# PROGRESS IN COMBINING THE WHEAT LEAF RUST IMMUNITY OF AGROPYRON ELONGATUM WITH THE QUALITY AND AGRONOMIC CHARACTERISTICS OF HARD RED WINTER WHEAT

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# PREFACE

Originally, there were two purposes for this study. The first was to determine what increment of quality could be added to agrotricums with each backcross to high quality wheats and to determine if there was a quality level, below that of the recurrent parent, which could not be exceeded. This purpose was not achieved because of the hail and excessive rainfall in the spring of 1957 which made the production of normal wheat impossible. The second purpose was to make selections in the segregating generations from each backcross in an attempt to derive leaf rust immune, high quality lines that might be potential varieties. This objective was partly achieved, though it now appears that low yield in rust immune selections may be more difficult to overcome than low quality.

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Appreciation for many things also is extended to my good parents, Mr. and Mrs. W. H. Frazier, to my wife, Ruth, and to my sons, Floyd Wendell and Stephen Paul.

F. W. F.

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# INTRODUCTION

Hard Red Winter Wheat is the most important crop grown in Oklahoma with production ranging up to over 100 million bushels per year having a value of over 200 million dollars. The average annual loss of production due to leaf rust (Puccinia recondita Rob. ex Desm.) has been estimated at 5 percent of the wheat crop. This would be up to 10 million dollars annual loss due to leaf rust in Oklahoma alone. Because of these losses here and elsewhere, plant breeders throughout the world have attempted to develop leaf rust resistant wheat varieties for many years. Many varieties of wheat have been released which were resistant to the races of leaf rust that were prevalent at the time and in the area of their release. All of the older and some of the more recently released varieties have become susceptible to leaf rust because of changes in the prevalence of the various leaf rust races. This changing race population has caused wheat breeders to look for a new type of leaf rust resistance, one which would interact with some physiological factor characteristic of the leaf rust species, rather than the older types which interact with factors which vary among physiological races of leaf rust. It also is desirable that the effectiveness of the resistance be great enough to completely prevent reproduction of the rust. While this is desirable for the purpose of eliminating inoculum, which can cause some damage even on partially resistant plants, it is of much greater importance in preventing opportunity for the development of new virulent types. Thus, any type of resistance which does not prevent reproduction of the fungus may not be long lasting.

Among the possible sources of this new type of leaf rust resistance for wheat are certain selections from hybrids between Agropyron elongatum and wheat. These selections have the desired type of rust resistance, in this case actual immunity in the field, cross readily with wheat, and produce fertile hybrids. The primary purpose of these studies was to try to combine the rust immunity of these selections with the high grain quality of certain hard red winter wheats into a single strain. Since certain other agronomic characteristics are necessary before a variety is desirable commercially, selection for yield was attempted, and the effect of the rust immunity gene on date-of-maturity and height-of-plant was studied.

# REVIEW OF THE LITERATURE

## General Reports of Triticum-Agropyron Hybrids

Verushkine and Shechurdine (66)[1] reported in 1933 that Zizine (more recently translated as Tzitzin) had made the first successful cross of Triticum x Agropyron. Following this first cross of T. vulgare x A. intermedium, Verushkine, Shechurdine, and Zizine attempted many other crosses and succeeded in crossing many varieties of T. vulgare and T. durum with both A. intermedium and A. elongatum. In 1938 Tschermak-Seysenegg (63), according to Swarup et al. (62), first used the name agrotricum for hybrids between Triticum and Agropyron. This name now has been adopted widely. Tzitzin (64) in 1940 reported that agrotricums had been produced that were more winterhardy than the hardiest rye. Others outyielded standard wheat varieties by 50 to 71 percent, and many of them had great drought resistance. Another strain had resistance to bunt and smut, frost, lodging and shedding, and had exceptionally high baking quality. Some were perennial with superior winter survival, yield, great disease resistance, and unusually high grain quality. By 1943 Cicin (9) reported that an agrotricum had

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[1] Figures in parentheses refer to "Literature Cited," page 66.

been produced that was non-segregating, perennial, resistant to drought, disease, and lodging and produced each year a grain crop and an aftermath hay crop. Seleznev (55) in 1957 reported that hybrids 1, 186, and 599 had been introduced into commercial production and were outyielding standard wheats in several provinces of the Russian Soviet Federated Socialist Republics, and hybrid 1 also outyielded standard wheats in Estonia and Lithuania.

In America no commercial varieties have been produced from agrotricums. Smith (59) and White (68) have given good reviews of the rather extensive literature on the subject as well as describing their own crossing experiments. White believes, because of the low percentage of leaf rust susceptible plants in segregating generations even after backcrossing to susceptible wheats, that there are several factors for leaf rust resistance in A. elongatum. He also found that derivatives of wheat x A. glaucum sometimes had extensive rhizome development but that the perennial derivatives from A. elongatum had a bunch habit of growth. A suggestion that genomes homologous with those of wheat can be derived from various related species and may be desirable sources of germplasm in wheat breeding is made by McFadden and Sears (37). They report considerable success in producing synthetic amphiploids with genomes homologous with those of vulgare wheat but derived from related species.
In later generations of agrotricums, American investigators have observed certain difficulties. Armstrong and

Stevenson (4) found that continuous selection for wheat-like characters in agrotricums gradually reduced the number of Agropyron chromosomes and also the disease resistance derived from *A. elongatum*. Schmidt et al. (49) found their agrotricums to lack winter hardiness, and though there was enough resistance to several diseases to warrant further research, it was found only in the grass-like and intermediate types. The wheat-like segregates were completely susceptible. In California, Suneson and Pope (60) have attempted to select perennial types but have had very low yields which have been still lower in the second and later years after planting. Sando (47) found numerous agrotricums resistant to both stem and leaf rust, but all had speltoid-like spikes and other undesirable Agropyron characters. Fellows and Schmidt (13), Swarup et al. (62) and Schmidt et al. (50) all found that agrotricums resistant to yellow streak mosaic were grass-like or intermediate, and when chromosomes were examined there was always at least one Agropyron chromosome, non-homologous with wheat chromosomes, present. Marshall and Schmidt (36) studied the meiotic stability of agrotricums in advanced generations and found that even though they were morphologically stable they were, in general, highly unstable meiotically. They also found highly significant correlations between meiotic index and kernel weight index, percent germination, and percent normal pollen. Sachs (46) found that 19 of 24 amphiploids in the triticinae which he examined produced chromosome mosaics in the anthers at meiosis. The anthers with mosaics contain, at meiosis, a mixture of cells with complete amphiploid and various reduced aneuploid numbers of chromosomes. He hypothesized that mosaics probably arose by gene-controlled spindle abnormalities just before meiosis since his plants bred true for mosaic formation or the lack of it. Cells with the reduced chromosome number resulting from these mosaics were able to function as gametes and thus produce new completely aneuploid plants.

Most investigators, after making crosses between agrotricums and wheat, have reported that the results in the segregating generation fit no known genetic ratio. One exception is the paper by Shebeski and Wu (56). These authors, after rejecting several simple hypotheses because of a poor fit, settled on the following system for stem rust resistance in the cross between Red Egyption and Perennial Wheat 357-5, both of which are resistant to stem rust.

(a) P. W. 357-5 resistance which is $P_1$ $P_2$ $P_3$.

(b) Red Egyption resistance which is $r_1r_1$ or $r_2r_2$.

(c) Complementary action of $r_1$ with any one of $P_1$, $P_2$, or $P_3$.

(d) Complementary action of $r_2$ with $P_1P_2$ but not with $P_1P_3$ or $P_2P_3$.

This gave a the theoretical ratio of 925 resistant to 99 susceptible, which fits their results acceptably.

## Genetics of Leaf Rust Resistance

In crosses of wheat x wheat it generally has not been too difficult to determine the mode of inheritance of leaf rust resistance. Ausemus et al. (7) give a good review of the genetics of leaf rust resistance as it had been investigated up to 1946. The inheritance of mature plant leaf rust resistance is given by two of the papers which they review as monogenic. Two other papers report digenic inheritance of resistance, and three papers report crosses in which the inheritance of leaf rust resistance by mature plants seems to be multigenic. Another paper reports that the physiological resistance to different races of leaf rust was found to be either monogenic or digenic. No new types of leaf rust resistance have been found since in crosses of wheat x wheat. After testing 27 varieties of common wheat, Johnson and Melchers (30) reported that some varieties were susceptible to leaf rust in the seedling stage and resistant at the heading stage. Other varieties were susceptible as seedlings and remained susceptible at heading. All varieties that were resistant as seedlings remained resistant at the heading stage.

Due to the low percentage of susceptible plants in the segregating generations from the cross wheat x *A. elongatum*, White (68) believes that there are several factors for mature plant leaf rust immunity in *A. elongatum*. Schmidt et al. (49) and Sando (47) found that leaf rust immunity was tightly linked with grass-like characters but did not explain its mode of inheritance.

## Milling and Baking Quality

In 1921 Percival (44) wrote:

> So-called "strength" of grain is important, but wheats of the highest quality in this respect invariably give low yields. It usually pays the producer to grow wheat of inferior milling quality, and this has been adopted as a sound policy by wheat growers during the last 200 years. Throughout Western Europe, wheats of the highest quality have been abandoned, and in other regions, wheats of high quality and low yield are being replaced by better yielding sorts of inferior quality.

In 1957 Bell and Bingham (8) state that British farmers are still growing high yielding, low quality wheats. They believe that breeders could produce a wheat for Great Britain which would have a low but acceptable protein level and a high protein quality without sacrificing yield.

In the U. S. A. Geddes (17) writes that no reputable wheat breeder would consider releasing a new variety without exhaustive milling and baking tests. He also states that, while kernel texture and test weight are good indices of quality within a variety, they are much less reliable indices of milling and baking value between varieties. He gives the objective of the wheat breeder as the production of varieties as nearly similar as possible in milling and baking characters to those to which the trade is accustomed, since practices in any country are adapted to the wheat which is available. This does not mean that undesirable characteristics should be reproduced or that desirable characteristics should not be increased, but rather it means that the variety must give satisfactory results when treated according to present procedures. Recently Reitz (45) has written that breeders should develop varieties with "built in" safety margins of quality. Some of these safety zones of quality are long mixing time and high mixing tolerance, high protein percent, very hard nonweathering kernels, high test weight, high flour yield, and a protein quality that is not easily affected by adverse environment and that gives high loaf volume and small thin-walled loaf cells.

Though it was necessary in this study to select for hard grain texture in order to improve the milling quality, the following papers leave some doubt as to the effect of this selection on other quality characteristics of the grain. Shellenberger and Coleman (58) concluded that dark, vitreous grain is decidedly superior to starchy grain from the same variety for breadmaking. In another paper, Shellenberger and Kyle (57) reported that samples with a high percentage of dark, hard vitreous kernels were higher in protein, and the highest protein percent was found in wheat with a test weight of 54 pounds. Newton et al. (41) reported that harder kernels had a higher protein percent, while Hayes et al. (24) observed that, among diverse strains of spring and winter wheat, protein content and texture were not significantly correlated, nor was there any significant correlation between either protein content or kernel texture and loaf volume. Clark (2) and Clark and Hooker (3) reported that, in a cross between Marquis and Hard Federation, they were unable to select $F_3$ lines with a protein percent equal to that of Marquis, but they found many $F_3$ lines that produced more total protein than Marquis. They had little difficulty in selecting for hard texture and suggested that texture is not a good indication of protein percent and that in any cross at least one parent should have a protein percent equal to that desired in the strains resulting from the cross.

Ausemus et al. (7) reviewed 12 references to the inheritance of gluten strength ranging from monogenic to multigenic. Using the wheat meal fermentation time as a test, Worzella (69) was able to recover the quality of the parents in $F_3$ families from the cross Trumbull x Michikof. He hypothesized three non-dominant cumulative factors for quality difference between these two parents. Single $F_2$ plants and $F_3$ lines had a quality correlation coefficient of +0.842 which indicates that quality evaluation should begin in early generations. Starchy grain texture was reported by Aamodt et al. (1) to be dominant over vitreous texture and to be multi-factoral. Nakagawa and Watanabe (40) believed that three loci each with multiple allels controlled grain texture in eight varieties of Japanese wheat. According to Schlehuber (48) Heyne and Finney (26) suggest that, in breeding for quality, tests be made on $F_4$ material from $F_2$ derived lines. Harlan et al. (20), in contrast to some of the other papers cited herein, found in 329 barley crosses that high quality and high yield were highly correlated.

Tzitzin (64) reports high baking quality in some of his agrotricums, and Armstrong and Stevenson (4) found that their agrotricums had much more protein than wheat. In discussing wheat quality in North America, Schlehuber (48) tells of the efforts of wheat breeders to insure that their releases have acceptable quality and makes the statement that no agrotricums will be released by the Oklahoma Experiment Station unless highly acceptable quality is indicated.

The methods of determining breadmaking quality in wheat are reviewed by Miller and Johnson (39). They state that the baking test is the final criterion of quality and that the percent of protein is the best single predictive test. However, other chemical tests are giving way to physical dough tests. In a discussion of the value of the mixogram in predicting baking results, Johnson et al. (31) conclude that it gives information regarding mixing requirement, mixing tolerance, and varietal pattern. By comparing the mixogram of a flour being tested with the mixogram of flours of known quality, good predictions of the baking quality can be made. Copp (10) observed that the sedimentation test gave a high correlation ($r = 0.89$) with baking test scores within varieties but gave a low correlation ($r = 0.08$) with baking test scores between varieties. In spite of this he was able to isolate high quality lines by applying this test to individual plants. In contrast to this, Harris and

Sibbitt (23) found that the sedimentation and protein determinations were useful only in isolating the very poor quality lines. For wheats of generally superior quality, protein content and sedimentation value had little relation to loaf volume.

## Breeding for Yield in Wheat

The early literature on breeding wheat for yield is reviewed by Percival (44) who discusses the success of some workers in isolating superior pure lines from mixed populations, the failure of the second round of selection because the workers were attempting to select within pure lines, the belief of some workers that acquired characters were inherited and cumulative and their attempts to improve wheat by super-fertilization of individual plants, and, finally, he tells of a few wheat breeders who make artificial crosses between wheat varieties and make selections in the hybrid progeny. Ausemus et al. (7) list nine references, all of which state that the inheritance of yield is multigenic. Hagedoorn (19) recommends the bulk hybrid method of breeding self-pollinated crops because of the low labor requirement and acceptable results. Hayes et al. (25) state that methods have been standardized to a considerable extent with self-pollinated crops. They describe both the pedigree and the bulk methods and state that selection usually is based on the judgement of the observer, and most workers prefer not to make yield trials until the $F_5$ or $F_6$ derived lines are obtained, although early testing for yield has been tried occasionally.

Mass selection was recommended by Leighty (33), although he did not specify that it was to be used in hybrid populations. On the same symposium Love (34) discussed the use of the bulk and the pedigree methods and a combination method which is now called the $F_2$ derived line method. Palmer (43) found that the selection of individual plants in either the $F_2$ or $F_8$ was ineffective except for grain size and that size of grain was negatively correlated with yield. Immer (28) suggests bulk yield tests beginning with the $F_2$ for selecting the better crosses. This contrasts with the experience of Grafius et al. (18) who report that the average yield of the parents is the best measure of the value of a cross in barley. They also report that the selection of individual $F_2$ plants is ineffective and consider this to be due to dominance and epistasis. Harlan et al. (20) also found that poor yielding varieties made poor parents, although some varieties that were not quite equal to the best ones in plot tests made excellent parents, and high yielding bulks produced high yielding selections. Atkins and Murphy (6), on the contrary, did not find agreement between early generation bulk tests with oat crosses and later selections from these bulks. Frey (16) reported that $F_2$ derived lines in barley gave such good indications of the yields of $F_3$ derived lines that the use of $F_3$

derived lines was not warranted. It is reported by Harrington (21,22) that those $F_2$ bulks which express the most heterosis also produce the best selections, and he suggests growing segregating generations in bulk until a good year for selecting for some important character and then making individual plant selections and growing them in progeny rows the following years. This procedure may be repeated if conditions are right.

Weibel (67) calculated that the heritability of yield in wheat was only 7.7 percent and did not recommend making selections for yield in early generations. Florell (14) handled 19 crosses by the bulk method, and since 73.3 percent of the $F_7$ and $F_8$ selections were better than the check variety, he considered it a successful method.

Laude and Swanson (32) observed that, in mixtures of Kanred with Harvest Queen or Kanred with Currell, competition increased the percentage of Kanred to almost a pure stand in nine years. They suggest that in a hybrid population natural selection soon would eliminate most of the non-competitive types. Working with mixtures of barley and also with mixtures of wheat, Suneson and Wiebe (61) also found that certain varieties were eliminated quickly, but those that survived were not necessarily the varieties that yielded best in pure stands. They concluded that this puts a decided limitation on the success of the bulked population method of plant breeding.

Fowler and Heyne (15) reported that, while there was a highly significant correlation between bulk hybrids and selections from them in regard to plant height, date of flowering, and test weight, equally good results could have been obtained by selection of the parents to be crossed. In regard to yield, the correlation between bulk hybrids and selections was small but significant. The correlation between parents and selections was larger but non-significant. They say that indications are that selection during segregating generations should emphasize characteristics other than yield. A scheme which they call the "pedigree-trial method" is reported by Lupton and Whitehouse (35) to have given good results. Visual selection is made of $F_2$ plants and of $F_3$ and $F_4$ single plant progeny rows. Yield trials are conducted with remnant seed in $F_5$, $F_6$, and $F_7$ to test the plants selected in the $F_3$, $F_4$, and $F_5$, respectively. Van Der Kley (65) discusses the bulk selection method, the pedigree method, and the mass pedigree method. He concludes that "gradual selection" should be used in which a gradually increasing number of recessive detrimental genes be eliminated during consecutive generations. Schlehuber (48) quotes A. B. Campbell as writing "We will forgo preliminary yield tests in favor of quality prediction tests." This is in agreement with Fowler and Heyne as noted above. Asana et al. (5) observed that, in 17 varieties of Indian wheat grown under drought conditions, the number of grains per ear was the most important component of yield, but under adequate soil moisture conditions ears per plant were a more important component. This suggests that under drought conditions selection for large ears is a desirable breeding method.

# MATERIALS AND METHODS

## Triticum sp.-Agropyron elongatum x Pawnee Selections

The selections which were the source of leaf rust immunity used in this study had the pedigree, Triticum sp.-Agropyron elongatum x Pawnee. The original cross was made by W. J. Sando, circa 1935, between an unrecorded common wheat and Agropyron elongatum. Selections were made from the segregates from this cross, and some of them were sent to the California Agricultural Experiment Station at Davis, California. They were re-selected at Davis, and some of the selections were sent to the Kansas Agricultural Experiment Station at Manhattan, Kansas. In the spring of 1947 selections from this material were sent to the Oklahoma Agricultural Experiment Station where they were spring planted and the more wheat-like types selected. Prior to this time no intentional crosses had been made with this material since the first intergeneric cross was made by Sando. However, due to the fact that crosses of this type have a high degree of self-sterility in the early segregating generations, and because of the rather wheat-like appearance of the material, it is believed that some natural crosses with wheat may have occurred. In 1948 at the Oklahoma Agricultural Experiment Station crosses between this material and the hard red winter wheat variety Pawnee were made. Selection for rust immune wheat-like plants was made on an individual plant basis in the segregating material from this cross until 1952 when selected $F_4$ plant rows were bulked and subsequently evaluated for agronomic characteristics and grain quality.

Using the first letter of the words Triticum, Agropyron, and Pawnee, the name TAP was coined for these selections. By adding the last two digits of the 1952 Stillwater selection number, the different selections are identified. The selections which were used in this study are TAP48, which previously had been shown to have 44 chromosomes, and TAP45, TAP47, TAP64, and TAP67, each of which has 42 chromosomes. These selections are uniformly resistant to leaf rust in the seedling stage and immune or very nearly immune as adult plants in the field. The grain yield of these selections varies from moderate to low, and the grain is soft and unsuited for bread making. The test weight of the grain varies from low to very low, and the flour produced from it has a mixing time varying from short to very short. The lodging resistance of these selections is at least equal to that of the best wheats.

## Recurrent Wheat Parents

As sources of the desirable agronomic and quality characteristics which were lacking in the above selections, the wheat varieties, Comanche C.I.[2] 11673 and Ponca C.I. 12128, and the experimental strain C.I. 12406 were used. Comanche is moderately high yielding, is rather susceptible to lodging, and produces grain of good test weight and good milling and baking characteristics. The mixing time of Comanche flour is only moderately long. Ponca is moderately high yielding, has good resistance to lodging, is somewhat lacking in winter hardiness, and produces grain of good test weight and good milling and baking characteristics. The mixing time of Ponca flour is generally long. C.I. 12406 is a selection from the cross Marquillo-Oro x Oro-Tenmarq; it is moderate in yield and loding resistance and produces grain of good test weight and good milling and baking characteristics. The mixing time of C.I. 12406 flour is generally extremely long.

## Breeding Methods

In 1953 each of the TAP selections involved in this study was crossed with both Comanche and Ponca. The $F_1$ plants from these crosses were growing in the field when the author started to work on this project in February, 1954. Information concerning the extremely long mixing time of C.I. 12406 had become available, so it was added as one of

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[2] C.I. refers to accession number of the Cereal Crops Section, Field Crops Research Branch, United States Department of Agriculture.

the recurrent parents. Because of the extremely short mixing time of TAP64 and the low grain yield and test weight of TAP45, the $F_1$ plants involving these parents were not used for backcrossing. Backcrossing the rust immune or resistant plants to the above-mentioned wheat parents was continued in the greenhouse in 1955, 1956, and 1957. From each backcross generation a series of segregating generations was grown in which to make selections.

In 1956, because of the observation that the mature plant type of resistance that was expressed in the greenhouse was becoming weaker with each backcross, it was decided to start a new attempt to produce an agrotricum with good grain quality and with as little wheat inheritance as possible. Accordingly, Triticum sp. x A. elongatum was crossed with C.I. 12406. The particular plant of T. sp. x A. elongatum used in this cross proved to have green seed. An examination of these green seeds showed the color to be due to a blue aleurone covered by an amber color layer in the testa.

A pedigree chart of these crosses and of the selections made from them is shown in Figure 1.

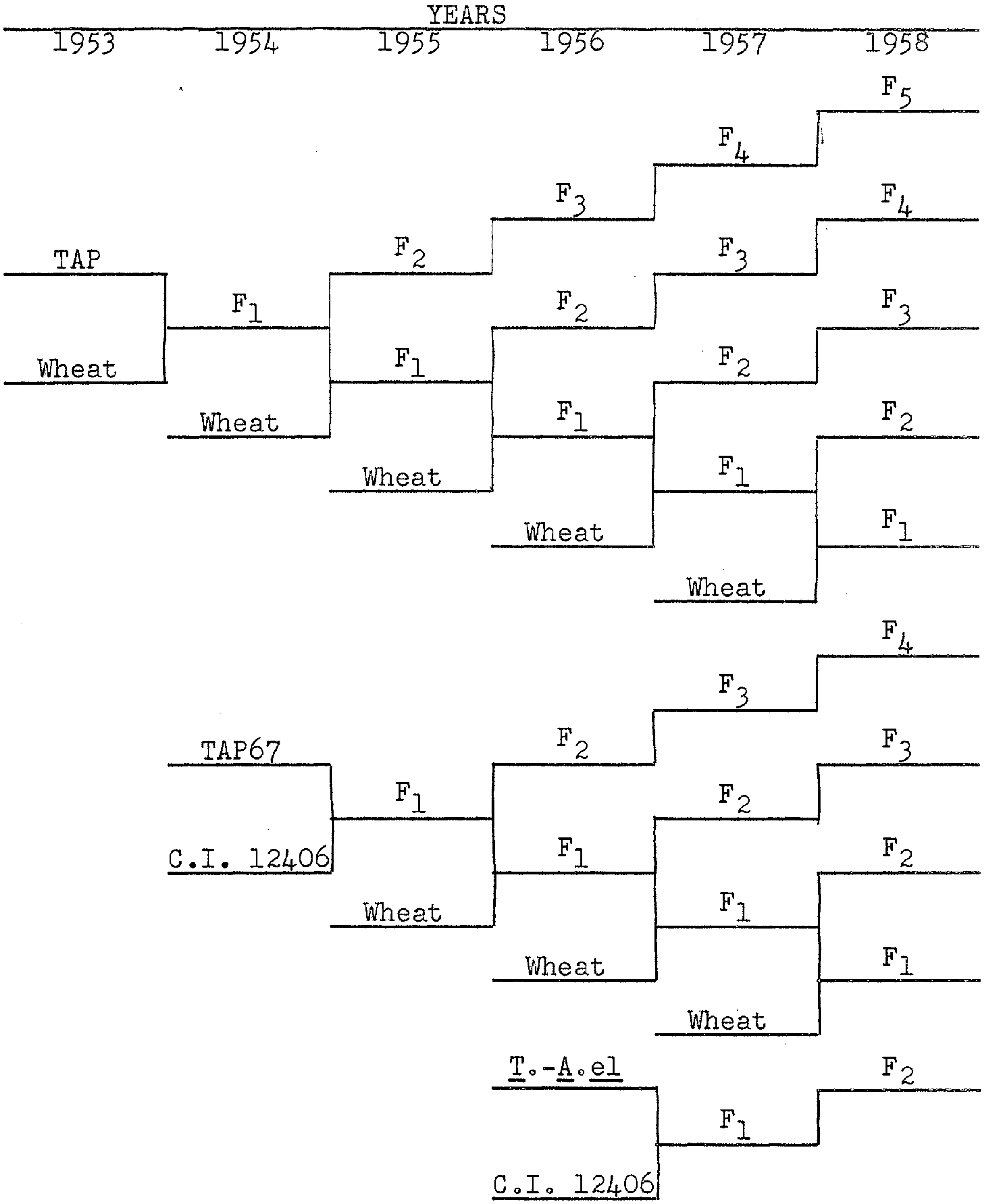

Figure 1.--Pedigree of the crosses and selections that concern this study.

## Selection Methods

### For Leaf Rust Resistance

The first selection for rust resistance was made in the greenhouse in 1955 on $F_1$ material with the general pedigree of $\text{Wheat}^2$ x TAP and also $F_1$ material with the pedigree of TAP67 x C.I. 12406. This material was artificially inoculated with leaf rust race 105-B,[3/] which is the most virulent race of leaf rust occurring in Oklahoma if virulence is measured as the number of strains of wheat which are susceptible to its attack. This inoculation was made at a time estimated to be 10 days prior to heading of the most advanced plants so that the immune or resistant plants could be used as parents in additional backcrosses. It was thought that this timing would give the same reaction as occurred in the field on mature plants. This same type of test was carried out on the backcross material that was available in 1956 and again in 1957 with the resistant plants being used as parents for further backcrosses and the susceptible plants discarded. In the fall of 1957 the backcrossed seed produced that year were grown in plant bands, tested for rust reaction as seedlings, and the resistant plants transplanted to six-inch pots for growing to maturity.

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[3/] A subrace of race 105 virulent on the supplemental differential wheat varieties Westar C.I. 12110 and Wesel C.I. 13090.

In the field in 1955 $F_2$ segregating populations from each of the $F_1$ plants that were grown the previous year were subjected to an extremely heavy, late, naturally occurring rust attack. These plants were space-planted, and the rust reaction of each was recorded and the plants harvested individually. Only the rust immune plants were considered in selecting those to be planted the following year. In 1956 there was no naturally occurring rust in the field and, therefore, no selection for rust immunity could be made.

In 1957 three space-planted nurseries were grown in the field and subjected to an extremely heavy, late, naturally occurring rust attack. In the $F_2$ nursery the plots had the pedigree of $Wheat^3$ x TAP or $Wheat^2$ x TAP and were grown from plants that had been resistant or highly resistant in the greenhouse the previous year. One head from each rust immune plant was harvested for planting. The $F_3$ nursery had pedigrees of $Wheat^2$ x TAP or Wheat x TAP. The $F_4$ nursery had a pedigree of Wheat x TAP. Only rust immune plants were considered in selecting plants from these nurseries, and those plants grown in homozygous immune lines were favored over those grown in lines segregating for rust immunity.

### For Yield and Other Agronomic Characteristics

The season of 1954-1955 was characterized by extreme drought and the $F_2$ field nurseries by an extremely variable response to drought. These factors made it unwise to give yield factors much weight in making selections. However, two selection methods for yield were tried. Because of the drought most of the plants produced a low weight of grain per head, with the range being from 0.0 to 1.2 grams per head. It was decided to eliminate from consideration those plants that produced less than 0.6 gram of seed per head. Since a surplus of plants remained after other selection factors had been applied, the number was reduced further by eliminating those with a total grain yield of less than 15 grams per plant.

Plant heights and maturity dates were recorded for each plant but were not used in selection since no plants were of excessive height, and most of the late plants were eliminated because of shriveled grain.

Only one head per plant was harvested from the 1956 $F_2$ nursery because this method was many times faster than harvesting plants individually. No intentional selection for yield was made; however, all heads having less than 30 seeds remaining after one or two seeds had been tested for texture were discarded because it was desired to use 30 seeds for evaluation the next year. This may have had some effect on yield. The 1956 $F_3$ nursery was a yield nursery consisting of 40 $F_3$ strains and three entries each of Ponca and Comanche. This nursery was planted in three replicates, with the plot size being a single five-foot row of 10 plants. These plants were harvested and threshed individually, but only the total yield of each plot was recorded. Based on the mean grain yield and the quality of these 40 strains, six strains were selected to be planted in an $F_4$ nursery. Each of the 174 plants in these selected lines became a separate line in the $F_4$ nursery. Maturity dates and plant heights were recorded for each line but were not considered in making selections.

The 1956-1957 growing season was normal until April when a series of heavy rains began which, combined with one severe hail storm, caused the loss of all small grain yield nurseries at Stillwater except those discussed in this paper. The reduction in yield and test weight caused by excess moisture and hail, however, raised the question of whether the yields would be valid comparisons of what might be expected in a more nearly normal year. No yield or other agronomic data were considered in selecting the $F_2$ plants to be continued. In the $F_3$ and $F_4$ nurseries most of the lines did not produce the required 120 grams of grain with the 48 pounds per bushel test weight needed for testing in the quality laboratory. Most of the lines were discarded for this reason. Of those lines remaining that were rust immune or segregating for rust immunity, all of the lines that were well above average for yield, test weight, or mixing time were saved for replanting. One head from each plant had been harvested separately. The heads from rust immune plants in segregating lines had been tagged in advance. The remainder of each line had been harvested in bulk for quality and yield determinations.

For Quality

In the 1955 $F_2$ nursery only those plants which rated 90 or better in plumpness and whose texture, as determined by biting, was hard or very hard were selected for further planting. In the 1956 $F_2$ nursery the same standards were used except that for those plants of the cross, TAP67 x C.I. 12406, the standards were relaxed somewhat in order not to discard all of them. The 1956 $F_3$ nursery produced enough seed that, by compositing the seed from the three replicates of each strain, test weights could be determined, and 150 gram samples could be submitted to the Oklahoma State Quality Laboratory for testing of protein percent, mixing time, and sedimentation time. The total yield of protein for all three replicates in grams was calculated, after which each line was scored for three characteristics in the following way:

Score for Test Weight = 20 (lbs./bu. - 57)
Score for Mixing Time = 25 (Mixing Time in minutes - $\frac{1}{4}$)
Score for Yield of Protein = 4 (Yield of Protein in gms. - 33.5)

These scoring systems were designed to give a score of 100 to the line that was highest for each characteristic and a score of 50 for the nursery mean. The three scores of each line were added, and the six lines with the highest total score were selected for growing the following year.

Due to the very abnormal season of 1956-1957 and to the unexpected results of the quality tests of the check varieties, it was felt that the results of the quality tests of the $F_3$ and $F_4$ lines should not be given much weight. Accordingly, no scores were calculated in 1957, but a large number of the lines that were excellent in some one or more characters and a few lines that were good in all characters were saved for replanting. All of the rust immune $F_2$ plants also were saved without regard to quality.

## Disposition of the Material

Three hundred and thirty-one $F_5$ plant rows, 291 $F_4$ plant rows, and 90 $F_3$ plant rows, together with appropriate checks, were planted in the field in the fall of 1957. Each of these plant rows was the progeny of a plant that was leaf rust immune in the 1956-57 nurseries, and many $F_5$ and $F_4$ plant rows were from lines that appeared to be homozygous immune. In Tables I and II the $F_3$ and $F_4$ plants selected and the data for selection are listed. From each of 16 $F_1$ plants that were rust resistant in the greenhouse in 1956-57, a space-planted plot was seeded in the fall of 1957. Ninety $F_1$ plants and 10 $F_2$ plants resistant to rust in the greenhouse test in the fall of 1957 were transplanted to six-inch pots for the production of seed.

TABLE I

1957 $F_4$ PLANTS SELECTED FOR CONTINUATION IN 1957-58 ALONG WITH SELECTION DATA

| | 1957 | | | | | | | | 1956 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cross | No. of Plants Continued | Plot No. | Rust a/ Reaction | Yield gms. | lbs. bu. | Percent Protein | Specific Sedimentation | Mixing Time (mins.) | lbs. bu. | Percent Protein | Specific Sedimentation | Mixing Time (mins.) |
| TAP67 x Com. | 14 | 7544 | I | 171 | 49.0 | 17.9 | 2.75 | 2.75 | 61.5 | 18.5 | 3.54 | 2 7/8 |
| TAP67 x Com. | 19 | 7566 | I | 219 | 54.0 | 16.8 | 2.87 | 3.00 | | | | |
| TAP67 x Com. | 12 | 7584 | I | 206 | 50.0 | 18.7 | 3.28 | 3.75 | | | | |
| TAP67 x Com. | 10 | 7618 | I | 131 | 49.0 | 18.8 | 3.01 | 2.75 | | | | |
| TAP67 x Com. | 12 | 7650 | I | 136 | 50.5 | 19.8 | 2.63 | 3.38 | | | | |
| TAP67 x Com. | 19 | 7680 | I | 201 | 51.0 | 17.7 | 3.41 | 3.38 | | | | |
| TAP67 x Com. | 12 | 7570 | Seg. | 220 | 50.5 | 18.0 | 3.53 | 4.13 | | | | |
| Com. x TAP64 | 15 | 7630 | I | 211 | 49.0 | 18.1 | 2.74 | 2.00 | 59.0 | 16.6 | 3.97 | 3 |
| Com. x TAP64 | 14 | 7637 | I | 173 | 48.5 | 16.7 | 3.03 | 2.50 | | | | |
| Com. x TAP64 | 10 | 7577 | Seg. | 176 | 48.0 | 17.3 | 3.07 | 2.50 | | | | |
| TAP47 x Com. | 3 | 7590 | Seg. | 112 | 43.0 | | | | 59.5 | 17.1 | 3.91 | 2 1/4 |
| TAP47 x Com. | 5 | 7651 | Seg. | 105 | 41.5 | | | | | | | |
| TAP47 x Com. | 6 | 7669 | Seg. | 105 | 42.5 | | | | | | | |
| TAP47 x Com. | 3 | 7672 | Seg. | 102 | 43.5 | | | | | | | |
| Ponca x TAP45 | 11 | 7532 | I | 126 | 52.0 | | | | 60.0 | 19.0 | 3.31 | 4 1/4 |
| Ponca x TAP45 | 14 | 7591 | I | 141 | 52.5 | 18.6 | 2.44 | 2.88 | | | | |
| Ponca x TAP45 | 19 | 7665 | I | 184 | 51.0 | 17.0 | 2.90 | 3.00 | | | | |
| Ponca x TAP45 | 20 | 7666 | I | 181 | 53.0 | 18.1 | 2.69 | 3.75 | | | | |
| Ponca x TAP45 | 9 | 7539 | Seg. | 154 | 49.0 | 17.1 | 3.09 | 3.50 | | | | |
| TAP48 x Ponca | 12 | 7571 | Seg. | 174 | 49.0 | 17.0 | 3.17 | 2.50 | 62.0 | 18.3 | 3.10 | 1 7/8 |
| TAP48 x Ponca | 15 | 7572 | Seg. | 193 | 51.0 | 16.5 | 2.90 | 2.38 | | | | |
| TAP48 x Ponca | 13 | 7667 | Seg. | 171 | 52.0 | 15.5 | 2.68 | 2.13 | | | | |
| TAP48 x Ponca | 20 | 7679 | Seg. | 139 | 50.0 | 15.9 | 2.94 | 2.75 | | | | |

I = Immune, Seg. = Segregating, Immune and Susceptible.

TABLE II

1957 $F_3$ PLANTS SELECTED FOR CONTINUATION IN 1957-58 WITH SELECTION DATA

| Cross | No. of Plants Selected | Plot No. 1957 | Rust[a] Reaction | Yield Grams | Lbs. Bu. | Percent Protein | Sp. Sed. | Mix. Time Mins. |
|---|---|---|---|---|---|---|---|---|
| Ponca x TAP48-Ponca | 15 | 13205 | I | 177 | 54.0 | 18.9 | 1.74 | 2.00 |
| C.I. 12406 x TAP48-Ponca | 13 | 13011 | Seg. | 147 | 51.5 | 16.5 | 2.89 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 11 | 13268 | I | 138 | 50.0 | 17.7 | 3.18 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 14 | 13378 | I | 132 | 50.5 | 18.0 | 2.55 | 4.00 |
| C.I. 12406 x TAP47-Ponca | 7 | 13032 | Seg. | 178 | 52.0 | 18.3 | 2.66 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 4 | 13223 | Seg. | 163 | 53.5 | 18.3 | 2.87 | 3.88 |
| C.I. 12406 x TAP47-Ponca | 6 | 13267 | Seg. | 178 | 51.0 | 17.2 | 2.82 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 5 | 13323 | Seg. | 133 | 50.5 | 17.8 | 3.06 | 3.66 |
| Com. x TAP47-Com. | 18 | 13059 | I | 135 | 52.0 | | | |
| Com. x TAP67-Com. | 8 | 13109 | I | 118 | 48.0 | | | |
| Com. x TAP67-Com. | 8 | 13138 | I | 127 | 44.0 | | | |
| Com. x TAP67-Com. | 5 | 13060 | Seg. | 152 | 46.0 | 18.2 | 3.07 | 2.63 |
| C.I. 12406 x TAP47-Com. | 3 | 13108 | Seg. | 141 | 49.0 | 17.5 | 3.79 | 5.00 |
| C.I. 12406 x TAP47-Com. | 3 | 13277 | Seg. | 140 | 48.5 | 17.0 | 4.03 | 3.38 |
| C.I. 12406 x TAP47-Com. | 1 | 13284 | Seg. | 146 | 50.0 | 16.2 | 3.48 | 3.33[b] |
| C.I. 12406 x TAP47-Com. | 9 | 13329 | Seg. | 184 | 54.0 | 17.5 | 3.29 | 4.66[b] |
| TAP67 x C.I. 12406 | 17 | 13041 | I | 186 | 53.0 | 16.6 | 2.78 | 2.88 |
| TAP67 x C.I. 12406 | 16 | 13070 | I | 209 | 52.5 | 16.3 | 2.19 | 3.25 |
| TAP67 x C.I. 12406 | 14 | 13077 | I | 186 | 51.0 | 17.3 | 2.70 | 3.00 |
| TAP67 x C.I. 12406 | 21 | 13121 | I | 155 | 52.5 | 16.9 | 2.20 | 2.50 |
| TAP67 x C.I. 12406 | 18 | 13163 | I | 192 | 52.0 | 17.0 | 2.50 | 2.63 |
| TAP67 x C.I. 12406 | 17 | 13204 | I | 196 | 53.5 | 16.7 | 2.00 | 2.25 |
| TAP67 x C.I. 12406 | 18 | 13270 | I | 164 | 54.0 | 16.5 | 2.40 | 3.00 |
| TAP67 x C.I. 12406 | 15 | 13333 | I | 141 | 54.5 | 15.8 | 2.92 | 3.13 |
| TAP67 x C.I. 12406 | 10 | 13316 | Seg. | 161 | 49.5 | 16.7 | 3.18 | 3.00 |

[a] I = Immune, Seg. = Segregating, Immune and Susceptible.
[b] Too soft for proper milling in 1957.

## EXPERIMENTAL RESULTS

### Leaf Rust Resistance

In 1954, 49 $F_1$ plants of the cross TAP x wheat were apparently immune to leaf rust in the field. The reciprocal cross also produced mostly immune plants, but five plants of the cross Comanche x TAP had a mesothetic[4/] reaction, and 11 plants were susceptible and were believed to be "selfs." From a total of 80 plants that were judged to be "crosses," immunity was dominant in 75 instances and intermediate in five. In 1955, 11 $F_1$ plants of the cross TAP67 x C.I. 12406 were all immune to leaf rust race 105B, when tested in the greenhouse in the mature plant stage, and 14 plants from the same cross were all immune in the field.

The rust reactions of 57 plants with the pedigree of wheat$^2$ x TAP which were grown in the greenhouse in 1955 were 21 immune, 35 susceptible, and one plant highly resistant. In the field this cross produced 22 immune and 51 susceptible plants from a total of 73. In 1956 three very highly resistant and two susceptible plants with the pedigree C.I. 12406$^2$ x TAP67 were grown in the greenhouse. The rust

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[4/] Mesothetic refers to an intermediate reaction with a pustule type of from 1 to 4 on the same leaf.

reactions of 45 plants with the pedigree wheat$^3$ x TAP were one very highly resistant, 20 highly resistant, and 24 with various degrees of susceptibility.

The 1957 greenhouse rust tests resulted in three plants with a mesothetic reaction, 18 resistant, and 10 susceptible from a total of 31 plants with the pedigree wheat$^3$ x TAP. From 34 plants with the pedigree wheat$^4$ x TAP, there were two plants with a mesothetic reaction, three resistant, and 29 susceptible. One plant from the cross C.I. 12406 x *Triticum* sp.-*Agropyron elongatum* was resistant.

The 1958 greenhouse-grown plants were tested in the seedling stage to race 105B of leaf rust. The reactions of 192 plants with the pedigree wheat$^4$ x TAP were 52 resistant and 140 susceptible, while the tests of 30 plants with the pedigree of wheat$^5$ x TAP resulted in four resistant and 26 susceptible. The pustule type of these seedling resistant plants was a 0; to 2+, the same as the TAP67 resistant check. Thus, while the proportion of the resistant plants falling in the less highly resistant classes has increased with each additional cross to a susceptible wheat variety, when tested as mature plants in the greenhouse, the seedling reaction of the resistant plants remains as good as the resistant parent.

Six green seed and nine amber seed from the $F_1$ plant C.I. 12406 x *T.*-*A. elongatum* produced plants that were tested for rust reaction. All of the plants grown from green seed were rust resistant, but of the plants produced by the amber seed five were susceptible and four were resistant.

In the 1955 $F_2$ nursery the rust readings were as shown in Table III. The low proportion of immune plants in crosses involving TAP48, the 44 chromosome selection, should be noted and compared with the results obtained in 1957, as shown in Table IV. The small number of immune plants with the pedigrees of Com. x TAP45 and Com. x TAP47 may be related to the mesothetic reaction of the $F_1$ plants of the same crosses as contrasted with the immune reaction of the other $F_1$ plants. The later ripening of the rust immune plants is also notable.

In 1956 there was no rust in the field-grown nurseries.

The leaf rust reactions in the families that could be read easily in the 1957 $F_4$ nursery are shown in Table IV. A transformation of the percentage of immune plants in each replicate of each segregating line was carried out using the formula, angle = arc sin $\sqrt{\text{percentage}}$, and an analysis of variance was made of the resulting angles. The mean percentages given below were recovered from the mean angle for each cross. The analysis of variance is shown in Table V.

## TABLE III

## 1955 $F_2$ PLANTS LISTED BY PEDIGREE, DATE OF RIPENING AND REACTION TO LEAF RUST

| Cross | Rust Reaction | 6-10 + 6-11 | 6-13 | 6-16 | 6-20 + 6-21 | 6-23 + 6-24 | 6-29 + 7-1 | 7-6 + 7-7 | Total |
|---|---|---|---|---|---|---|---|---|---|
| TAP48 x Ponca | I[a] | 10 | 0 | 4 | 4 | 2 | 5 | 3 | 28 |
| | S[b] | 46 | 2 | 11 | 7 | 12 | 5 | 0 | 83 |
| TAP48 x Com. | I | 2 | 0 | 2 | 0 | 2 | 12 | 6 | 24 |
| | S | 34 | 7 | 14 | 14 | 11 | 11 | 0 | 91 |
| Ponca x TAP45 | I | 5 | 2 | 12 | 7 | 10 | 21 | 13 | 70 |
| | S | 8 | 4 | 4 | 6 | 8 | 15 | 0 | 45 |
| Com. x TAP45 | I | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 5 |
| | S | 40 | 2 | 4 | 1 | 10 | 14 | 0 | 71 |
| TAP45 x Com. | I | 1 | 2 | 2 | 1 | 0 | 8 | 1 | 15 |
| | S | 0 | 2 | 2 | 3 | 0 | 1 | 0 | 8 |
| Ponca x TAP47 | I | 0 | 0 | 4 | 8 | 3 | 10 | 6 | 31 |
| | S | 10 | 2 | 7 | 7 | 6 | 10 | 1 | 43 |
| TAP47 x Ponca | I | 4 | 2 | 4 | 9 | 14 | 60 | 47 | 140 |
| | S | 9 | 2 | 14 | 46 | 36 | 24 | 2 | 133 |
| Com. x TAP47 | I | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 4 |
| | S | 3 | 3 | 6 | 12 | 4 | 2 | 1 | 31 |
| TAP47 x Com. | I | 12 | 7 | 7 | 14 | 14 | 51 | 16 | 121 |
| | S | 46 | 17 | 7 | 25 | 12 | 12 | 3 | 122 |
| Ponca x TAP64 | I | 1 | 0 | 0 | 1 | 7 | 17 | 3 | 29 |
| | S | 3 | 1 | 2 | 4 | 8 | 3 | 0 | 21 |
| Com. x TAP64 | I | 0 | 0 | 1 | 2 | 1 | 10 | 13 | 27 |
| | S | 5 | 1 | 4 | 7 | 9 | 3 | 1 | 30 |
| TAP64 x Com. | I | 2 | 0 | 0 | 4 | 17 | 73 | 77 | 173 |
| | S | 1 | 0 | 1 | 19 | 27 | 13 | 1 | 62 |

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[a] I = Immune

[b] S = Susceptible

TABLE III--Continued

| Cross | Rust Reaction | 6-10 + 6-11 | 6-13 | 6-16 | 6-20 + 6-21 | 6-23 + 6-24 | 6-29 + 7-1 | 7-6 + 7-7 | Total |
|---|---|---|---|---|---|---|---|---|---|
| TAP67 x Ponca | I | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 4 |
| | S | 1 | 0 | 1 | 2 | 2 | 2 | 0 | 8 |
| TAP67 x Com. | I | 1 | 0 | 2 | 1 | 8 | 20 | 28 | 60 |
| | S | 3 | 0 | 3 | 8 | 8 | 7 | 1 | 30 |
| Total | I | 41 | 13 | 38 | 52 | 80 | 294 | 213 | 731 |
| | S | 209 | 43 | 80 | 161 | 153 | 122 | 10 | 778 |

## TABLE IV

## LEAF RUST REACTION OF FIVE FAMILIES OF $F_4$ PLANTS GROWN IN 1957

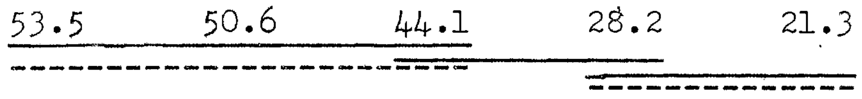
| Cross | Lines | | | Mean Percentage of Immune Plants in Segregating Lines |
|---|---|---|---|---|
| | Susc. | Seg. | Imm. | |
| Ponca x TAP45 | 12 | 7 | 10 | 53.5 |
| TAP67 x Com. | 13 | 6 | 10 | 50.6 |
| Com. x TAP64 | 18 | 7 | 3 | 44.1 |
| TAP48 x Ponca | 21 | 9 | 0 | 28.2 |
| TAP47 x Com. | 23 | 7 | 0 | 21.3 |

## TABLE V

## ANALYSIS OF VARIANCE OF THE TRANSFORMED PERCENTAGES OF RUST IMMUNE PLANTS IN FIVE $F_4$ FAMILIES OF AGROTRICUMS GROWN IN 1957

| Source | Degrees of freedom | Sum of squares | Mean square | F | $F_{0.01}$ |
|---|---|---|---|---|---|
| Total | 107 | 24340 | | | |
| Blocks | 2 | 485 | 242.5 | 2.63 | 4.92 |
| Lines | 35 | 17396 | 497.0 | 5.38 | 1.93 |
| Crosses | 4 | 6195 | 1548.8 | 16.78 | 3.60 |
| Lines within crosses | 31 | 11201 | 361.3 | 3.91 | 1.97 |
| Error | 70 | 6459 | 92.3 | | |

The multiple range test applied to the mean percentages of immune plants is shown below. Those percentages not underlined by the same solid line are significantly different at the 1 percent level. Those percentages not underlined by the same broken line are significantly different at the 5 percent level.



In addition, there was another family of lines which originated from a different $F_2$ plant of the cross TAP48 x Ponca which segregated for both the TAP48 immunity and the Ponca type of mature plant resistance. This family had four completely susceptible lines, nine lines with Ponca type resistance, and 15 lines that were segregating for TAP48 immunity and Ponca resistance. No attempt was made to read the reactions of the individual plants.

The $F_3$ nursery in 1957 contained 17 rust immune lines, 73 lines segregating for immunity, and 297 completely susceptible lines. Since these lines had been selected for seed type and texture the previous year, these figures may be biased, and no explanation of the mode of inheritance of rust immunity should be based on them. The $F_2$ nursery in 1957 contained four plots derived from $F_1$ plants which had only a fleck type of reaction in 1956. These plots produced 145 immune plants and 270 susceptible plants. Also contained in this nursery were 17 plots from plants that had produced a few small pustules in 1956. Eleven of these plots were completely susceptible, and the remaining six plots contained 17 immune plants and 71 susceptible plants. There was no apparent difference in the immune plants arising from these two sources.

## Quality

The $F_2$ nursery grown in 1955 contained 520 rust immune plants that were rated as hard or very hard and 211 plants that were rated soft or intermediate in texture. The immune plants also were rated for plumpness. A total of 373 of them were rated 90 or 95 in plumpness, and 358 of them were rated 85 or lower in plumpness. To try to determine the effect of the factor for rust immunity on quality, 200 susceptible and 200 immune plants were paired for plot and date of ripening and then were bulked to make a susceptible composite and an immune composite. These composites were submitted to the Oklahoma State University Wheat Quality Laboratory for evaluation with the following results (Table VI):

TABLE VI

QUALITY CHARACTERISTICS OF IMMUNE AND SUSCEPTIBLE COMPOSITES OF $F_2$ PLANTS GROWN IN 1955

| | Lbs. Bu. | Percent Protein | Flour Yield Percent | Flour Ash Percent | Mixing Time |
|---|---|---|---|---|---|
| Immune Composite | 56.5 | 18.3 | 65.3 | 0.69 | 1.5 min. |
| Susceptible Composite | 55.5 | 17.8 | 67.1 | 0.74 | 2.0 min. |

The $F_3$ nursery grown in 1956 from 40 rust immune plants selected from the above nursery produced enough grain for micro quality evaluations of each line. The averages of the hybrid strains are compared with the averages of the Ponca and Comanche checks in Table VII. The $F_2$ nursery in 1956 contained 2691 plants, 1631 of which were discarded because they were too soft and/or shriveled.

In 1957, due to the excess rainfall and hail, only 29 of the 174 strains included in the $F_4$ nursery, plus three

Ponca checks, produced the necessary 120 grams of grain with at least a test weight of 48 pounds per bushel which was needed for a quality test. The results of these tests by the Oklahoma State University Wheat Quality Laboratory along with other data are given in Table VIII.

In the $F_3$ nursery grown in 1957 only 31 strains of hybrids plus seven check strains produced the necessary quantity and test weight of seed for quality tests. The results of the quality tests and other data are shown in Table IX. In Table X are shown the average of the quality data of the hybrids and check varieties of both the $F_3$ and $F_4$ nurseries grown in 1957.

TABLE VII

A COMPARISON OF THE QUALITY OF THE 1956 $F_3$ AGROTRICUMS WITH TWO WHEAT CHECKS

|  | Mixing Time | Specific Sedimentation | % Protein | Lbs. Bu. |
|---|---|---|---|---|
| Hybrids | 2.24 | 3.11 | 18.5 | 59.3 |
| Ponca | 2.83 | 3.47 | 17.9 | 60.8 |
| Comanche | 2.00 | 3.18 | 18.0 | 60.5 |

## TABLE VIII

## QUALITY AND OTHER DATA OF THE TESTED $F_4$ LINES AND CHECKS GROWN IN 1957

| Variety or Cross | Plot No. | Lbs./Bu. | Yield, grams | Rust Reaction[a] | Protein Percent | Specific Sedimentation | Mixing Time Minutes |
|---|---|---|---|---|---|---|---|
| Ponca | 7503 | 48.0 | 179 | R | 16.9 | 2.96 | 2.75 |
| Ponca | 7599 | 48.0 | 152 | R | 16.9 | 3.09 | 2.63 |
| Ponca | 7638 | 48.5 | 175 | R | 16.0 | 2.96 | 2.50 |
| Ponca x TAP45 | 7591 | 52.5 | 141 | I | 18.6 | 2.44 | 2.88 |
| Ponca x TAP45 | 7665 | 51.0 | 184 | I | 17.0 | 2.90 | 3.00 |
| Ponca x TAP45 | 7666 | 53.0 | 181 | I | 18.1 | 2.69 | 3.75 |
| Ponca x TAP45 | 7539 | 49.0 | 154 | Seg | 17.1 | 3.09 | 3.50 |
| TAP48 x Ponca | 7545 | 49.5 | 159 | I&R | 16.1 | 2.80 | 2.25 |
| TAP48 x Ponca | 7558 | 49.5 | 157 | I&R | 16.7 | 2.97 | 2.33 |
| TAP48 x Ponca | 7571 | 49.0 | 174 | I&R | 17.0 | 3.17 | 2.50 |
| TAP48 x Ponca | 7572 | 51.0 | 193 | I&R | 16.5 | 2.90 | 2.38 |
| TAP48 x Ponca | 7617 | 48.0 | 122 | I&R | 16.4 | 2.81 | 2.38 |
| TAP48 x Ponca | 7667 | 52.0 | 171 | I&R | 15.5 | 2.68 | 2.13 |
| TAP48 x Ponca | 7674 | 48.5 | 137 | I&R | 16.4 | 2.82 | 2.25 |
| TAP48 x Ponca | 7679 | 50.0 | 139 | I&R | 15.9 | 2.94 | 2.75 |
| TAP48 x Ponca | 7501 | 50.0 | 140 | R | 16.0 | 2.56 | 2.38 |
| TAP48 x Ponca | 7516 | 51.0 | 159 | R | 16.4 | 3.08 | 2.50 |
| TAP48 x Ponca | 7631 | 48.0 | 170 | R | 16.4 | 2.88 | 2.00 |
| TAP48 x Ponca | 7657 | 49.5 | 152 | R | 15.9 | 3.19 | 2.63 |
| TAP48 x Ponca | 7655 | 51.0 | 142 | S | 16.4 | 2.94 | 2.13 |
| TAP48 x Ponca | 7678 | 48.0 | 152 | S | 16.6 | 2.74 | 2.13 |
| Com. x TAP64 | 7630 | 49.0 | 211 | I | 16.1 | 2.74 | 2.00 |
| Com. x TAP64 | 7637 | 48.5 | 173 | I | 16.7 | 3.03 | 2.60 |
| Com. x TAP64 | 7577 | 48.0 | 176 | Seg | 17.3 | 3.07 | 2.50 |
| TAP67 x Com. | 7544 | 49.0 | 171 | I | 17.9 | 2.75 | 2.75 |
| TAP67 x Com. | 7566 | 54.0 | 219 | I | 16.8 | 2.87 | 3.00 |
| TAP67 x Com. | 7584 | 50.0 | 206 | I | 18.7 | 3.28 | 3.75 |
| TAP67 x Com. | 7618 | 49.0 | 131 | I | 18.8 | 3.01 | 2.75 |
| TAP67 x Com. | 7650 | 50.5 | 136 | I | 19.8 | 2.63 | 3.38 |
| TAP67 x Com. | 7680 | 51.0 | 201 | I | 17.7 | 3.41 | 3.38 |
| TAP67 x Com. | 7548 | 49.0 | 168 | Seg | 17.9 | 3.01 | 2.88 |
| TAP67 x Com. | 7570 | 50.5 | 220 | Seg | 18.0 | 3.53 | 4.13 |

[a] I = Immune, R = Ponca type of resistance,
Seg = Immune and completely susceptible types.

## TABLE IX

## QUALITY AND OTHER DATA OF THE TESTED $F_3$ LINES AND CHECKS GROWN IN 1957

| Cross, Strain or Variety | Plot No. -13000 | Lbs./Bu. | Yield, grams | Rust Reaction[a] | Protein Percent | Specific Sedimentation | Mixing Time Minutes |
|---|---|---|---|---|---|---|---|
| Ponca | 334 | 52.5 | 196 | R | 16.7 | 3.01 | 3.00 |
| Comanche | 251 | 49.0 | 156 | S | 16.8 | 2.98 | 3.38 |
| TAP67 | 146 | 50.5 | 143 | I | 16.3 | 2.71 | 2.63 |
| TAP67 | 148 | 51.0 | 159 | I | 16.4 | 2.80 | 2.63 |
| C.I. 12406 | 260 | 51.0 | 151 | S | 17.9 | 2.82 | 2.75 |
| C.I. 12406 | 395 | 50.0 | 144 | S | 18.2 | 2.89 | 3.00 |
| TAP67 x C.I. 12406 | 41 | 53.0 | 186 | I | 16.6 | 2.78 | 2.88 |
| TAP67 x C.I. 12406 | 70 | 52.5 | 209 | I | 16.3 | 2.19 | 3.25 |
| TAP67 x C.I. 12406 | 77 | 51.0 | 186 | I | 17.3 | 2.70 | 3.00 |
| TAP67 x C.I. 12406 | 121 | 52.5 | 155 | I | 16.9 | 2.20 | 2.50 |
| TAP67 x C.I. 12406 | 163 | 52.0 | 192 | I | 17.0 | 2.50 | 2.63 |
| TAP67 x C.I. 12406 | 204 | 53.5 | 196 | I | 16.7 | 2.00 | 2.25 |
| TAP67 x C.I. 12406 | 270 | 54.0 | 164 | I | 16.5 | 2.40 | 3.00 |
| TAP67 x C.I. 12406 | 333 | 54.5 | 141 | I | 15.8 | 2.92 | 3.13 |
| TAP67 x C.I. 12406 | 24 | 49.5 | 144 | Seg | 16.9 | 2.24 | 2.00 |
| TAP67 x C.I. 12406 | 159 | 52.5 | 177 | Seg | 16.7 | 2.10 | 1.63 |
| TAP67 x C.I. 12406 | 170 | 48.0 | 147 | Seg | 17.8 | 2.71 | 2.00 |
| TAP67 x C.I. 12406 | 316 | 49.5 | 161 | Seg | 16.7 | 3.18 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 268 | 50.0 | 138 | I | 17.7 | 3.18 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 378 | 50.5 | 132 | I | 18.0 | 2.55 | 4.00 |
| C.I. 12406 x TAP47-Ponca | 32 | 52.0 | 178 | Seg | 18.3 | 2.66 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 223 | 53.5 | 163 | Seg | 18.3 | 2.87 | 3.88 |
| C.I. 12406 x TAP47-Ponca | 267 | 51.0 | 178 | Seg | 18.2 | 2.82 | 3.00 |
| C.I. 12406 x TAP47-Ponca | 323 | 50.5 | 133 | Seg | 17.8 | 3.06 | 3.66 |
| C.I. 12406 x TAP47-Ponca | 353 | 52.5 | 137 | Seg | 17.6 | 2.14 | 2.13 |
| C.I. 12406 x TAP47-Ponca | 1 | 48.5 | 172 | S | 18.1 | 3.78 | 4.75 |
| C.I. 12406 x TAP48-Ponca | 11 | 51.5 | 147 | I&R | 16.5 | 2.89 | 3.00 |
| C.I. 12406 x TAP48-Ponca | 45 | 49.0 | 163 | Seg | 16.9 | 3.21 | 2.75 |
| C.I. 12406 x TAP48-Ponca | 244 | 49.5 | 135 | Seg | 17.2 | 2.90 | 2.13 |
| C.I. 12406 x TAP47-Com. | 108 | 49.0 | 141 | Seg | 17.5 | 3.79 | 5.00 |
| C.I. 12406 x TAP47-Com. | 277 | 48.5 | 140 | Seg | 17.0 | 4.03 | 3.38 |
| C.I. 12406 x TAP47-Com. | 284 | 50.0 | 146 | Seg | 16.2 | 3.48 | 3.33 |
| C.I. 12406 x TAP47-Com. | 329 | 54.0 | 184 | Seg | 17.5 | 3.29 | 4.66 |
| Ponca x TAP48-Ponca | 205 | 54.0 | 177 | I | 18.9 | 1.74 | 2.00 |
| Com. x TAP67-Com. | 60 | 46.0 | 152 | Seg | 18.2 | 3.07 | 2.63 |

[a] I = Immune, R = Ponca type of resistance, S = Susceptible, Seg = Immune and completely susceptible types.

## TABLE X

### A COMPARISON OF THE QUALITY OF THE 1957 AGROTRICUMS AND CHECK VARIETIES

| Material Compared | Mixing Time | Specific Sedimentation | Percent Protein | Lbs. Bu. |
|---|---|---|---|---|
| $F_4$ Hybrids | 2.72 | 2.93 | 17.1 | 50.0 |
| Homozygous Imm. $F_4$ Hybrids | 3.01 | 2.89 | 18.0 | 50.7 |
| Ponca (ck.) | 2.63 | 3.00 | 16.6 | 48.2 |
| $F_3$ Hybrids | 3.02 | 2.81 | 17.0 | 51.1 |
| Homozygous Imm. $F_3$ Hybrids | 2.88 | 2.47 | 17.1 | 52.5 |
| TAP67 (ck.) | 2.63 | 2.75 | 16.3 | 50.7 |
| Ponca (ck.) | 3.00 | 3.01 | 16.7 | 52.5 |
| Comanche (ck.) | 3.38 | 2.98 | 16.8 | 49.0 |
| C.I. 12406 (ck.) | 2.88 | 2.86 | 18.0 | 50.5 |

### Yield

Due to the extreme drought in 1954-1955, many of the $F_2$ plants did not produce heads. Of those that did head, a few produced no seed, and the yield ranged upward to 42 grams for one plant. In choosing plants for the production of the $F_3$ generation, yield was considered only after rust reaction, texture, and plumpness had failed to reduce the plants to a manageable number.

The 1956 $F_3$ nursery was a replicated yield test. It proved to be quite successful, with a Coefficient of Variation of 14.8 percent, which is not too high for a good wheat yield test. The analysis of variance of yield is given in Table XI.

TABLE XI

ANALYSIS OF VARIANCE OF YIELD OF $F_3$ LINES AND CHECK VARIETIES IN 1956

| Source | Degrees of Freedom | Sum of Squares | Mean Square | F | $F_{0.01}$ |
|---|---|---|---|---|---|
| Total | 137 | 47333 | | | |
| Blocks | 2 | 2709 | 1354 | | |
| Lines | 45 | 31155 | 692 | 4.63 | 1.79 |
| Error | 90 | 13469 | 149 | | |

In 1957 both the $F_3$ and $F_4$ nurseries were planned as yield tests; however, due to the abnormal season and the high proportion of rust susceptible lines in the $F_3$ nursery, it was decided to harvest only a part of the $F_3$ nursery. The $F_4$ nursery was harvested, and the analysis of variance of yield is given in Table XII.

## TABLE XII

### ANALYSIS OF VARIANCE OF YIELD OF $F_4$ LINES AND CHECK VARIETIES IN 1957

| Source | Degrees of Freedom | Sum of Squares | Mean Square | F | $F_{0.01}$ |
|---|---|---|---|---|---|
| Total | 539 | 118302 | | | |
| Blocks | 2 | 4906 | | | |
| Lines | 179 | 80508 | 450 | 4.90 | 1.33 |
| Families of Lines | 7 | 34898 | 4985 | 54.27 | 2.78 |
| Lines within Families | 172 | 45610 | 265 | 2.89 | 1.33 |
| Error | 358 | 32888 | 92 | | |

### Plant Height

Though plant heights were recorded on all nurseries grown, they were not used as a basis for selection, and no analysis of heights was made in most nurseries. In 1957 plant growth was apparently normal until after the nurseries were headed and plant height recorded. The severe rust infection that occurred soon afterwards made it possible to find three groups of lines containing both rust immune and completely susceptible lines. Each group was descended from a single $F_2$ plant. The average plant heights by pedigree and disease reaction are presented in Table XIII. The analysis of variance of the original data is shown in Table XIV. Since the numbers of immune and susceptible lines were unequal, the addition theorem for sums of squares does not apply, and the sums of squares for crosses, disease reaction, and interaction between them were calculated by the method known as "Weighted Means of Squares."

TABLE XIII

PLANT HEIGHT IN 1957 BY PEDIGREE AND RUST REACTION

| Cross | Rust Reaction | No. of Plots | Mean Height Inches |
|---|---|---|---|
| Ponca x TAP45 | Immune | 30 | 38.7 |
| | Susceptible | 36 | 42.2 |
| TAP64 x Com. | Immune | 9 | 41.4 |
| | Susceptible | 54 | 44.2 |
| Com. x TAP67 | Immune | 30 | 43.0 |
| | Susceptible | 39 | 44.9 |

## TABLE XIV

## ANALYSIS OF VARIANCE OF PLANT HEIGHT OF THE RUST IMMUNE AND SUSCEPTIBLE LINES IN THREE $F_4$ FAMILIES IN 1957

| Source | Degrees of Freedom | Sum of Squares | Mean Square | F | |
|---|---|---|---|---|---|
| Total | 197 | 1854 | | | |
| Blocks | 2 | 25 | | | |
| Lines | 65 | 1315 | 20.2 | 5.11 | $F_{0.01}=1.61$ |
| Groups with same Cross and Disease Reaction | 5 | 808 | 161.6 | 40.91 | $F_{0.01}=3.16$ |
| Lines within groups | 60 | 507 | 8.5 | 2.14 | $F_{0.01}=1.63$ |
| Crosses | 2 | 416 | 208.0 | 52.66 | $F_{0.01}=4.78$ |
| Disease Reactions | 1 | 264 | 264.0 | 66.83 | $F_{0.01}=6.84$ |
| Interactions between Disease Reactions and Crosses | 2 | 24 | 12.0 | 3.03 | $F_{0.05}=3.07$ |
| Error | 130 | 514 | 3.95 | | |

### Maturity Date

In 1955 it was noted that the earlier ripening plants were mostly rust susceptible, and as the season progressed a much higher proportion of the plants ripening were rust immune. Since it is not valid to test an hypothesis with the data from which the hypothesis is derived, no analysis of these data was made. In 1957 the normal plant growth, which continued until after the heading dates were recorded, followed by severe rust infection furnish data that could be used for testing the hypothesis that this type of rust immunity is associated with delayed maturity. The average heading date by pedigree and disease reaction are presented in Table XV. The analysis of variance of the original data, calculated as explained under the heading "Plant Height," is presented in Table XVI.

TABLE XV

DATE-OF-MATURITY IN 1957 BY PEDIGREE AND RUST REACTION

| Cross | Rust Reaction | No. of Plots | Mean Heading Date in May |
|---|---|---|---|
| Ponca x TAP45 | Immune | 30 | 17.3 |
| | Susceptible | 36 | 15.6 |
| TAP64 x Com. | Immune | 9 | 15.9 |
| | Susceptible | 54 | 14.2 |
| Com. x TAP67 | Immune | 30 | 15.7 |
| | Susceptible | 39 | 15.6 |

## TABLE XVI

## ANALYSIS OF VARIANCE OF DATE-OF-MATURITY OF THE RUST IMMUNE AND SUSCEPTIBLE LINES IN THREE $F_4$ FAMILIES IN 1957

| Source | Degrees of Freedom | Sum of Squares | Mean Square | F | $F_{0.01}$ |
|---|---|---|---|---|---|
| Total | 197 | 559 | | | |
| Blocks | 2 | 50 | | | |
| Lines | 65 | 399 | 6.1 | 7.2 | 1.61 |
| Groups with same Cross and Disease Reaction | 5 | 197 | 39.4 | 46.6 | 3.16 |
| Lines within groups | 60 | 202 | 3.4 | 4.0 | 1.63 |
| Crosses | 2 | 45 | 22.7 | 26.8 | 4.78 |
| Disease Reactions | 1 | 48 | 48.0 | 56.6 | 6.84 |
| Interactions between Disease Reactions and Crosses | 2 | 26 | 12.7 | 15.0 | 4.78 |
| Error | 130 | 110 | 0.846 | | |

# DISCUSSION

## Genetics of Leaf Rust Resistance

Since the mechanism which controls mature plant leaf rust immunity in the crosses under consideration is dominant but does not give the usual Mendelian ratios, some mechanism other than genic segregation must be involved. The fact that resistant or immune plants have occurred in the $F_1$, $BC_1$, $BC_2$, $BC_3$, and $BC_4$ generations of crosses in which the recurrent parent was completely susceptible is considered ample proof that the immunity is dominant. Additional proof is shown by the large number of susceptible and segregating lines in the $F_4$ nursery grown in 1957. All of them were descended from six plants that had been immune in 1955. Since all plants known to be rust susceptible were discarded, it is not known what the breeding behavior of susceptible plants would have been, but it is assumed that they would have produced all susceptible plants.

The close approach to a ratio of three susceptible to one immune plant that occurs in the crosses involving TAP48 in Table III, and in the crosses TAP48 x Ponca and TAP47 x Comanche in the $F_4$ nursery of 1957, could lead to the erroneous conclusion that immunity was a simple Mendelian recessive if proof that it is dominant were not available.

The cross Concho x Triticum sp.-Agropyron elongatum was studied by Merkle (38) who, basing his opinion on the ratio of susceptible to immune plants, stated that his data indicated that the inheritance of immunity was on a monohybrid basis with immunity being recessive. The heterogenity of the results presented in Table III indicate that the inheritance of rust immunity in this material is complex.

Since TAP48 has 44 chromosomes, it is logical to assume that the extra pair is derived from Agropyron elongatum and that they carry the rust immunity. The other TAP lines that have been examined have had 42 chromosomes. It is hypothesized here that two of these are Agropyron elongatum chromosomes substituted for wheat chromosomes. In addition, it is hypothesized that all TAP lines have gene substitutions from Agropyron elongatum caused by crossing-over of wheat and Agropyron chromosomes that are homologous. Since no cytological examination was made of the plants involved in this thesis, the behavior of the added or substituted chromosomes must be inferred from the breeding behavior of the plants or from the behavior of chromosomes in similar situations.

Extensive experiments by Sears (53) with monosomics in wheat indicate that 75 percent of the megaspores produced by monosomics have only 20 chromosomes. This could be caused by 50 percent of the univalent chromosomes lagging so far in moving to the poles that they are not included in either cell of the diad. Sears also found that monosomes produced from 0.9 to 7.6 percent of nullisomic plants. This could mean that, if 20 chromosome microspores are produced in the same proportion as the megaspore, their effectiveness is reduced by gamete selection so that only 1.2 to 10 percent of the functioning male gametes have 20 chromosomes. Sears (52) also reported that univalents from Haynaldia villosa in a common wheat background were not distributed at random but tended to be transmitted as a group and that, due to their lagging at first prophase, a loss of about 50 percent of them is normal. With a single monosome from H. villosa added to common wheat, Hyde (27) found that it was transmitted through the female gamete 25 percent of the time, but male transmission occurred only when some aberration caused little normal pollen to be formed. Similar gamete competition was noted by O'Mara (42) who found that the percentage of male gamete successes from wheat plants heterozygous for a rye chromosome substitution were: 60 percent normal gametes, 26 percent substitution gametes, 8 percent gametes with both chromosomes, and 6 percent nullisomic gametes.

If the unpaired chromosomes in plants heterozygous for an addition or substitution carrying rust immunity follow this same pattern, the following results would be expected. In plants heterozygous for an addition, 75 percent of the ova would not carry the addition and would not contribute to rust immunity. Seventy-five percent of the male gametes would not carry the addition and would have a competitive advantage over the gametes with the extra chromosome. Multiplying the above two percentages gives 56 percent of the selfed seed with no immunity. Actually, the percentage of immune plants in lines segregating for an addition has been only a little over 25 percent on the average. One factor that could be reducing the percentage of immune plants in these lines would be the formation of chromosome mosaics just prior to meiosis as described by Sachs (42). If spore mother cells which do not have the addition chromosome are sometimes formed, this would reduce the percentage of immune plants and also explain the occurrence of occasional rust susceptible plants in pure lines of TAP48 which the author has noted. It is believed that the major part of the reduction in percentage of immune plants is due to gamete competition. If this is true, one would expect the percentage of heterozygous immune plants to approximate the percentage of immunity transmitted by the ova. Homozygous immune plants would be rare. This expectation is borne out by the family of lines grown in 1957 with the pedigree of TAP48 x Ponca. Thirty unselected $F_3$ plants grown from the same $F_2$ plant produced 21 completely susceptible lines, nine segregating lines, and no homozygous immune lines. The mean percentage of immune plants in the segregating lines was 28.2 percent.

In plants heterozygous for a substitution, the situation is more complicated. Figure 2 shows what the distribution of chromosome types in the gametes and embryos would be if chromosome mosaics and gamete competition did not occur and assuming that 50 percent of the unpaired chromosomes are lost during meiosis. It is assumed, however, that the sperm with 20 wheat chromosomes or with 21 wheat chromosomes and an *Agropyron* chromosome compete successfully only in trace amounts.

| | | | | | |
|---|---|---|---|---|---|
| percentage . . . . . . . . . . . | | 56.25 | 18.75 | 18.75 | 6.25 |
| chromosomes of sperm . . . . | | 20 | 21 | 20+A[a] | 21+A |
| | ova | zygotes | | | |
| percentage. . . . . | 56.25 | 31.64 | 10.55 | 10.55 | 3.52 |
| chromosomes . . . . | 20 | 40 | 41 | 40+A | 41+A |
| percentage. . . . . | 18.75 | 10.55 | 3.52 | 3.52 | 1.17 |
| chromosomes . . . . | 21 | 41 | 42 | 41+A | 42+A |
| percentage. . . . . | 18.75 | 10.55 | 3.52 | 3.52 | 1.17 |
| chromosomes . . . . | 20+A | 40+A | 41+A | 40+AA | 41+AA |
| percentage. . . . . | 6.25 | 3.52 | 1.17 | 1.17 | 0.39 |
| chromosomes . . . . | 21+A | 41+A | 42+A | 41+AA | 42+AA |

---

[a] A = chromosome from *Agropyron*

Figure 2.--Theoretical distribution of chromosomes in gametes and zygotes resulting from selfing an $F_1$ produced by crossing a substitution line with common wheat, assuming no gamete competition.

If sperm with 21 wheat chromosomes fertilize the ova shown in Figure 2, plants would be produced in the proportion of three susceptible to one immune. Plants produced from sperm with 20 wheat chromosomes and one *Agropyron* chromosome would produce all immune plants, so that if the two types of gametes were equally competitive, the over-all ratio would be three susceptible plants to five immune. In order to produce a ratio of one susceptible to one immune plant, as has sometimes occurred, it would be necessary for the sperm with 21 wheat chromosomes to produce twice as many successful matings as those with 20 wheat chromosomes and an *Agropyron* chromosome.

It can be hypothesized from these studies that the *Agropyron* genes carried on chromosomes that are homologous in wheat and *Agropyron* have the following effects. First, the male gametes which have an *Agropyron* chromosome substitution compete more successfully if many *Agropyron* genes are present. Second, as the number of *Agropyron* genes decreases, the effect of the *Agropyron* chromosome substitution changes from rust immunity to very high resistance, to high resistance, to resistance, to a mesothetic reaction. This effect has been observed only in the mature plant stage of greenhouse grown plants when the chromosome substitution was in the heterozygous condition. A difference in number of homologous *Agropyron* genes may explain some of the difference in ratios of immune and susceptible plants in the various substitution lines shown in Table III.

In 1957 three families of segregating lines had, respectively, 53.5 percent, 50.6 percent, and 44.1 percent of immune plants. These percentages were not significantly different from each other, but they did differ significantly from the 28.2 percent of immune plants in the family of lines derived from TAP48, the 44-chromosome strain. They also differed significantly from the 21.3 percent of immune plants in the family of lines derived from TAP47, a 42-chromosome strain. It is hypothesized that the $F_2$ plant from which this family was derived was heterozygous for an addition, since this is one of the possible segregates from a plant heterozygous for a substitution.

## Quality

In 1955 the rust immune composite had 0.5 percent higher protein and 0.5 minute shorter mixing time than the susceptible composite. Since an unknown proportion of the immune plants was heterozygous, and the dominance effects concerning protein percent and mixing time are unknown, the direction but not the magnitude of the effects when homozygous is indicated.

Since a higher protein percent is a desirable quality characteristic, it partially offsets the undesirable effects of the shorter mixing time. Many wheats have a longer mixing time than is necessary and, therefore, it should be possible to breed a wheat with a satisfactory mixing time even though it carries a factor for shorter mixing time associated with this type of rust immunity.

In 1956 $F_3$ hybrid lines had mixing times of up to 4.25 minutes compared to the best plots of Ponca with 2.88 minutes. The average of the hybrids in this nursery was 2.24 minutes, and though no rust was present, the 1957 tests showed that all lines, selected as having a good combination of quality and yield, were heterozygous for rust immunity.

In the 1957 nurseries the longest mixing times for homozygous and segregating immune lines were four and five minutes, respectively. Since this is more than adequate, it would seem that in so far as mixing time is a measure of quality, the detrimental effects of this source of rust immunity are not insurmountable.

It is not known whether the soft texture of the TAP selections is associated with rust immunity, but it has been necessary to select away from this soft texture. Selection has been quite effective. None of the $F_3$ lines grown in 1956 was too soft for proper milling, and this improvement came about by a single cycle of selection. In 1957 four of the 58 $F_3$ and $F_4$ hybrid lines submitted for testing were too soft for proper milling. In view of the excessive rain in 1957 and because of their otherwise excellent quality characteristics, these lines have not been discarded; however, if they remain too soft in a normal year and do not segregate for texture, they will be discarded. Under the present marketing system, test weight is a quality characteristic, and none of the TAP selections are better than moderately low for this characteristic. The test weights in the 1956 $F_3$ yield nursery averaged lower than the check varieties; however, some hybrid lines exceeded the best of the checks. In the 1957 $F_3$ and $F_4$ nurseries the rust-immune lines were much higher in test weight, as a group, than other lines, including checks. This is believed to be due to their disease reaction, however, and may be reversed in a year with little rust. The question of whether high test weight can be combined with rust immunity from this source is yet to be answered, though some of the selections now growing may provide an answer.

## Yield

The TAP selections, in several years of testing, have never equaled their Pawnee parent in yield, though at times TAP67 has been very close. Recent wheat variety releases outyield Pawnee by a substantial margin so that the TAP selections can only be classed as low yielding by modern standards.

Since the only purpose in breeding a rust resistant wheat is to increase yield and test weight in the years in which rust occurs, the yield of any variety produced must be better than the best rust susceptible varieties in years with heavy rust infection. A small decrease in yield can be tolerated in years with little or no rust infection as an insurance premium on a rust damage policy. The loss in yield accumulated in years of little rust damage must be almost regained in the years of heavy rust damage to make it economically sound.

In 1956 there was no rust, and some of the $F_3$ hybrids were substantially better than the average of the checks in yield, though they were not significantly better than the check average using the Multiple Range test of significance. In 1957 a very severe rust infection occurred rather late in the season and this, together with hail and too much rain, reduced the yield and test weight of all strains. The rust immune hybrids suffered the least and were greatly superior to the susceptible hybrids and checks. It is believed that 1957 was too abnormal a year to serve as a test of the relation of yield to rust reaction. At the time that rust readings were made in 1957, the plants had headed but had not yet been harmed much by rust. In the segregating lines the individual rust immune plants appeared at this time to be less vigorous and to have smaller heads than the susceptible plants. Even if the best of these rust immune lines are equal to the better wheat varieties in yield, it is possible that they could be made still higher yielding by replacing their rust immunity with rust susceptibility through the backcross method of plant breeding.

The possibility of selecting for yield within segregating populations by means of the progeny test was investigated during the years of 1956 and 1957. In 1956, 40 $F_3$ lines, each derived from a single $F_2$ plant, were grown in triplicate yield plots. Only 10 plants were grown in each plot, and there were no border rows or discarded row ends. These features of the nursery probably increased the error term, and thus the size of the Coefficient of Variation, and decreased the sensitivity of the test. Even so, the analysis of variance indicated almost a null possibility that the differences in mean yield of the strains were due to chance rather than to genetic differences in the $F_2$ plants from which they were derived. When the 174 $F_3$ plants from six of these lines were grown as $F_4$ lines, a similar high significance for the differences between lines was obtained. The sum of squares for lines in the $F_4$ nursery then was subdivided. One component was the sum of squares due to the variation between the eight groups of lines which were derived from six different $F_2$ plants and two check varieties. The other component was the sum of squares due to the variation of lines within the $F_2$ derived groups and the check varieties. These two components showed that the significance of the differences between groups of lines was far greater than the significance of the differences between lines within groups. This is, of course, exactly according to genetic theory. Even though the $F_3$ derived lines were less variable than the $F_2$ derived lines, they still had so much variability that $F_4$ derived lines seem to offer promise of additional improvement. Accordingly, $F_4$ derived lines have been planted for increase so that selections from them can be tested in regular nursery yield plots.

## General

The transfer of genes conditioning disease resistance from related species to _Triticum_ _vulgare_ often has been attempted in the past. Transfers from the emmers, which have chromosomes homologous with some of the common wheat chromosomes, generally have been successful. In recent years transfer of genes from T. *timopheevi*, which has one genome not homologous with any genome of common wheat, has been accomplished. The transfer of genes to common wheat through still wider crosses, while often attempted, has seldom been successful. This apparently has been due to the fact that the desired genes have been located on chromosomes that are not homologous with any wheat chromosome. Because of this no crossing over occurs with wheat chromosomes and, therefore, the chromosome with the desirable gene is inherited as a unit. Sears (53) has shown that an extra pair of chromosomes has a deleterious effect on the vigor of wheat plants carrying them, and it may be assumed that extra chromosomes from another species also would have a depressing effect on yield. In the case of a substituted chromosome, there might be a compensating effect so that the vigor of the plant might be unharmed. With either an addition or substitution, however, there would be a large number of genes tending to make the wheat plant more like the donor species. As a general rule this lowers both the grain yield and quality. Sears (54) has succeeded in eliminating most of the detrimental effects of a chromosome from *Aegilops umbellulata* while retaining the rust resistance carried on that chromosome. He did this by X-raying a plant with the added chromosome and selecting from its progeny a plant with a small intercalary translocation which carried the rust resistance. Elliott (11,12) also has used various sources of irridation to induce translocation of genes for bunt and stem rust resistance from Agropyron elongatum chromosomes to those of common wheat. Jenkins (24), on the other hand, reports that he is using various combinations of intact chromosomes from Aegilops squarrosa, Agropyron elongatum, Secale cereale, Aegilops longissima, and Haynaldia villosa substituted for some of the chromosomes of common wheat. He hopes by this process to create more productive species of food plants.

The data from this thesis indicate that, if a chromosome substitution is the source of rust immunity in this material, such a substitution is detrimental to both grain yield and quality. The data also indicate that through selection certain gene combinations have been isolated which compensate for the substitution and thus produce wheat plants which are equal to the check varieties in yield and grain quality.

## Recommendations

The following recommendations for further research with this material are suggested. In order to determine more accurately the present status of the problem, a few selected lines from the more advanced segregating populations should be increased and entered in regular nursery yield tests.

With the greater amounts of grain available, quality tests should be made. Lines isogenic except for a difference in rust reaction should be produced by maintaining some of the segregating lines until the $F_8$ generation, after which near isogenic pairs of lines can be selected. These lines then can be used to determine the effects of the chromosome bearing the genes for rust immunity on other agronomic and quality characteristics.

If the hypothesis, that an addition or substitution chromosome from Agropyron elongatum is the source of the rust immunity, proves to be correct, the chromosome should be added to a known variety and then substituted in turn for each of the 21 pairs of chromosomes of this variety. Sears (53) gives a method for producing these substitution lines from addition lines. Homoeologous group seven consisting of chromosomes VII, XI, and XXI, which are least essential to the wheat plant, might afford the best substitution sites; however, it is possible that the Agropyron elongatum chromosome might better compensate for the loss of some other chromosome, and thus another substitution site might be better. That chromosomes from different genomes of a polyploid species may have enough genes in common that a tetrasome of one can partially compensate for a nullisome of another even when they do not retain enough structural homology to pair at meiosis was reported by Sears (51). It now appears that this homoeology of chromosomes may extend to genomes from different species. Even if the chromosome carrying the rust immunity is homoeologous with the one for which it is substituted, there should be two other sites for which it could compensate in part and which might be better than the one which it now occupies.

Crosses between homozygous rust immune lines with complementary characteristics should be made. These crosses would have the advantages that no elimination of a chromosome carrying susceptibility would be necessary, and some selection toward a genotype compensating for the loss of a wheat chromosome already would have been made.

The possibility that more than one chromosome of *Agropyron elongatum* carries effective genes for leaf rust immunity should be investigated. That there may be a chromosome which carries genes for both blue aluerone color and rust immunity is indicated by the segregation in the $F_2$ of the cross C.I. 12406 x *T.-A. elongatum*. Six $F_1$ seed from this cross with blue aluerone all produced immune plants, whereas nine seed with colorless aluerone produced five susceptible and four immune plants. This difference in rust reaction, if not due to chance, might indicate that blue aluerone and rust immunity are carried on the same chromosome. The other sources of rust immunity studied in this material have not been associated with blue aluerone and thus must be located on a different chromosome. An alternative hypothesis is that there is but one chromosome which carries rust immunity and that this chromosome and another one are both necessary for the production of blue aluerone.

Other experiment stations also have wheat-like agrotricums with leaf rust immunity which may or may not be carried on the same chromosome as the immunity in this study.

# SUMMARY

The possibility of combining leaf rust immunity from selections of Triticum sp.-Agropyron elongatum x Pawnee with good grain quality, high yield, and other desirable agronomic characteristics of hard red winter wheat was investigated in this study. Incidental to the primary purpose, an effort was made to explain the mode of inheritance of this type of leaf rust immunity and to determine if a progeny test method of breeding for yield would be effective. Preliminary results indicate that the primary objective may have been achieved, since some selected lines have been homozygous rust immune and have exceeded the check varieties in grain quality and yield. Most of the rust immune lines also have had a higher protein percentage than the check varieties.

In this material rust immunity was inherited as a dominant; however, the ratios of immune to susceptible plants which were obtained in the backcross and segregating generations proved to be quite complex and did not fit any Mendelian ratio. Most segregating populations were near either a three susceptible to one immune ratio or a one susceptible to one immune ratio. Several of the populations with 25 percent immune plants were known to have originated from immune plants which had 44 chromosomes. The hypothesis

is offered that all populations segregating with near 25 percent immune plants were segregating for an addition chromosome and that the populations segregating with near 50 percent immune plants were segregating for a substitution chromosome. It also is hypothesized that chromosome mosaics, lagging chromosomes during meiosis, and gamete selection in pollen are the factors that reduce the percentage of immune plants in the segregating populations.

The analysis of variance indicated that the progeny test was quite effective in the $F_3$ and $F_4$ generations for selecting high yielding lines. Additional populations tested for more generations would be needed to more completely evaluate the progeny test for wheat breeding.

Data presented in this thesis seem to indicate that rust immunity in this material is associated with lower yield, lower quality, later maturity, shorter straw, and a higher percentage of protein in the grain. The data also indicate that the tendency toward low yield and low quality can be overcome by selection.

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