

REACTION OF F₃ LINES OF THE CROSS
WICHITA 5 X CHINESE AND AEGILOPS UMBELLULATA
TO SEVERAL RACES OF LEAF RUST

by

ATEF SHAFIK SOLIMAN

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INTRODUCTION

Leaf rust of wheat, Puccinia recondita Rob. ex Desm., Cummins and Caldwell (15) is one of the most severe diseases attacking wheat and is found wherever wheat is grown. Leaf rust has been found to be the most destructive disease of wheat in Kansas Huffmann and Johnston (34). Leaf rust in Kansas was extremely heavy on volunteer and early sown wheat in the fall of 1960 as stated in the Wheat Newsletter (90). It was reported also by Hansing, et al. (25) that heavy infections of leaf rust were present on volunteer and early sown wheat in the eastern two thirds of the state in the fall of 1958. They mentioned that the loss due to leaf rust was estimated at 10 percent. The damage caused by the leaf rust disease usually is underestimated because it never totally destroys a Kansas crop and seldom causes severe shrivelling of the grain. However, it has been proved that leaf rust reduces the number of kernels per head and the size of kernels per head, and the size of the kernels as reported by Pady, et al. (62).

Leaf rust resistant varieties offer the chief means of control of this disease. However, the problem of breeding resistant varieties is greatly complicated by the occurrence of many physiologic races of the fungus as reported by Johnston (38, 39, 45) and Mains (57). At present 183 physiologic races are recognized by Johnston (43). These races include the 18 races recognized by Basile (6) on the basis proposed by Johnston (40) of consolidation of closely related physiologic races of Puccinia rubigo-vera (D.C.). She used eight differential varieties to identify these races.

One of the objectives of the wheat breeding program at the Kansas

Agricultural Experiment Station is to introduce agronomic characters (disease resistance, insect resistance, winter hardiness, etc.) into the hard red winter wheats adapted to Kansas conditions, and which are extensively grown in Kansas, e.g., Wichita, Triumph and Bison, Wheat Newsletter (89,90). It was shown this can be accomplished by chromosome substitution from related genera and species. Agropyron derivatives are good sources for leaf rust resistance as well as for good agronomic characters that were reported by Knott (49), Schmidt and Heyne (76). Aegilops derivatives also are good sources of leaf rust resistance, Sears (71) and Watanabe (87). Triticum species crosses, diploid and tetraploid, were used as a source of desired characters, Abe (4), Kihara (48), Kostov (51), Tochinal and Kihara (81) and Kostov (52).

It was found that the transfer of characters from one species or genus to another is not only of great potential practical importance, but is of considerable genetic interest as well. In general, the wider the transfer the more interesting it is genetically, Sears (71), Smith (80) and Vavilov (83). From a practical standpoint, the greater the distance over which transfers can be made, the greater the possibility of introducing useful characters not present in the host species. It is therefore important to extend the limits of transfer as far as possible. Significant progress has already been made in this direction and has been reviewed by Elliot (17), Hays (27) and Heyne (28).

This thesis is concerned about the inheritance of leaf rust resistance of Aegilops umbellulata transferred into cytologically stable hexaploid hard red winter wheats.

REVIEW OF LITERATURE

The inheritance of leaf rust resistance was carefully studied by Chester (13), Heyne (30,31). It was stated by Chester (13) that in general, leaf rust is inherited in simple mendelian fashion. In many cases resistance is governed by a single factor as reported by Heyne and Livers (29), Heyne and Johnston (30, 31), Mode (60), Schulte (79) and Bueno (12). The resistance derived from related genera and species has also been studied. Nyquist (61) studied the inheritance of resistance to leaf rust in hybrids involving a common wheat strain derived from Triticum timopheevi. Similar work on the genetic studies of derived resistance was done by Shands (73) and Shebeski (74). Sears (72) concluded that the wheat chromosome carrying leaf rust resistance from Aegilops umbellulata was chromosome X (6B) and that the translocated segment from Aegilops is small and intercalary. The F_2 data, obtained from the cross of strain 47 (sometimes referred to under the name Transfer) and mono - chromosome X (6B), gave 479 resistant and 180 susceptible plants, a reasonable fit to a 3:1 ratio. These data indicated that the resistance to leaf rust derived from Aegilops umbellulata was simply transmitted.

As the inheritance of leaf rust resistance was carefully reviewed by other workers, Bueno (12), this review will cover the transfer of useful agronomic characters from one species or genus to another.

The problems of interspecific and intergeneric hybridization are sterility, irregularities in chromosome behavior during the meiotic division, Beasley (7) and male sterility, Fukasawa (20). It was found that certain wide crosses can be made to succeed by doubling the

chromosome number of one parent. The work done by Bernstrom (8) on *Lamium*, and Livermore and Johnstone (56) on potatoes are good examples. Other methods used are to overcome the barrier to successful crosses is embryo transplantation Hall (24) and growing the young embryos in nutrient solution, Keim (47) and Laibach (54). Brock (11) used hormones in inducing pear-apple hybrids. Emsweller and Stewart (18) found that naphthene acetamide, was very effective in crosses between different species of *Lamium*. Allard (5) and Watanabe et al. (84, 85, 86, 87) found that by backcrossing the hybrids to the recurrent parent they were able to decrease irregularities of chromosome behavior during the meiotic division. Watanabe et al. (84, 85, 86, 87) were able to get more or less fertile hybrids from the crosses T. timopheevi x T. vulgare, five species of Dinkel group x T. timopheevi x Aegilops longissima.

Sources of resistance to leaf rust and stem rust were reviewed by Chester (13) and the reaction to leaf rust of some of these sources and several hybrids between wheat x rye were studied by Johnston (37). He also studied seedling reaction of some varieties which may be used as a source of resistance (41). Some of these varieties which are susceptible became resistant at maturity. Johnston (42) called this phenomenon, the maturative type of resistance.

Clayton (14) has made the following suggestions in selecting wild species for interspecific transfer of disease resistance:

1. By repeated evaluations of the disease resistance of available species narrow the choice to those that are uniformly highly resistant or immune.

2. Measure the disease reaction of these species in direct comparisons with the allopolyploids or F_1 's that they form with the crop plant.

3. If possible, use for interspecific work a species that produces an allopolyploid or F_1 which shows the full resistance of the resistant parent. Tochinal and Kihara (81) in a series of crosses involving Triticum vulgare, dicoccum, durum, turgidum, compactum, polonicum, spelta and Dinkel wheats, obtained progeny with varying chromosomes up to ($2n=41$). The F_1 hybrids were generally susceptible, i.e., resistance was recessive and in later generations the segregates reacted toward rust similarly to the parent which they most resembled in morphology and chromosome number.

McFadden (58) succeeded in transfer of emmer characters to vulgare wheat. He used Yaroslav emmer, a variety of Triticum dicoccum, and Marquis, a variety of Triticum vulgare. Abe and Matsumura (4) crossed the rust resistant T. durum ($n=14$) with susceptible T. vulgare ($n=21$). In the progeny with $2n$ chromosome numbers from 28 to 35, susceptibility was progressively higher with the increase in the chromosome number. Guard (23) crossed the seedling susceptible T. vulgare Chinese ($n=21$) with the resistant T. dicoccum ($n=14$). The F_1 plants showed mesothetic or "X" type reactions and had 14 bivalent and 7 univalent chromosomes. In the F_2 to F_6 generations the plants with 14 chromosomes were all rust resistant, and those with 21 chromosomes had ratios of 11 resistant to 6 susceptible. The chromosome behavior during the meiotic division in the hybrids obtained from the following crosses (T. timopheevi x T. vulgare) and five species in Dinkel groups

and Triticum timopheevi, were studied by Watanabe and Mukade (84, 85). They found a considerable decrease in the number of multivalents and univalents and increase in bivalents by crossing the hybrids to their parents. The irregularities in chromosomes has been observed in both interspecific and intergeneric crosses.

Wheat x rye hybrids are normally susceptible to wheat leaf rust in the F_1 generation, hence resistance is recessive. An exception was seen in Guard's crosses (23) between T. vulgare Chinese ($n=21$) and Abruzzes rye ($n=7$), Secale montanum. He obtained amphidiploids with 28 chromosomes in which wheat leaf rust resistance was dominant. O'Mara (65) explained a method for substitution of a specific rye chromosome for a specific Triticum vulgare chromosome.

O'Mara (64) outlined also a method of combining characters of two species or genera by the addition of one or more chromosomes from one species to the full diploid complement of the other species. Such a procedure has been carried out in wheat with addition from rye by Florell (19) and Haynaldia villosa Hyde (35). Hyde (35) obtained five of the seven possible addition disomics. He found obvious modification of the wheat plant caused by the addition of individual Haynaldia chromosomes. Chromosome pairs are limited to increase in spike density, change of coleoptile color, increase in asynapsis and a general decrease in vigor and fertility. Kattermann (46) developed a wheat line with 20 pairs of wheat chromosomes and a pair of rye chromosomes. This work was part of the program in Germany to obtain wheat which has high yield, resistance to lodging and to diseases and early maturity.

Sears (67) obtained a hybrid between Triticum dicoccoides (a wild

tetraploid wheat) and Haynaldia villosa ($2n=14$) and he doubled that hybrid to ($2n=42$). This amphidiploid was used in crosses with common wheat to produce types which contained the villosa complement plus the variable wheat complement.

The evaluation of individual chromosomes by monosomic analysis is very important in the field of chromosome substitution. An example of monosomic analysis was done by Heyne and Livers (29). They concluded that Pawnee wheat has one major factor for resistance to race 9 of leaf rust located in chromosome X (6B). By applying this type of analysis it is possible to make chromosome substitution much easier.

Sears (69, 70) showed the relation of chromosome substitution and nullisomic analysis. He reported that there are two main purposes of chromosome substitution in wheat; first to determine the effects of individual chromosomes in a variety when transferred to a common background, generally through the use of monosomes; and second to demonstrate that disease resistance or some other desirable feature is conditioned by a certain chromosome. The next step is to substitute this chromosome into other acceptable variety by backcrossing to that variety until the backcrossed plants have the desired chromosome in the recurrent parent. The above work indicated the importance of monosomic and nullisomic analysis for evaluation of chromosomes.

The investigations of Kihara and Lillienfield (48) and Kostov (51) showed that hybrids obtained from interspecific and intergeneric crosses are highly self-sterile. The cytological investigations of T. timopheevi in Japan, Kihara and Lillienfield (48) using cyclic crosses with different species, Aegilops and Secale, have shown that in

T. timopheevi there is a distinct assortment of seven chromosomes which are different from those of other wheat species. Pridham (63) obtained a successful cross between Triticum vulgare and Triticum timopheevi. He obtained lines that were resistant to stem and leaf rust and T. vulgare in type. Shands (73) made crosses between Triticum timopheevi and a number of varieties of T. vulgare. There was no difficulty however in obtaining seed when T. vulgare was used as a female. He was able to transfer Triticum timopheevi characters including resistance to mildew, leaf rust and stem rust to fertile types of T. vulgare and, furthermore, that several of these plant lines are fertile in hybrids with other varieties of common wheat. Kostov (52) obtained a highly immune wheat experimentally which he named Triticum timococcum.

Sando (66) reviewed the early literature involving hybridization of Triticum, Aegilops and Secale and the morphological differences between the crosses of these genera. He obtained seeds from mature F_1 plants of Haynaldia villosa on Triticum aegilopoides, T. timopheevi, T. dicoccoides, T. dicoccum, T. durum, T. turgidum, T. polonicum and Secale fragile. A critical study showed that 52 morphological characters possessed by the parents and the F_1 hybrids were intermediate between those of the parents. Some characters of the F_1 plants show, however, a decided increase in degree of expression over those of either parents, while others show a dominance of the one or the other parent.

The study of the cytology of wheat and its derivatives is very important from the chromosome transfer standpoint. The cytology of Triticum, Secale and Aegilops hybrids with reference to phylogeny was

studied extensively by Aase (1, 2, 3) and briefly by Sears (68). The reaction to leaf rust Puccinia triticina in some of these above genera was recorded by Hiratsuka (32).

A large amount of work has been done recently on chromosome transfer or segments of chromosomes from the two genera Aegilops and Agropyron to Triticum because of the importance and outstanding characters they have. Jenkins (36) showed the chromosome homologies in wheat and Aegilops. Watanabe et al. (86) tried to synthesize 6 amphidiploids by the artificial hybridization between T. timopheevi and Aegilops longissima. The aim was to combine leaf rust resistance genes possessed separately by these two species into a single species. They obtained the desired hybrid which was crossable with both parents and, furthermore, crossed rather easily with the cultivated varieties of T. vulgare and also with other species of Triticinaea.

The work done by Sears (71) is the most outstanding work so far. He made a cross of Triticum aestivum with amphidiploid T. dicoccoides x Aegilops umbellulata followed by two backcrosses to the former followed by selection and produced a T. aestivum plant with a single added Aegilops chromosome. Plants, with the added derived iso-chromosome carrying the resistance to leaf rust, were X-rayed prior to meiosis and the pollen produced was used on normal untreated plants. Of the 6091 offspring 132 were resistant including 40 with translocated chromosomes. Most of these translocations involved the chromosome which had the Aegilops centromere. This indicated the gene for resistance to leaf rust was located near the centromere. One intercalary translocation obtained gave nearly normal pollen trans-

mission, and was cytologically undetectable. Homozygous plants are distinguishable from normal plants only by rust resistance and slightly later maturity.

The procedures, involved in the various phases of chromosome substitution in common wheat, were outlined and explained by Unrau, et al. (93). They discussed the development of chromosome deficient lines to develop substitution and combination of two chromosome substitutions into a single line. They used Thatcher lines, alien substitution, and combination of two chromosome substitutions into a single line. They used Thatcher lines monosomic for chromosome X (6B) having substituted the same Timstein chromosome carrying the stem rust resistance. In addition they set up a program to substitute chromosome XX (2D) from McMurachy which carries additional stem rust resistance to a Thatcher line monosomic for that chromosome. By combining the two substitution lines, they will have a Thatcher derivative carrying both chromosome X (6B) from Timstein and chromosome XX (2D) from McMurachy.

The importance of the Agropyron derivatives in intergeneric crosses with wheat were reported by Larter and Elliot (55), White (91), Smith (80), Aase (2, 3) Sears (68), Tzitizin (82) and Schmidt, et al. (75). The problem of Agroticum hybridization was reviewed by Schmidt (77), Kovaleva (53), Schindermann (79), and McFadden and Sears (59). The following attributes of the Agropyron species that might be transferred to the wheats were listed: perennial habit, resistance to heat and drought, extreme winter hardiness, resistance to alkaline and acid soil conditions, resistance to various diseases and wide geographic

adaptation. Schmidt, et al. (75) reviewed most of the work done to emphasize the importance of the genus Agropyron in wheat crosses. They reported that other investigators had obtained hybrids between wheat and Agropyron elongatum, A. elongatum derivatives and A. trichophorum. They concluded that the most valuable hybrids isolated were the morphologically intermediate types characterized by harsh foliage, stiff straw, long lax spike, brittle rachis, partly adhering glume and a wheat like kernel. That type proved to be a valuable source of germ plasm for disease resistance, leaf and stem rusts, bunt, loose smut, mildew, speckled leaf blotch, yellow streak mosaic and wheat jointworm insect.

Watanabe and Mukade (87) made a cross between Agropyron glaucum and common wheat. They used Agropyron glaucum as a source of resistance to disease and for its perennial habit. They obtained an F_1 , which was similar to Agropyron glaucum and its fertility was slightly increased by backcrossing with the pollen of the vulgare parent. They reported also that the F_1 's were resistant to diseases, drought and were winterhardy, and that tillering ability especially was superior. Knott (50) succeeded in transferring stem rust resistance from Agropyron elongatum to common wheat by the transfer of the Agropyron genes for resistant to common wheat. He reported that wheat plants having 21_{11} of wheat chromosomes plus a single added Agropyron chromosome were resistant to stem rust. Spikes of these plants were irradiated with thermal neutrons. As a result of irradiation the gene or genes carrying rust resistance was transferred to a wheat chromosome. He reported that one of the translocations was transmitted normally through the gametes.

As far as the work done on crops other than wheat, Gerstel's (21) work on tobacco deserves consideration in this connection. He reported on the effects of the addition of individual Nicotiana glutinosa chromosomes to tobacco (N. tabacum). The later case 4x Nicotina tabacum was crossed to 2x N. glutinosa and the F₁ hybrid backcrossed to 2x N. tabacum. The addition types, including one carrying the mosaic resistance of N. glutinosa, were isolated by selfing. Gerstel (22) also reported the mechanisms of chromosome substitution in N. tabacum. Holmes (33) transferred the mosaic resistance of Nicotina glutinosa through the use of a synthetic amphidiploid species N. digluta to tobacco. Backcrossed progeny of mosaic resistant hybrid derivatives crossed to N. glutinosa. Homozygous resistant tobacco selections were obtained by selfing.

Brink, et al. (10) made a hybrid between Hordeum jubatum (n=14) x Secale cereal (n=7). The hybrid obtained had 21 chromosomes and was intermediate between the parents in habit of growth and sterile. Webster (88) made a successful interspecific cross between Melilotus alba and Melilotus officinalis using embryo culture. The fertile interspecific hybrid between the two species mentioned had failed because of early abortion of the embryo. These crosses were made to transfer low coumarin determining genes to M. officinalis from M. alba. The low coumarin character of M. alba was originally derived as a result of hybridization of this species with M. dentata. It was mentioned by Webster that attempts were made by Stevenson and Kirk (1935) to obtain intergeneric hybrids by crossing Melilotus, Medicago and Trigonella, but no seeds were obtained from these attempts.

Beasley and Brown (7) succeeded in obtaining hyperploid plants carrying an extra pair of chromosomes in addition to the normal chromosome complex of upland cotton ($2n=52$). These were produced from hybrids of upland cotton, with each of two, 13 chromosome species, cultivated Asiatic species, and wild American species. The initial $3x$ hybrids were doubled by the colchicine treatment to produce fertile hexaploids. By repeated backcrossing with upland pollen $26_{11}+1_1$ plants were obtained. These were selfed with a limited amount of pollen. Among the progeny of such $26_{11}+1_1$ plants, four plants having 27 pairs were identified, three having an extra pair of chromosomes from an Asiatic species, Gossypium arboreum var Naking, and one having an extra pair from G. harknesii, a species native to lower California. Two of the upland Asiatic plants are polyploid in appearance, with thick stems, thick dark green, slightly ruffled leaves, broad buds, and flowers with ruffled petals.

Vavilov (83) stated that vegetative reproduction gives the possibility of a wider utilization of distant hybrids in fruit and berry crops, potatoes and sugarcane. In this connection the work of Bremer (9) on sugarcane in Java has particular interest. He crossed the cultivated cane Saccharum officinarum with the wild cane S. spontaneum, the latter being resistant to two virus diseases of this plant, the mosaic disease "Gelestrepenziekte" and "Sereh" which resemble leaf curl in potatoes. The crosses between these species of cane produced fertile hybrids, although S. officinarum has 40 chromosomes (haploid number) and S. spontaneum has 56 in the F_1 . The number of chromosomes was 136 ($2n$) instead of the expected 96 which was associated with

doubling of the chromosomes in the 40 chromosome maternal parent, either at the time of fertilization or in the zygote directly after fertilization. This doubling of the chromosomes often takes place in S. officinarum when it is crossed with distantly related species. Meanwhile a doubling of the chromosomes in the sperm nucleus did not occur. The first generation of hybrids of S. officinarum x S. spontaneum with 136 chromosomes was distinguished by immunity against both diseases, but their sugar content, as in F_1 , was still insufficient (less than the original cultivated parent). Continuing the improvement, plants that were obtained as a result of the first backcross were crossed again with S. officinarum. The plants obtained having approximately 114 chromosomes of which 100 came from S. officinarum and only 14 from S. spontaneum.

The plants obtained were very resistant to mosaic and entirely immune from the "Sereh" disease. They were high in sugar content, sometimes exceeding the cultivated parent in this respect. The immune variety, P. O. J. 2878 exceeded all the old Chinese cultivated varieties of sugarcane in sugar content.

MATERIAL AND METHODS

The seedling reaction of F_3 lines of the cross Wichita⁵ x Chinese + Aegilops umbellulata was tested in the greenhouse with races 9 and 15 of leaf rust during the fall of 1961. Some F_1 plants of advanced backcrosses to several Kansas hard winter wheat varieties were also studied.

There were 499 F_3 lines used in the study representing two different crosses and six families. These and the parents are listed

in Table 1 along with 1961 and 1962 identification numbers.

The two crosses X5967 and X5968 trace back to the same F_1 plant in the first backcrosses to Wichita, namely Wichita² x Chinese + Aegilops umbellulata, cross X5611, greenhouse pot number 95 in 1956. The original Chinese + Aegilops umbellulata material was obtained from Dr. E. R. Sears and the plant used in making the first cross to Wichita was identified as P 54-47. 4-6, greenhouse pot number B 121 in 1955. The "47" family is often referred to as Transfer, CI 13483, CI 13296.

F_2 seeds separately planted in the fall of 1960, were pulled, separated, classified for awns, and threshed separately in 1961. No leaf rust reading was made on F_2 plants because of late infection and heavy infection of stem rust.

Seed of each F_2 plant was packeted for planting in the field in the fall of 1961 and for seedling leaf rust tests to physiologic races 9 and 15. The seedling rust tests were conducted in isolated sections of the greenhouse with one race of rust in each section in the fall of 1961. The pure culture of races 9 and 15 used in the experiments were obtained from Mr. C. O. Johnston, Pathologist, United States Department of Agriculture, stationed at Kansas State University.

The method of inoculation was the same used and described by Bueno (12), El Hakim (16), Harris (26), Mode (60), Schulte (79) and Woodward (92). Approximately 30 seeds of each line were sown in 3-inch pots. Ten days after planting, the seedlings were inoculated with a pure culture of the desired physiologic race of leaf rust which had been propagated on the susceptible variety Wichita. The plants were then placed in a canvas moist chamber, moistened with water and dusted

Table 1. Crosses, families and parents of Wichita⁵ x Chinese + Aegilops umbellulata studied for reaction to races 9 and 15 of leaf rust in the seedling stage.

1962 line nos.	1961 family no.	Parent or Cross*	No. lines
5694 - 5698	R 1241	Wichita, parent	5
5699 - 5703	R 1242	Wi ⁴ x Cns + <u>Au</u> , parent	5
5704 - 5774	R 1243	Wi ⁵ x Cns + <u>Au</u> , X5967	71
5775 - 5858	R 1245	do	84
5859 - 5936	R 1246	do	78
5937 - 5941	R 1253	Wichita, parent	5
5942 - 5946	R 1254	Wi ⁴ x Cns + <u>Au</u> , parent	5
5947 - 6032	R 1255	Wi ⁵ x Cns + <u>Au</u> , X5968	86
6033 - 6126	R 1257	do	94
6127 - 6212	R 1258	do	86

* Wi = Wichita, Cns = Chinese, Au = Aegilops umbellulata

with urediospores from infected Wichita plants. One-hundred entries including appropriate leaf rust differential varieties to detect race purity were inoculated for each test. Pots were removed from the moist chamber approximately 12 hours after inoculation.

Ten to twelve days later, depending on temperature and light intensity, the plants were classified as to phenotype on the basis of type of uredia formed in six classes described by Johnston and Mains (45) and Mains and Jackson (57) as follows:

0 Highly resistant - No uredinia formed. Small flecks, chlorotic or necrotic areas more or less prevalent.

1 Very resistant - Uredinia few, small always in small necrotic spots. More or less necrotic areas produced without development of uredinia.

2 Moderately resistant - Uredinia fairly abundant. Of moderate size, always in necrotic areas, produced without development of uredinia.

3 Moderately susceptible - Uredinia fairly abundant. Of moderate size. No necrosis produced, but some times slight chlorosis immediately surrounding the uredinia.

4 Very susceptible - Uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occurring as green islands surrounded in each case by chlorotic ring.

X Intermediate - Two or more type reaction on the same leaf.

The reaction of the original parents had been made by Johnston (44). He stated that the variety (Chinese + Aegilops umbellulata), P 54-47. 4-6, was highly resistant to leaf rust races 1, 3, 5, 6, 9, 10, 11, 13, 15, 19, 20, 25, 35, 37, 54, 58, 68, 84, 93, 105, 122, 126, and he reported also that Wichita was susceptible to all races for which it had been tested.

The differential varieties used as checks were Webster, Mediter-

ranean, Carina and Malakof.

Chi-square was used to analyze the data obtained in order to see if each family gave a good fit for the ratio expected. Heterogeneity Chi-square was used in order to see if the families studied were from the same population. Moreover Chi-square of independence was used to see if the reaction to rust was linked with awnedness.

EXPERIMENTAL RESULTS

Reaction of the Parents of the Cross Wichita 5 x Chinese + Aegilops umbellulata to Leaf Rust Physiologic Races 9 and 15

The parents of the cross were tested to the races 9 and 15 and the result of these tests are presented in Table 2.

As shown in Table 2, the male parents used in making the backcrosses to Wichita were F_1 plants and were expected to be heterozygous. The F_3 plants selected at random from the Wi^4 x Cns + Au parents could give progeny that were homozygous resistant, homozygous susceptible or segregating for rust reaction. The Wi^4 x Cns + Au parent family number 1242 gave all five plants that were homozygous resistant to both races 9 and 15. In family 1254 progeny plant numbers 1 and 4 were homozygous susceptible and progeny plant numbers 2, 3 and 5 were homozygous resistant to both races. All Wichita progeny were susceptible to both races as expected.

The differentials used as checks were Webster, Mediterranean, Carina and Malakof. Their reaction to both races is shown in Table 3. This test was run to detect the purity of the races used in the experiment.

Table 2. Reaction of the parents of the cross Wichita⁵ x Chinese + Aegilops umbellulata to leaf rust physiologic races 9 and 15.

Family number and name*	Reaction to Race 9				
	Plant number				
	1	2	3	4	5
1241 Wichita	4	4	4	4	4
1242 Wi ⁴ x Cns + <u>Au</u>	0;	0;	0;	0;	0;
1253 Wichita	4	4	4	4	4
1254 Wi ⁴ x Cns + <u>Au</u>	4	0;	4	0;	0;

Family number and name*	Reaction to race 15				
	Plant number				
	1	2	3	4	5
1241 Wichita	4	4	4	4	4
1242 Wi ⁴ x Cns + <u>Au</u>	0;	0;	0;	0;	0;
1253 Wichita	4	4	4	4	4
1254 Wi ⁴ x Cns + <u>Au</u>	4	0;	4	0;	0;

* See Table 1 for explanation of abbreviations

Table 3. Reaction of the differentials which were used as checks for race purity to leaf rust physiologic races 9 and 15.

Name and CI numbers	Physiologic races	
	9	15
Webster 3780	4	0
Mediterranean 3332	0; (0-1)	4
Carina 3756	1-2	0
Malakof 4898	4	0

As shown in Table 3, the differentials showed the standard reaction to both races 9 and 15. The results in Table 3 indicate the purity of the two races used in the study of the inheritance of leaf rust in F_3 lines of the cross Wichita⁵ x Chinese + Aegilops umbellulata.

Reaction of F_3 Lines of the Cross
Wichita 5 x Chinese + Aegilops umbellulata
to Leaf Rust Physiologic Race 9

The reaction of F_3 lines to race 9 are shown in Table 4. These results were based on the fact that only two types of response to leaf rust occurred, i.e. type 0; and type 4. No other types of response were observed in the parent or segregating material. It appeared that the resistance to race 9 was completely dominant and due to one factor.

The results in Table 4 indicate that the six families came from the same population and the data fit a 1:2:1 ratio. The deviation of family 1255 from the ratio 1:2:1 may be due to chance because the whole

Table 4. Reaction of F₃ lines of the cross Wichita⁵ x Chinese + Aegilops umbellulata to leaf rust physiologic race 9 in the seedling stage.

Family number	Reaction to race 9			X ² goodness to fit
	Number of resistant lines	Number of segregating lines	Number of susceptible lines	
1243	21	35	14	1.400 ns
1245	23	45	16	1.595 ns
1246	23	35	19	1.052 ns
1255	29	45	12	6.907*
1257	22	48	23	0.118 ns
1258	15	53	17	5.282 ns
Total Chi-square	--	--	--	16.354
Chi-square of the total	133	261	101	5.610 ns
Heterogeneity Chi-square	--	--	--	10.744 ns

ns = non significant at 5% level

* = significant at 5% level

population fits the ratio 1:2:1, and the heterogeneity Chi-square was not significant.

A further check on segregation was made by counting the resistant and susceptible plants in the F_3 lines that were heterozygous for response to race 9. As resistance to race 9 was completely dominant, only two classes were present. The plant counts in segregating lines are given in Table 5.

As shown in Table 5, five of the six families fit the hypothesis that the segregation was 3:1. Data from family 1255 does not fit a 3:1 ratio. In that family there was an excess of resistant plants. Moreover in Table 4, family 1255 did not fit a 1:2:1 ratio for a similar reason that the homozygous susceptible class was deficient. The deviation of family 1255 apparently was sufficient to make the pooled data not fit the hypothesis. In fact four of the five families tended to be short in the expected number of susceptible plants. However the heterogeneity Chi-square was non-significant indicating that these six families came from the same population. However, when the data of family 1255 are omitted from the pooled data the hypothesis fits (Table 6).

As shown in Table 6, the five families fit the hypothesis that the segregation was 3:1. Moreover, the heterogeneity Chi-square is not significant, so we can pool the data of these families. The conclusion from Table 6 is that the pooled data fit the 3:1 ratio. It is evident that a single dominant factor is involved for resistance to race 9. The conclusion is based on the results in Tables 4 and 6. The deviation of the family 1255 is of unknown cause or could be due to chance.

Table 5. Reaction of segregating lines observed in F3 lines of the cross Wichita 5 x Chinese + Aegilops umbellulata to leaf rust physiologic race 9.

Family number	Reaction to race 9 number of plants		χ^2
	Resistant	Susceptible	
1243	1078	395	2.590 ns
1245	905	271	2.399 ns
1246	1131	348	1.705 ns
1255	1764	517	6.630*
1257	1625	504	1.999 ns
1258	2226	721	0.449 ns
Total Chi-square	--	--	15.772
Chi-square of the total	8729	2756	6.168*
Heterogeneity Chi-square	--	--	9.604 ns

ns = non significant at 5% level

* = significant at 5% level

Table 6. Reaction of the segregating lines (five families) of the cross Wichita 5 x Chinese + Aegilops umbellulata to leaf rust physiologic race 9.

Family number	Reaction to race 9 number of plants		χ^2
	Resistant	Susceptible	
1243	1078	395	2.590 ns
1245	905	271	2.399 ns
1246	1131	348	1.705 ns
1257	1625	504	1.999 ns
1258	2226	721	0.449 ns
Total Chi-square	--	--	9.142
Chi-square of the total	6965	2239	2.227 ns
Heterogeneity Chi-square	--	--	6.915 ns

ns = non significant at 5% level

The following lines were considered off-types and were classified according to their expected reaction. This classification was based on past experience. The lines showing reaction type 0; with one or two plants type 4 were considered type 0;. The following five lines showed that phenomena:

<u>line number</u>	<u>reaction to race 9</u>	
5771	39 = 0;	1 = 4
5848	24 = 0;	1 = 4
5973	57 = 0;	1 = 4
5985	57 = 0;	3 = 4
6114	29 = 0;	1 = 4

The lines showing reaction type 4 with one or two plants type 0; were classified as type 4. The following sixteen lines showed that phenomena:

<u>line number</u>	<u>reaction to race 9</u>	
5711	1 = 0;	38 = 4
5717	1 = 0;	42 = 4
5718	1 = 0;	37 = 4
5736	1 = 0;	52 = 4
5740	1 = 0;	52 = 4
5747	1 = 0;	13 = 4
5749	1 = 0;	42 = 4
5805	1 = 0;	22 = 4
5834	1 = 0;	29 = 4
5835	1 = 0;	32 = 4
5860	1 = 0;	25 = 4
5910	1 = 0;	44 = 4
5930	1 = 0;	57 = 4
5931	1 = 0;	50 = 4
5934	2 = 0;	51 = 4
6153	6 = 0;	45 = 4

The following lines were discarded on the basis that they probably were mixtures of two plants.

<u>line number</u>	<u>reaction to race 9</u>	
5733	23 = 0;	21 = 4
5899	16 = 0;	33 = 4
6042	27 = 0;	20 = 4
6202	46 = 0;	36 = 4

Reaction of F₃ lines of the Cross
Wichita 5 x Chinese + Aegilops umbellulata
to Leaf Rust Physiologic Race 15

The reaction of F₃ lines to race 15 are shown in Table 7. Here again only two types of response occurred. No intermediate types were present. It appeared that the resistance to race 15 was completely dominant and due to one factor.

The conclusion from Table 7 is that the six families came from the same population and the pooled data fit a 1:2:1 ratio. The deviation of family 1255 from the ratio 1:2:1 may be due to chance. The consistency of results, obtained from the reaction to races 9 and 15 indicate that the deviation of the family 1255 was not due to environmental factors. Moreover, the deficiency in the susceptible line tended to be consistent in this reaction to both races 9 and 15.

A check on segregation was made in the same manner as in the case of reaction to race 9, by counting the resistant and susceptible plants in the F₃ lines, that were heterozygous for response to race 15. As resistance to race 15 was completely dominant, only two classes were present. The plant counts in segregating lines are given in Table 8.

Five of the six families in Table 8 fit the hypothesis that the segregation was 3:1. The family 1255 did not fit the hypothesis. It showed the same response as in the case of reaction to race 9. Besides the four families which showed deficiency in the homozygous susceptible class in case of reaction to race 9 showed, more or less, the same tendency in the case of reaction to race 15. The deviation of family 1255 apparently was sufficient to make the pooled data

Table 7. Reaction of F₃ lines of the cross Wichita⁵ x Chinese + Aegilops umbellulata to leaf rust physiologic race 15 in the seedling stage.

Family number	Reaction to race 15			χ^2 goodness to fit
	Number of resistant lines	Number of segregating lines	Number of susceptible lines	
1243	21	35	14	1.400 ns
1245	23	45	16	1.595 ns
1246	23	35	19	1.052 ns
1255	29	45	12	6.907*
1257	22	48	23	0.118 ns
1258	15	53	17	5.282 ns
Total Chi-square	--	--	--	16.354
Chi-square of the total	133	261	101	5.610 ns
Heterogeneity Chi-square	--	--	--	10.744 ns

ns = non significant at 5% level

* = significant at 5% level

Table 8. Reaction of segregating lines observed in F3 lines of the cross Wichita 5 x Chinese + Aegilops umbellulata to leaf rust physiologic race 15.

Family number	Reaction to race 15 number of plants		χ^2
	Resistant	Susceptible	
1243	1035	339	.078 ns
1245	931	295	.575 ns
1246	944	293	1.138 ns
1255	1383	385	9.801**
1257	1470	459	1.494 ns
1258	1748	568	.278 ns
Total Chi-square	--	--	13.364
Chi-square of the total	7511	2339	8.258**
Heterogeneity Chi-square	--	--	5.106 ns

ns = non significant at 5% level

* = significant at 5% level

** = highly significant at 5% level

highly significant. Data without family 1255 are given in Table 9.

As in the case of resistance to race 9 some lines were apparent mixtures. Lines sharing reaction type 0; with one or two plants type 4 were considered as homozygous type 0;. The following two lines showed that phenomena:

5771	35 = 0;	1 = 4
6114	29 = 0;	1 = 4

The lines showing reaction type 4 with one or two plants were classified homozygous as type 4. The following three lines showed that phenomena:

5718	2 = 0;	36 = 4
5822	1 = 0;	36 = 4
5832	1 = 0;	30 = 4

The following four lines were discarded on the basis they were mixtures of two plants:

5733	23 = 0;	21 = 4
5899	16 = 0;	33 = 4
6042	27 = 0;	30 = 4
6202	46 = 0;	36 = 4

As shown in Table 9 the five families and the pooled data fit the hypothesis that the segregation is 3:1. Moreover the heterogeneity Chi-square is non-significant which indicates that the five families came from the same population and their data can be pooled. From Tables 4, 6, 7 and 9 we can conclude that the resistance to races 9 and 15 derived from Aegilops umbellulata is simply inherited and a single completely dominant factor is involved in that resistance.

Table 9. Reaction of the segregating lines (five families) of the cross Wichita 5 x Chinese + Aegilops umbellulata to leaf rust physiologic race 15.

Family number	Reaction to race 15 number of plants		χ^2
	Resistant	Susceptible	
1243	1035	339	.078 ns
1245	931	295	.575 ns
1246	944	293	1.138 ns
1257	1470	459	1.494 ns
1258	1748	568	.278 ns
Total Chi-square	--	--	3.563
Chi-square of the total	6128	1954	2.918 ns
Heterogeneity Chi-square	--	--	0.645 ns

ns = non significant at 5% level

Reaction of F₁ plants of the 4th, 5th
and 6th Backcrosses to Hard Red Winter
Wheat to Leaf Rust Physiologic Race 9

The data in Table 10 further emphasizes this conclusion. The data in Table 10 were obtained from the reaction of F₁ plants to race 9 of leaf rust of some advanced backcrosses involving the Aegilops factor.

As shown in Table 10 the data appeared to fit the hypothesis that the segregation was 1:1. The statistical analyses are presented in Table 11.

From Table 11 we can conclude that the samples came from the same population because heterogeneity Chi-square is non-significant and the pooled data fit the hypothesis that the segregation is 1:1. In fact, the data from Tables 10 and 11 are good evidence that the resistance to leaf rust race 9 is simply inherited and that a single completely dominant factor is involved in that resistance. From Tables 4, 6, 7, 9 and 11 it is clear that only a single completely dominant factor is involved for resistance to races 9 and 15 derived from Aegilops umbellulata.

Inheritance of Awns

The mature F₂ plants were separated and classified according to the awnedness appearance. It was observed that the segregating plants for the awnedness character varied greatly and it was difficult to set a hypothesis on that character because it is evident from the data in Table 12 that the awnedness character is not simply inherited. Evidence about complex inheritance of awns in Chinese was given by

Table 10. Reaction of F1 plants of the 4th, 5th, and 6th backcrosses to hard red winter wheat to leaf rust physiologic race 9.

Cross number	Cross*	Reaction to leaf rust	
		Resistant	Susceptible
X611	Bsn ³ x [Wi ² - Cns + Au x Bsn ₇]	8	9
X612	do	1	1
X613	do	2	1
X614	do	1	2
X615	do	3	3
X616	do	3	6
X617	do	4	2
X618	do	7	3
X619	Bsn ³ [Wi x Pn x Wi - Cns + Au ₇]	3	7
X6110	do	0	2
X6111	do	2	2
X6112	Wi ⁷ x Cns + Au	4	3
X6113	do	5	5
X6114	do	2	0
X6115	do	9	9
X6116	do	9	6
X6117	do	7	3
X6118	do	10	6
X6119	do	2	2
X6120	do ₄	0	2
X6121	Kaw x Bsn ² x Wi ⁴ - Cns + Au	7	6
X6122	do	1	8
Hays	Bsn ⁵ x Cns + Au	4	3

* Bsn = Bison, Wi = Wichita, Cns = Chinese, Au = Aegilops umbellulata, Pn = Pawnee

Table 11. Reaction of F1 plants of the 4th, 5th, and 6th backcrosses to hard red winter wheat to leaf rust physiologic race 9.

Cross number	Reaction to leaf rust race 9 number of plants		χ^2
	Resistant	Susceptible	
X611 - X618	29	27	.071 ns
X619 & X6110 - X6111	5	11	2.250 ns
X6112 - X6120	48	36	1.714 ns
X6121 - X6122	8	14	1.636 ns
Hays	4	3	.142 ns
Total Chi-square	--	--	5.813
Chi-square of the total	94	91	.048 ns
Heterogeneity Chi-square	--	--	5.765

ns = non significant at 5% level

Heyne and Livers (29).

As shown in Table 12 the inheritance of awns in the F_2 lines is not simple. The data cannot be pooled because the heterogeneity Chi-square is significant so we cannot derive any conclusions from these data of awnedness inheritance.

Table 12. Inheritance of awns of the F_2 lines of the cross Wichita⁵ x Chinese + Aegilops umbellulata.

Family	Awnedness character	
	A, A ^t	B
1243	55	15
1245	62	22
1246	64	13
1255	46	40
1257	43	50
1258	45	40
Total	315	180

A_t = awnless
 A^t = variable awn expression
 B = with awns

Association of the Leaf Rust
Resistance and Inheritance of Awns

The association of the two characters were studied. Chi-square of independence was used to show the relation of the two characters. Chi-square of independence was used because the genetic ratio of awnedness character is not known so it will fit our purpose here. As there was a consistent result obtained for the reaction to leaf rust race 9 and 15 the reaction to leaf rust in Table 13 is applicable to both races.

Table 13. Association of leaf rust resistance, and awnedness character for the F₃ lines of the cross Wichita 5 x Chinese + Aegilops umbellulata.

Awnedness character	Leaf rust resistance			Total
	resistant	number of plants segregating	susceptible	
A, A ^t	91	168	56	315
B	42	93	45	180
Total	133	261	101	495
Chi-square of independence - 4.301 non-significant at 5% level				

A = awnless

A^t = variable awn expression

B = with awns

As shown in Table 13 leaf rust resistance to races 9 and 15, and awnedness are independently inherited.

DISCUSSION

The information reported in this thesis is the study of inheritance of leaf rust resistance in common wheat derived from Aegilops umbellulata.

Aegilops umbellulata is a species of Aegilops that has no apparent homologies with Triticum. It has 14 chromosomes and the genome has been identified as C^u. In making the transfer to hexaploid wheat, Sears (72) indicated that only a very small piece of chromosome carrying the resistance gene to leaf rust was transferred without the undesirable characters of Aegilops.

Aegilops umbellulata has been resistant to all races of leaf rust to which it had been tested. Tests in Kansas have shown that the hexaploid wheats carrying this resistance are also resistant to all races tested and has been resistant under field conditions. This transfer to hexaploid wheats should offer an excellent source of resistance to leaf rust providing a new race does not occur which will attack these new types. Samborski [as reported in the Wheat Newsletter (90)] had indicated that such a race has been found in Canada. He reported that not all the resistance of Aegilops umbellulata has been transferred to hexaploid wheat. However, the race a variant of 15 gave a type 1 reaction instead of type 0.

The tests presented in this thesis were carried on using standard procedures for rust studies. The two individual races of leaf rust used in these experiments represented two important race groups. In

this manner if a certain gene is found to govern resistance to one race it can be assumed that it also is resistant to the other races in the same group.

It was stated by other workers that the transfer of character from one species or genus to another is important practically and very useful Vavilov (81). It was stated also that the wider the transfer the more interesting it is genetically Sears (71). Apparently the resistance of Aegilops umbellulata has been transferred to Wichita, a hard red winter wheat variety.

In Kansas as well as other states and countries there are sources of leaf rust resistance. One of the recent objectives in the field of breeding resistant varieties is to induce segments of chromosome or genes from alien genera and species. Moreover we may reach permanent protection against leaf rust and other diseases from further investigation in this field.

SUMMARY

The seedling reaction to races 9 and 15 studied in F_3 lines Wichita⁵ x Chinese + Aegilops umbellulata and F_1 of some of the advanced backcrosses indicate that resistance to leaf rust derived from Aegilops umbellulata is inherited in a simple manner. The results obtained indicate that this resistance is due to a single dominant factor as a small piece of chromosome. The factor controlling resistance to race 9 was the same as that controlling resistance to race 15. The deviation of one family from the expected segregation ratio could have been due to chance. It was not possible to reach a clear-cut

conclusion on the inheritance of awns because the results indicate this character was not simply inherited. Response to the leaf rust and awn development was not associated in inheritance.

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REACTION OF F3 LINES OF THE CROSS
WICHITA 5 X CHINESE AND AEGILOPS UMBELLULATA
TO SEVERAL RACES OF LEAF RUST

by

ATEF SHAFIK SOLIMAN

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Leaf rust, Puccinia recondita Rob. ex. Desm. is one of the most severe diseases attacking wheat throughout the world, and the most destructive disease in Kansas. The rust is composed of 183 physiologic races which are identified on eight differential varieties.

The production of resistant varieties offers the most effective means of control. At present there are a large number of resistant varieties available which are the result of breeding carried out in many parts of the world.

Extensive work has been done in the U.S.A. and Canada as well as other countries to transfer segments of chromosomes from alien genera and species to the adapted hexaploid wheat varieties to gain resistance to diseases or to obtain other economic characters.

Sears (1956) was able to transfer a small piece of chromosome carrying the genes for resistance to leaf rust from Aegilops umbellulata to hexaploid wheats. He identified the chromosome in which the segment was added or substituted as chromosome X (6B). He proved that the segment was small and intercalary.

In Kansas one of the objectives is to transfer leaf rust resistance from the variety Transfer CI 13483, (Chinese + Aegilops umbellulata) to cytologically stable hard red winter wheat such as Wichita.

The inheritance of leaf rust resistance derived from Aegilops umbellulata was studied in the cross Wichita⁵ x Chinese + Aegilops umbellulata. Races 9 and 15 of leaf rust were used in this study. Each race represented an important group of races found in Kansas. Standard inoculation techniques and classification methods were used.

The results of the study showed that the resistance derived from Aegilops was simply inherited and one dominant factor governed the resistance to leaf rust. However, there was one family which did not fit the expected ratio. The deviation of that family may be due to chance. The inheritance of awns was studied and the F_2 plants were classified according to that character, but the results indicate that the inheritance of that character is not simply inherited. The association of the two characters was also studied and it was found that the two characters, leaf rust resistance and awnedness, are independent. The conclusion from the study was that the leaf rust resistance derived from Aegilops umbellulata can be transferred to hard red winter wheats adapted to Kansas conditions without any objectionable features of the Aegilops genus.