate		36	27.0	9.0	12	21.0	-9.0	48	6.857	1-
Clavate		7	5.6	1.4	3	4.4	-1.4	10	0.768	30-50
Sub-total		103			91			194	15.760	1-
Ratio (%)			56.25%			43.75%		(9:7)		

Table 6. (Continued)

Head type	F_2 line No.	Resistant Obs.	Resistant Exp.	Resistant Dev.	Susceptible Obs.	Susceptible Exp.	Susceptible Dev.	Total	X^2	Pct. of time expected
Fusiform	6	92	115.9	-23.9	114	90.1	23.9	206	11.243	1-
Intermediate		67	52.3	14.7	26	40.7	-14.7	93	9.429	1-
Clavate		19	11.8	7.2	2	9.2	-7.2	21	10.004	1-
Sub-total		178			142			320	30.676	1-
Ratio (%)			56.25%			43.75%		(9:7)		
Fusiform	Total	432	492.5	-61.5	471	409.5	61.5	902	16.910	1-
Intermediate		203	157.2	45.8	85	130.8	-45.8	288	29.318	1-
Clavate		49	33.3	15.7	12	27.7	-15.7	61	16.282	1-
Grand Total		683			568			1,251	62.510	1-
Ratio (%)			54.60%			45.40%				
Grand Total Individual X^2 (d.f. = 15)									75.456	1-

Table 7. Chi-square test for independence upon seed color data of Hybrid No. 5 F_2. 1950.

	F_2 line no.	No. plants dark red	No. plants red	No. plants light red	No. plants golden	No. plants white	Total	X^2	Pct. of time expected
Observed	1	2	3	0	0	0	5	4.217	30-50%
Expected*		0.9	2.0	1.6	0.4	0.1			
Deviations		1.1	1.0	-1.6	-0.4	-0.1	0.0		
Observed	2	14	46	34	17	3	114	6.992	10-20
Expected*		19.7	44.6	37.4	10.2	2.0			
Deviations		-5.7	1.4	-3.4	6.8	1.0			
Observed	3	11	25	32	5	1	74	3.707	50-
Expected*		12.8	28.9	24.3	6.6	1.3			
Deviations		-1.8	-3.9	7.7	-1.6	-0.3	0.1		
Observed	4	5	19	12	2	1	39	2.192	70
Expected*		6.7	15.2	12.8	3.5	0.7			
Deviations		-1.7	3.7	-0.8	-1.5	0.3	0.0		
Observed	5	6	14	20	2	1	43	4.149	30-50
Expected*		7.4	16.8	14.1	3.9	0.8			
Deviations		-1.4	-2.8	5.9	-1.9	0.2	0.0		
Observed	6	20	24	12	4	0	60	13.328	1-
Expected		10.4	23.5	19.7	5.4	1.1			
Deviations		9.6	0.5	-7.7	-1.4	-1.1	-0.1		
	Total	58	131	110	30	6	335	34.585	5-10
	Ratio(%)	17.31%	39.10	32.84	8.96	1.76	100.0		

*Based on the ratio from the total data; no genetic ratio assumed.

Table 8. Chi-square test for goodness of fit to a 57 red : 6 golden : 1 white genetic ratio for seed color in Hybrid No. 5 F_2. 1950.

	F_2 line no.	No. plants red	No. plants gold	No. plants white	Total	X^2	Pct. of time expected
Observed	1	5	0	0	5	0.660	70-80%
Expected		4.4	0.5	0.1			
Deviations		0.6	-0.5	-0.1	0.0		
Observed	2	94	17	3	114	5.120	5-10
Expected		101.5	10.7	1.8			
Deviations		-7.5	6.3	1.2	0.0		
Observed	3	68	5	1	74	0.626	70-80
Expected		65.9	6.9	1.2			
Deviations		2.1	-1.9	-0.2	0.0		
Observed	4	36	2	1	39	1.046	50-70
Expected		34.7	3.7	0.6			
Deviations		1.3	-1.7	0.4	0.0		
Observed	5	40	2	1	43	1.261	50-70
Expected		38.3	4.0	0.7			
Deviations		1.7	-2.0	0.3	0.0		
Observed	6	56	4	0	60	1.531	30-50
Expected		53.44	5.6	0.9			
Deviations		2.6	-1.6	-0.9	0.1		
Observed	Total	299	30	6	335	0.178	90-95
Expected		298.3	31.4	5.2			
Deviations		0.7	-1.4	0.8	0.1		
	Ratio(%)	89.06	9.38	1.56	100.00		