REACTION OF F_4 LINES OF WICHITA X LOROS AND WICHITA X BREVIT TO SEVERAL RACES OF LEAF RUST

by

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TABLE OF CONTENTS

INTRODUCTION

Wheat leaf rust, Puccinia triticina Erikss., an obligate parasite, is one of the major wheat diseases in Kansas. The damage done by leaf rust has been greatly underestimated, because the losses are due to failure of the head to produce the normal number of kernels and the disease ordinarily does not completely destroy the crop nor causes severe shrivelling of the grain. However, it has been demonstrated that reductions in yield of 15 to 25 per cent are common. Certain varieties may be reduced as much as 50 to 97 per cent under extremely heavy infestations if they occur while the plants are in the seedling stage and remain infected to maturity.

Like all of the cereal rusts, leaf rust of wheat is composed of many physiologic races or strains. These cannot be distinguished by ordinary examination or microscopic differences, but they can be separated by their reaction on certain wheat varieties known as differential hosts, namely Malakof, Democrat, Mediterranean, Hussar, Loros, Brevit, Carina, and Webster.

Breeding leaf rust resistant wheat varieties has been and appears to be a profitable way for wheat improvement. However, breeding rust resistant varieties is a continuous one because of the appearance of new races. At present, according to Heyne (7) and Johnston (10) there are sources of resistance for all known races of leaf rust in wheat, but there are no commercial varieties available that are resistant to all races.

Studies concerning the inheritance of resistance among the eight differential varieties and the manner of transferring the genetic factors to the accepted wheat varieties adapted to Kansas as Wichita and Pawnee comprise one phase of an organized program at Kansas State College for breeding improved varieties of wheat. The study reported herein is a portion of that research.

REVIEW OF LITERATURE

It is not the intention to review here all of the literature cited pertaining to leaf rust of wheat, but merely to cite some of the important theories and concepts about physiologic specialization and the mode of inheritance of resistance to the disease.

As early as 1920 several workers noticed what seemed to be different forms of the disease that showed different reactions on different varieties of wheat. In 1926 Mains and Jackson (18) reported 12 physiologic races by their manner of reaction on 11 differential strains of wheat. They found 25 strains to be more or less resistant to one or more of these forms, and out of these 25 strains, 11 varieties comprising eight differential groups were found that best identified the 12 physiologic forms of leaf rust. No one of these physiologic forms has been found to which all of these varieties are susceptible. On the other hand, other than the variety Vernal Emmer S.D.293, no variety has been found which in the seedling stage in the greenhouse has proved highly resistant to all 12 of these forms. The authors added that the physiologic forms of the leaf rust of wheat are not found pure in the field but usually several are mixed together and that physiologic forms are neither fixed nor limited in their distribution.

Since then workers in many parts of the world undertook to analyze and classify the leaf rust population in their areas. As a result many new races were described. By 1955, according to the Fifth Revision of the International Register (11), the total number of leaf rust races was 163. A summary showing the author and the year of publication of all races described up to 1955 were given in the report.

New races of cereal rust have been thought to originate through selfing or crossing in areas where the alternate host, Thalictrum, is abundant. Allen (1) made a notable contribution to the knowledge of the fertilization process which proceeds the development of aeciospores on the alternate host medow-rue that illustrated how new races may arise by gene recombination. The possibility of the origin of new races by mutation has been suggested by many workers. Johnston (12) reported a new form of leaf rust found on the resistant variety Mediterranean. Greenhouse experiments demonstrated that this form differed from all other cultures studied. His conclusions were:

> It seems reasonable to suppose that if the rust fungus can mutate for such heritable characters as color, it also can mutate for the equally heritable character of physiologic specialization. It seems therefore through mutation we may find a possible origin of physiologic forms, as well as in the phenomenon of heterothallism.

At one time the "bridging host" hypothesis of Marshall Ward was given some consideration. "A race of rust can infect one host variety but not a second, may gain the ability to infect the second if it is first passed through an intermediate variety," and although this hypothesis does not give a satisfactory explanation for the differences between some of the leaf rust races, yet it may play an important part in changes in composition of race population.

There is experimental evidence that some of the physiologic races may be merely variants of other races arising from environmental condition. The response of leaf rust to a change in environment adds more to the complication of identification of races. Chester (2) supported by a number of investigators advanced the concept of environmental conditioned race groups. These being groups of races that may duplicate the reaction of others when subjected to certain environmental conditions. The majority of the groups have been shown to be uniform in their infection type on such stable differential varieties as Malakoff, Webster, Loros, Mediterranean, and Democrat. The environmentally induced instability has been limited to the varieties Carina, Brevit, and Hussar. Several workers have observed that the latter three varieties are consistently variable in their reaction and are unsuitable as differentials. Chester (2) advocated discarding these varieties. Johnston and Mains (13) ran a five-year experiment studying physiologic races of leaf rust; they pointed out that although many physiologic forms have been very constant in their behavior on differential varieties, certain forms have proved to be variable. They classified these varieties according to environmental conditions and to the small but inherent differences between components of a group of allied strains. They concluded that certain physiologic forms cannot be considered as basic units or genetic entities, but they apparently are groups of forms that probably could be further subdivided, although the economic necessity for finer divisions does not seem to be great.

Chester (2) reviewed the leaf rust genetic studies and listed crosses that had been studied for leaf rust reaction. He presented the studies published prior to 1940. The majority of these studies indicated that leaf rust resistance was inherited in a simple Mendelian manner. Generally one factor and occasionally two factors were reported controlling leaf rust reaction in different crosses. These factors were completely dominant, partially dominant, or recessive, according to the race or race group used in the experiment. A single factor often controls resistance to several races, but generally for each race there is one factor and probably more that are responsible for the resistant behavior of wheat varieties.

Mains et al (19) made many crosses using Malakoff and Kanred as the resistant parents. They found resistance was dominant, and concluded that resistance to various physiologic races of leaf rust was due to different factors inherited as a unit but independent from each other. It is worth mentioning that many of the resistant varieties known today trace their origin to Hope and H44. Both varieties were used in crosses with susceptible but otherwise desirable wheats to give many of the well adapted commercial wheats that are grown on substantial acreages in the United States and elsewhere in the world.

Leighty (16) reported a simple Mendelian ratio of three resistant to one susceptible when Malakof was used as the resistant parent, and when it was used as the susceptible parent he obtained a 1:2:1 ratio pointing to the fact that the factors involved were independently inherited. Leighty (17) also found that in the cross Fulcaster (resistant) X Kanred (susceptible) the F_1 generation was more resistant to race 9 than the susceptible parent. The F_2 generation segregated in the ratio of 1:2:1. In the cross Malakof X C13778 when tested with race 12 gave a 3:1 ratio with the resistance of Malakof as dominant, but the same cross when tested with race 5 the same ratio was obtained and resistance of C13778 was the dominant this time. The combined data gave a 9:3:3:1 ratio supporting the hypothesis that two independent factors were responsible for resistance to the races tested.

Wismer (29) from the cross of Oro (susceptible) X Tenmarq, Kansas Sel. 2637 (moderately susceptible) obtained numerous F_4 lines which were resistant to leaf rust in the adult stage under field conditions. These results indicated that in some cases recombination of factors for resistance may occur and the mode of inheritance is not simple. Swenson et al (26) crossed two susceptible varieties of wheat, Thatcher and Triunfo. From this cross plants and lines highly resistant to leaf rust were obtained. The segregating material exhibited all degrees of infection from highly resistant to very susceptible. The F_2 ratio of resistant to susceptible plants fit a 9:7 ratio, suggesting that each parent contributed one of the two complementary genes for resistance. An alternative hypothesis was also suggested by the same authors in which they stated, two genes none complementary to each other are contributed by one parent and these two genes are complementary either singly or in combination with one gene contributed by the other parent.

Wells and Swenson (27) reported a single factor pair for resistance to leaf rust in the cross (H-44- Reward x Baringa) X (Hard Federation X Dicklow). They also reported linkage between stem rust and leaf rust.

Woodward (30) studied the inheritance of resistance to physiologic races 9, 15, and 58 in the crosses Malakof X Democrat and Democrat X Mediterranean. He concluded that two recessive factors carried by Democrat apparently govern resistance to race 9 of leaf rust. The F_2 progeny segregated into 8 susceptible to 7 resistant to 1 intermediate which is a modified dihybrid ratio. Malakof had a single factor for resistance to race 15 and 58. Both races are inherited independently of race 9. The cross Democrat X Mediterranean resulted in no segregation when tested with all three races, indicating similar factors are responsible for resistance or susceptibility carried by the two parents.

Heyne and Livers (8) located the gene for resistance to race 9 of leaf rust in Pawnee on chromosome X by means of monosomic analysis. The authors suggested that resistance to race 9 of leaf rust in Pawnee in certain crosses is due to more than one factor. As other studies indicated that Pawnee had one major factor for resistance to race 9 they put an alternative hypothesis in which they stated that Chinese may have contributed a factor for susceptibility that was partially epistatic to the resistant reaction of the factor from Pawnee, or Pawnee may have complementary factors for leaf rust resistance.

Wu and Ausemus (31) reported that the resistance of the Lee variety was differentiated from the susceptibility of Mida variety by two pairs of independently inherited recessive genes. The genes were additive in effect and susceptibility appeared to be partially dominant. The authors stated that F_4 progenies studied in the greenhouse with reference to reaction to individual races of leaf rust showed that the resistance of Lee to race 126 was governed by a single recessive factor and to race 5 by a single dominant factor and these two factors were linked with recombination percentage of 21 ± 2.7. Also the Lee factors for resistance to leaf rust races 9, 5, and 126 in the seedling stage, whether dominant or recessive, as well as one of the two factors for mature plant resistance in the field all appeared to be associated in inheritance.

Mode (20) studied the reaction of several crosses to leaf rust races 5, 9, 15, and 58. He found that Webster had one dominant factor for resistance to all races studied. Mediterranean had one incompletely dominant factor for resistance to race 9, being inherited independently of that to race 5, 15, and 58. He reported one dominant factor for resistance to race 5 carried by Webster in the cross Webster X Pawnee. Also Carina and Hussar have different factors for resistance to all four races with the Carina reaction to races 5 and 15 was epistatic to the Hussar reaction when Carina genes for resistance were homozygous. Brevit and Hussar carried different factors for resistance to races 15 and 9 but the reactions were associated. The resistance of Loros to race 5 was differentiated from susceptibility of Pawnee by a single incompletely dominant gene.

Heyne and Johnston (9) concluded from a study of crosses among Timstein, Pawnee and RedChief wheats that Timstein appeared to have one major recessive factor and one or more modifying factors for adult plant resistance to leaf rust. Pawnee had one major factor for resistance to race 9 in the seedling stage that was non allelic to the Timstein factor.

Harris (6) studied the reaction of F_3 progeny of some differential crosses of wheat to four races of leaf rust. He also reported on the F_2 progeny of the crosses Brevit X Mediterranean, Brevit X Carina, Webster X Brevit and Loros X Webster to race 5. These were grown to maturity and tested to races 9 and 126. Inconclusive results were obtained in the crosses involving Hussar when tested with races 5 and 35 in the F_3 generation due to environmental conditions.

Mediterranean, Hussar, and Democrat were resistant to races 9 and 11 but segregation occurred in these crosses indicating each had different factors for resistance. Brevit, Carina, Webster and Loros appeared to have one dominant identical factor for resistance to race 5. Brevit was recessive to two complementary dominant factors for susceptibility to race 9.

Jones and Ausemus (15) concluded that the seedling reaction to leaf rust race 5 was inherited on a monogenic basis in the cross Frontana X (Mida - Kenya 117 A) and was controlled by two independent genes in the cross Kenya 58-Newthatch X Frontana cross. Inheritance of resistance to race 15 was conditioned by two independently inherited genes in both crosses.

Wells et al (28) reported on the cross Michigan Amber X Coker 47-27 after testing F_2 and F_3 progenies with races 5, 58, and 122. In the F_2 generation there were too many susceptible plants for a good fit to a one factor pair. The observations on the F_3 lines indicated one major factor pair governing leaf rust reaction.

Schulte (25) reported on genetic studies in F_3 involving the cross Wichita X Malakof, Wichita X Hussar, Wichita X Mediterranean, and Pawnee X Mediterranean. He mentioned that Mediterranean appeared to have one partially dominant factor for resistance to race 9 in the cross Wichita X Mediterranean. Malakof had a single dominant factor for resistance to race 15 in the cross Wichita X Malakof. Hussar had a single partially dominant factor for resistance to both races 5 and 15 in the cross Wichita X Hussar. Mediterranean and Pawnee appeared to carry the same factor or factors for resistance to race 9.

Nyquist (22) studied the inheritance of resistance to leaf rust involving the common wheat strain CI 12633 derived from Triticum timopheevi crossed with three susceptible varieties. He reported two different ratios in F_2 and one partially dominant major gene was responsible for resistance of CI 12633 to race 11 in the crosses CI 12633 X White Federation and Federation. In the cross with Romana, resistance was controlled by two partially dominant complementary major genes while in the cross with the resistant Chinese spring wheat no susceptible plants occurred and he concluded that the genes studied in CI 12633 were allelic to genes for resistance in Chinese Spring.

Gonzales (5) studied the seedling reaction of F_4 lines to races 15, 5, 9, 105 in the crosses Wichita X Carina and Wichita X Webster. He reported Webster to have a single completely dominant gene for resistance to race 5 and 15 in the cross Wichita X Webster and that no transgressive segregation was obtained in the cross when tested to race 9. Inconclusive results were obtained testing the cross to race 105. Carina appeared to have a single partially dominant gene for resistance to race 5 and 15 in the cross Wichita X Carina. The factors for resistance of Carina to race 9 and 105 appeared to respond in a recessive manner but were different for the two races. Part of the variability in reaction obtained in this cross was explained as being due to environmental factors, modifying genes, or specific interaction between host plant and the pathogen.

MATERIAL AND METHOD

F_4 progenies of the two crosses Wichita X Loros and Wichita X Brevit were studied for seedling reaction to four races of leaf rust in the greenhouse during the winter of 1957-1958. Races 9, 5, 15, and 105 were chosen for this study because of their importance and prevalence in the wheat growing region of the Great Plains. Also each race is an important component of different race groups. The original crosses were made at Manhattan, Kansas in the year 1953-54.

The parental varieties Brevit and Loros are two of the eight differential varieties used for identifying leaf rust races. Wichita is a commercially grown variety in Kansas.

Brevit is an annual variety characterized from other spring wheats by its short beak. It has somewhat stiff straw but is inclined to lodge at the time of maturity. Loros has long beaks, which in the greenhouse are as long as the awns. Under field conditions it stands somewhat better than Brevit and it is inclined to have darker brown glumes. In the seedling stage in the greenhouse, this variety shows a physiologic weakness in that the first seedling leaf shows chlorophyll changes. This condition is manifested by a somewhat water-soaked appearance of the tissues even before inoculation and often bright yellow colored areas about the pustules. Wichita is a selection from a cross between Tenmarq and Early Blackhull. The cross was made at Kansas State College. It is an early maturing hard red winter wheat variety that yields well and has a good test weight. It is adapted to the entire hard winter wheat areas of Kansas.

The reaction of the parents to the four leaf rust races used in this study are given in Table 1.

The F_4 lines were obtained from the Kansas wheat research project. There were 297 lines from the cross Wichita X Loros and 91 lines from the cross Wichita X Brevit. All these lines were tested to race 15 and the lines homozygous resistant or susceptible to race 15 were tested to the other three races.

Table 1. The reaction of Loros, Brevit, and Wichita to the four races of leaf rust used in the study:

Physiologic races	Parents: Loros	Parents: Brevit	Parents: Wichita
	Type of Reaction		
9	4	1-2	4
15	0,(0-1)	0-1	4
5	1-(0-1)	0-1	4
105	4 (3±)	3±	4

Tests for rust resistance to each race were done separately in isolated areas in the greenhouse. The technique followed in the inoculation was similar to that described by Mode (20), Harris (6), and Schulte (25). Twenty-five to 30 seeds of each line were grown in three-inch pots. The seedlings were considered ready for inoculation about ten days after planting, or when the primary leaves were fully developed. One hundred pots of F_4 lines and four differential varieties for detecting race purity were studied at a time. All pots were labled to maintain the identity of the lines. At the time of inoculation the pots and walls of the incubation chamber were moistened with water. The leaves of the seedlings were moistened by the use of a sprayer, so fine mist-like droplets of water covered the leaves. This procedure provided optimum conditions for germination of the urediospores and maximum infection. After moistening the plants, they were dusted with urediospores of the desired physiologic race which had been propagated on the susceptible variety Cheyenne. Inoculation was usually made in the evening to provide continued cool and humid environment. Plants were removed from the moist chamber approximately 12 hours after inoculation. The same procedure was followed throughout the experiment. The four races used were supplied by Mr. C. O. Johnston, Pathologist U.S.D.A. stationed at Manhattan, Kansas.

Readings to determine the infection types were taken approximately ten days after inoculation. The lines were classified homozygous resistant, homozygous susceptible, or segregating for rust reaction. In the segregating lines, individual plants were classified as to their reaction type. However, these were subjected to errors due to environmental condition affecting the development of both the host and the parasite. The classification of the reaction types used in identifying the type of uredia formed was made according to the standard reaction types described by Mains and Jackson (18) and Johnston and Mains (13).

The scale used ranged from 0, which is highly resistant with only chlorotic or necrotic areas, to four-type reaction which is highly susceptible with abundance of pustules. Intermediate or variable reactions varied from moderately resistant to moderately susceptible at different times, but consistent on a given leaf.

EXPERIMENTAL RESULTS

Reaction of F_4 Progeny of Wichita X Loros to Race 15

The Wichita parent gave a 4-type reaction to race 15, and Loros had 0; (zero fleck) reaction. There were 297 hybrid lines tested to race 15. These lines reacted in the following manner:

Homozygous resistant	55
Homozygous susceptible	88
Segregating	154

The lines showing 0; type reaction with one or two plants with different reaction and those showing 4-type reaction with one or two plants with different response were classified as homozygous lines. A random sample of the hybrid population was not available so the data were not analyzed statistically. However, the above data suggest a monohybrid ratio, with a goodness of fit test being significant at the 5 per cent level but not at the 1 per cent level. Chi-square analysis of the data showed that most of the deviation was attributed to the shortage of homozygous resistant lines. This might suggest the presence of minor or modifying genes, in addition to a major gene for resistance. These modifying factors when present in the homozygous condition, might affect the gene for resistance to the extent that its reaction is altered. Therefore, all plants with genotype AABB are susceptible due to the presence of BB. This genotype constitutes one-sixteenth of the total lines. In other words 19 out of 297 lines reacted differently from what was expected; being susceptible whereas they should be resistant. Now, as stated before, the big deviation of Chi-square resulted from the homozygous resistant lines due to the fact that our observed value is less than the expected value by 19.25, which is exactly the same number of lines that showed susceptible reaction because of the presence of the modifiers. On the other hand, when the segregating lines were classified according to their individual plant reaction, they gave 2548 resistant plants to 1079 susceptible ones. This will support the suggested 3:1 ratio. It is apparent therefore that a major factor pair and minor genes probably are envolved in the inheritance of resistance to race 15 of leaf rust in the above cross.

Reaction of F_4 Progeny of Wichita X Loros to Races 9 and 105

The number of lines tested to races 9 and 105 was carried out on 118 homozygous lines resistant or susceptible to race 15. The two parental varieties, Wichita and Loros had a uniform susceptible reaction to races 9 and 105. Loros has been reported to have 3-type reaction to race 105, however, it had 4-type reaction under the conditions of these experiments.

The reaction of the 118 lines to races 15, 9, 105, and 5 of leaf rust are given in Table 2.

As was expected the F_4 progeny of the above cross gave the same uniform susceptible reaction to both races. The evidence for transgressive segregation for resistance was not observed.

Reaction of F_4 Progeny of Wichita X Loros to Race 5

The Wichita parent had 4-type reaction and Loros gave 1+(0-1) reaction to race 5. The same 118 lines tested to races 9, and 105 were tested for reaction to race 5 (Table 2). The results are summarized as follows:

Homozygous resistant lines, 27

Homozygous susceptible lines, 63

Segregating lines, 28

The total number of resistant plants in the segregating lines was 564 and for the susceptible plants was 124. The above data do not fit a simple factor explanation for resistance. Examining Table 2, it is observed that the lines which breed true for resistance or susceptibility to race 5 also showed the same reaction to race 15 but with varying degree, i.e. a line with 4-type reaction to race 5 also showed 4-type reaction to race 15 and that with 1-type reaction to race 5 showed 0;-type reaction to race15. Exception to this phenomenon are found in lines number 12900, 12901, 13004, 13005, 13011, and 13003. The first four lines showed reversal of reaction and in all probability this might be due to mis-recording. The latter two lines might have escaped infection. It can be concluded that it is most likely that resistance or susceptibility to both races 15 and 5 in the cross Wichita X Loros is controlled, by the same major gene or

Table 2. Reaction of F_4 progenies of Wichita X Loros to the four races of leaf rust used in the study.

Line No.	Pr.15	Pr.5	Pr.9	Pr.105	Line No.	Pr.15	Pr.5	Pr.9	Pr.105
12772	S	S	S	S	12855	S	S	S	S
12779	S	S	S	S	12857	S	S	S	S
12783	S	S	S	S	12859	S	S	S	S
12786	S	S	S	S	12860	S	S	S	S
12787	S	S	S	S	12862	S	S	S	S
12796	S	S	S	S	12867	S	S	S	S
12804	S	S	S	S	12868	S	S	S	S
12805	S	S	S	S	12870	S	S	S	S
12810	S	S	S	S	12871	S	S	S	S
12812	S	S	S	S	12876	S	S	S	S
12818	S	S	S	S	12881	S	S	S	S
12819	S	S	S	S	12883	S	S	S	S
12824	S	S	S	S	12884	S	S	S	S
12825	S	S	S	S	12888	S	S	S	S
12843	S	S	S	S	12889	S	S	S	S
12851	S	S	S	S	12891	S	S	S	S

Table 2 (concl.).

Line No.	Pr.15	Pr.5	Pr.9	Pr.105	Line No.	Pr.15	Pr.5	Pr.9	Pr.105
12892	S	S	S	S	12791	R	R	S	S
12904	S	S	S	S	12799	R	R	S	S
12906	S	S	S	S	12803	R	R	S	S
12910	S	S	S	S	12809	R	R	S	S
12913	S	S	S	S	12829	R	R	S	S
12915	S	S	S	S	12853	R	R	S	S
12916	S	S	S	S	12912	R	R	S	S
12920	S	S	S	S	12919	R	R	S	S
12921	S	S	S	S	12923	R	R	S	S
12925	S	S	S	S	12934	R	R	S	S
12929	S	S	S	S	12958	R	R	S	S
12944	S	S	S	S	12961	R	R	S	S
12945	S	S	S	S	12964	R	R	S	S
12948	S	S	S	S	12968	R	R	S	S
12956	S	S	S	S	12969	R	R	S	S
12957	S	S	S	S	12992	R	R	S	S
12965	S	S	S	S	12997	R	R	S	S
12977	S	S	S	S	13001	R	R	S	S
12980	S	S	S	S	13025	R	R	S	S
12988	S	S	S	S	13045	R	R	S	S
12999	S	S	S	S	13062	R	R	S	S
13000	S	S	S	S	12806	R	Seg	S	S
13014	S	S	S	S	12882	R	Seg	S	S
13032	S	S	S	S	12909	R	Seg	S	S
13037	S	S	S	S	12927	R	Seg	S	S
13044	S	S	S	S	12951	R	Seg	S	S
13046	S	S	S	S	12960	R	Seg	S	S
13054	S	S	S	S	12983	R	Seg	S	S
13074	S	S	S	S	12993	R	Seg	S	S
12823	S	Seg	S	S	13006	R	Seg	S	S
12877	S	Seg	S	S	13036	R	Seg	S	S
12902	S	Seg	S	S	13040	R	Seg	S	S
12911	S	Seg	S	S	13051	R	Seg	S	S
12981	S	Seg	S	S	13058	R	Seg	S	S
13026	S	Seg	S	S	13059	R	Seg	S	S
13031	S	Seg	S	S	13061	R	Seg	S	S
13047	S	Seg	S	S	13063	R	Seg	S	S
12900	S	R	S	S	13064	R	Seg	S	S
13003	S	R	S	S	13065	R	Seg	S	S
13005	S	R	S	S	13066	R	Seg	S	S
13011	S	R	S	S	13071	R	Seg	S	S
12781	R	R	S	S	12901	R	S	S	S
12782	R	R	S	S	13004	R	S	S	S

Pr = Physiologic race
S = Susceptible
R = Resistant
Seg = Segregating

genes which are closely linked. This idea might be supported by the occurrence of segregation in some of the lines that were homozygous to race 15 when tested to race 5.

Test for independence of inheritance to physiologic races 15 and 5 in the cross Wichita X Loros is given in Table 3.

The hypothesis that races 15 and 5 are independently inherited is rejected on the basis of the highly significant Chi-square value. Therefore, the factors for resistance to race 15 are associated with the factors for resistance to race 5 or as mentioned previously the exceptions are due to escape from infection or incorrect labeling of lines in the successive tests.

Table 3. Contingency table for response of lines of Wichita X Loros and their reaction to races 15 and 5 of leaf rust.

Physiologic race 15 reaction		Physiologic race 5 reaction: res.	sus.	seg.	total
res.	obs.	25	0	20	45
	exp.	10.3	24.1	10.6	
sus.	obs.	2	63	8	
	exp.	16.7	38.9	17.4	73
Total		27	63	28	118

Chi-sq. = 88 df. = 2 P 0.005

Reaction of F_4 Progeny of Wichita X Brevit to Race 15

There were 91 lines each representing an F_2 plant; studied in the cross Wichita X Brevit to race 15. Wichita has been reported to be susceptible and Brevit has (0-1) type reaction to race 15. Responses of the 48 lines studied for reaction to races 15, 5, 105, and 9 are given in Table 4. The results obtained were:

53 lines were homozygous susceptible

37 lines were segregating

1 line was resistant

Table 4. The seedling reaction of F_4 progenies of Wichita X Brevit to the four races of leaf rust.

Line No.	Pr.15	Pr.9	Pr.5	Pr.105	Line No.	Pr.15	Pr.9	Pr.5	Pr.105
13078	S	S	S	S	13175	S	Seg	S	S
13092	S	S	S	S	13160	R	S	Seg	S
13097	S	S	S	S	13173	S	S	Seg	S
13124	S	S	S	S	13119	S			
13126	S	S	S	S	13123	S			
13127	S	S	S	S	13161	S			
13128	S	S	S	S	13171	S			
13129	S	S	S	S	13174	S			
13131	S	S	S	S	13176	S			
13134	S	S	S	S	13080	Seg			
13136	S	S	S	S	13081	Seg			
13141	S	S	S	S	13082	Seg			
13149	S	S	S	S	13084	Seg			
13151	S	S	S	S	13085	Seg			
13152	S	S	S	S	13086	Seg			
13153	S	S	S	S	13087	Seg			
13154	S	S	S	S	13088	Seg			
13116	S	R	S	S	13089	Seg			
13122	S	R	S	S	13093	Seg			
13125	S	R	S	S	13094	Seg			
13135	S	R	S	S	13095	Seg			
13140	S	R	S	S	13096	Seg			
13142	S	R	S	S	13098	Seg			
13143	S	R	S	S	13099	Seg			
13079	S	Seg	S	S	13100	Seg			
13091	S	Seg	S	S	13104	Seg			
13103	S	Seg	S	S	13105	Seg			
13114	S	Seg	S	S	13107	Seg			
13115	S	Seg	S	S	13108	Seg			
13117	S	Seg	S	S	13109	Seg			
13118	S	Seg	S	S	13110	Seg			
13120	S	Seg	S	S	13111	Seg			
13121	S	Seg	S	S	13113	Seg			
13130	S	Seg	S	S	13155	Seg			
13132	S	Seg	S	S	13156	Seg			
13133	S	Seg	S	S	13158	Seg			
13137	S	Seg	S	S	13159	Seg			
13138	S	Seg	S	S	13162	Seg			
13139	S	Seg	S	S	13164	Seg			
13144	S	Seg	S	S	13165	Seg			
13145	S	Seg	S	S	13166	Seg			
13146	S	Seg	S	S	13167	Seg			
13147	S	Seg	S	S	13168	Seg			
13150	S	Seg	S	S	13169	Seg			
13157	S	Seg	S	S	13177	Seg			
					13180	Seg			

Pr. = Physiologic race S = Susception
Seg = Segregating R = Resistant

It is to be noted that the only one resistant line (13160) observed in the above cross showed three plants with 1-type reaction, and the rest of the plants were of 0;-type. The segregating lines gave 240 resistant plants to 228 intermediate to 213 susceptible, which correspond to 1:1:1 ratio. This ratio does not correspond to a known genetic ratio. The number and nature of genes involved in the reaction of Wichita X Brevit cannot be determined on the basis of these results, because of their inconsistency. Also, the lack of more lines than one resistant to race 15 indicates that something is wrong with the cross. Some one or several of the following possibilities may account for the response obtained.

It was possible that the Brevit used in the cross was not an actual Brevit plant. Non randomness of the sample added to the selection of the homozygous lines might suggest the cause.

Environmental conditions have many times been reported to change the reaction type of Brevit.

A mutation might have occurred in the Brevit plant used as the parent.

Reaction of F_4 Progeny of Wichita X Brevit to Race 9

Resistance to physiologic race 9 of leaf rust came from the Brevit parent which has an average response of 1-2 reaction. Because of the results obtained with race 15, i.e. that one explanation of the unexpected results is that this is not a cross of Wichita X Brevit, makes any analysis of the results merely a speculation. Of the 48 lines tested for reaction to race 9, 7 were homozygous resistant, 23 segregated, and 18 were homozygous susceptible. Although the number of the tested lines is small 48, above figures suggest a dihybrid ratio of 3 resistant to 6 segregating to 7 susceptible. It is likely that two complementary genes, one of which AA has to be homozygous dominant and the other can either be homozygous dominant or heterozygous to produce resistance. Chi-square analysis applied to this hypothesis gives a fit to the proposed ratio. However, the hypothesis suggested was not supported by the data obtained from individual plant classification. About 136 resistant and 381 susceptible plants were obtained from F_4 segregating lines.

Chester (2) reported that variation in response of Brevit to several races had been observed due to environmental factors. Newton and Johnson (21) reported many cases in which the reaction of Brevit changed from resistant to susceptible form or vice versa with increase of temperature. In about 53 per cent of their tests, Brevit changed from resistant type at lower, to susceptible type at higher temperature. According to Chester (2) various workers have found that light, humidity, type of soil and its fertility also affect the reaction of leaf rust of wheat. In general all factors that favor the vegetative growth of the wheat plant tend to increase the susceptibility of wheat to leaf rust. The sensitivity of Brevit to changes in environment might account for the increase of the number of susceptible plants in the segregating lines. The reaction of Wichita X Brevit lines to race 9 were made in late March and considerable variations occurred in temperature and light compared to other tests made in January. Although there appeared to be considerable discrepancy of the data with the hypothesis, the one given appeared to be the most logical.

Reaction of F_4 Progeny of Wichita X Brevit to Race 105

Both parents were susceptible to race 105. All the tested lines gave the same susceptible reaction. The results obtained showed no evidence of transgressive segregation for resistance to race 105 (Table 4).

Reaction of F_4 Progeny of Wichita X Brevit to Race 5

Brevit has been reported to be resistant and Wichita susceptible to race 5 of the leaf rust of wheat. The results obtained from the 48 tested lines to this race showed 46 lines to be susceptible as the Wichita parent. (Lines number 13160 and 13173 were segregating. Table 4). The reaction of susceptibility in almost all the tested lines to race 5, was not expected. This might support the previous discussed possibilities stated when dealing with race 15.

DISCUSSION

Plant breeders are often interested in breeding for disease resistance. Many breeding programs center around the addition or recombination of disease resistance with other important agronomic characteristics. The first step in achieving a successful breeding program for resistance to diseases is the assembling of information regarding the reaction of species or varieties believed or known to carry factors for resistance. A search for new and superior germplasm should be regarded as a permanent objective of a sound breeding program. The fact that wheat is a self-fertilized crop results in rather uniform populations of the plants that are homozygous for most characters and reduces the possibility of finding new genotypes. However, many wheats are phenotypically alike but quite different genotypically. Through hybridization of different wheat lines plant breeders are able to produce new variants which result from the segregation and recombination of different genes. Selfing tends to bring about homozygosity in varieties and thus eliminates much of the variation commonly observed in populations of cross fertilized crops. There are several sources of germplasm available for wheat breeders. In some areas the present varieties are merely heterogeneous populations made up of strains differing in their genotypic behavior. The fact that in studies involving hybrid material new characters are recombined, while others show transgressive inheritence clearly indicate that the present wheats are genotypically different and possess different genetic factors for the same character.

It has been emphasised that to breed intelligently for specific purpose, as for resistance to leaf rust of wheat, breeders need more fundamental information about (a) the genetic and cytogenetic basis of inheritance, (b) knowledge of the inter-relationship between the pathogen and the host, and (c) the nature and cause of leaf rust resistance. The latter is not fully understood and has been claimed by some investigators to be of secondary importance from the practical standpoint of breeding. These phases related to breeding for resistance to diseases should not be considered of routine nature. The nature of disease resistance and the hereditary studies of resistance to diseases are as important as the routine work related to breeding.

Genetically speaking, resistance to leaf rust is often inherited in a simple manner. In most cases one or two factors govern the reaction. The literature bearing directly or indirectly on the inheritance of leaf rust of wheat has already become extensive. The fact that a single gene may govern resistance to several rust races indicates that it is possible to obtain a variety that carries resistance to many of the prevalent races of rust in a locality. In the experiment reported in this thesis, Loros appeared to carry a major and a minor factor for resistance to races 15 and 5. From such situations we can see that the genetic background of the inheritance of resistance of leaf rust offers promise in the breeding of resistant wheat varieties.

The monosomic method of analysis is a relatively new tool for studying the inheritance of Mendelian factors in polyploid species. The use of monosomics may lead to additional genetic information which is of practical value to plant breeders. The breeder may be able to transfer parts of chromosomes or an entire chromosome carrying the factor for resistance to leaf rust from a doner source (same or related species) to a variety of wheat. Sears (23) transferred a piece of a chromosome carrying the gene for resistance to leaf rust from Aegilops umbellulata to common wheat. Heyne and Livers (8) located the gene for resistance to race 9 of leaf rust in Pawnee on chromosome X by means of monosomic analysis.

The relationship between the host plant and the rust fungus has more in common with symbiosis than the host-parasite relationships of many other fungi. The physiology of parasitism is concerned with the interaction of two biological entities. This interaction cannot be separated from the interplay of environmental factors. The host plant serves as the substrate for the parasite which can utilize this environment as a growth medium. Considered from the nutritional viewpoint of the host, the substrate may be adequate or inadequate, and the host may have inhibitory factors that are effective or ineffective. Then the leaf rust fungus will show virulence when the substrate is adequate and the inhibitory factors are ineffective (Garber, (4). Many strains of wheat can be studied for their reaction to rusts in the seedling stage as those reported in this thesis. The responses of the plant may be different at various stages of growth and vary from season to season. It is the tendency of the plant to react in a particular way in a certain environment but is not the character itself that is inherited. Seedlings of a variety of wheat may be susceptible to a race of rust but resistant in the adult stage. Johnston (14) called this phenomenon, the maturative type of resistance, as seen in Tenmarq and Chinese spring wheats. In contrast, there are no clear cases of varieties that are leaf rust resistant as seedlings but become susceptible with increasing age. Harris (6) reported that Carina and Brevit were resistant to leaf rust races 9 and 126 in the seedling stage respectively but susceptible in the adult stage. Such exceptions have not been reported many times in the literature, but changes from seedling susceptibility to mature plant resistance is found in varieties that exhibit an intermediate rust reaction. Thus, when the seedling reaction is of a resistant type, it is a satisfactory guide to the reaction of the adult plant to the same race. Such responses are important toward an understanding of the host-pathogen inter-relationship.

At present time much remains to be known about various causes of leaf rust resistance in wheat. The resistance of some wheat varieties to leaf rust may be classified as morphological or structural and physiological or protoplasmic. The structural resistance appears to be of little importance in case of leaf rust. The parasite appears to enter the stomata and penetrate the cell walls of resistant and susceptible varieties with equal facilities. However, susceptibility varies widely in degree and possibly may be influenced by the waxy coatings which may afford protection by increasing the difficulty of wetting the surface of the leaves, which is a prerequisite condition for the germination of spores. Small size of stomata and their late opening by the plant may exclude the fungal hyphae and be considered at least a part of the mechanism of resistance. This may be appreciated when one considers the success and dominance of the fungus diseases lies in the fact that these organisms are too small to fit into environmental niches, which expose them to conditions very different from those surrounding the plant. The internal structure of the wheat plant may affect the relative shape of the pustules but has little or no bearing on resistance, since seedlings of same age of wheat may show a wide range of resistance to leaf rust.

Physiological resistance is protoplasmic in nature and dependent upon the reaction of the host and invading pathogen. One hypothesis is that the cell tissues surrounding an infection are killed so quickly that the fungus is isolated from living tissues of the plant which limits the development of the fungus. Increased rust development may be due to the removal of inhibitory substances or to the increase of substances essential to the rust development. Phenolic compounds are known that are toxic to micro-organisms which may affect the host-parasite relationship through their action in the indoleacetic acid oxidase system.

There is no direct evidence on specific nutritional requirements of rust fungi, but it has been inferred that availability of amino acids is of particular importance to rust development. Wheat plants grown with high nitrogen or low potassium supply were more susceptible to leaf rust than those grown with low nitrogen or high potassium. Low potassium may result in accumulation of amino acids in the leaves.

It has been observed that high rust susceptibility is associated with a high degree of vigor in the host plant. Increased vigor is expressed in increased carbohydrate metabolism which is also associated with high protein content of the host. The increase in resistance with low light intensity is generally regarded as due to inadequate photosynthesis which is expressed in less amount of carbohydrates. Therefore, there may be some relationship between sugars and disease susceptibility. It is most probable that the simple sugars are the ones concerned. Pustules of leaf rust which developed on or near areas infected with mildew, were flourishing and reproductive, whereas those developed at some distance, were weak and small. This might be due to the decomposition of complex forms of sugars into simpler forms by the mildew that provided a nutritional medium for the leaf rust fungus to develop. Very recently Samborski, et al (24) reported on the metabolic changes in detached leaves floated on benzimidazole and the effect of these changes on rust reaction. They emphasized the relation between supply of substrate and the development of the rust, and concluded that breaking down of resistance of Khapli, a resistant stem rust wheat variety, was associated with a decrease of protein and increase in amino acids and alcohol soluble carbohydrates. In a similar study, Forsyth and Samborski (3) broke down the resistance of Khapli wheat to a number of stem rust races after treatment with DDT, or "searing" (heat treatment at the base of the leaf). The effect of the treatments was a marked increase in the carbohydrates and soluble nitrogen levels. Since the amino acids, which are present in small quantities, and simple sugars appeared to be critical in the development of the rust fungus in these studies. Further evaluation along these lines may be useful in explaining the cause of resistance.

SUMMARY

The seedling reaction to races 15, 9, 5, and 105 of wheat leaf rust was studied in the F_4 lines of the crosses Wichita X Loros and Wichita X Brevit.

Loros appeared to have a major and a minor factor for resistance to races 15 and 5 in the cross Wichita X Loros. When lines of the same cross were tested to races 9 and 105, they gave the same uniform susceptible reaction as their parents. Evidence of transgressive segregation for resistance was not observed.

Unexpected results were obtained with the F_4 progenies of the cross Wichita X Brevit. The lack of more than one resistant line out of 91 tested lines to race 15 and two lines out of 48 tested lines to race 5 in the cross, indicated that something was wrong with the cross or at least one or several of the following possibilities might be the cause for the behaviour. It might be possible that the Brevit plant used in the original cross was not an actual

Brevit plant or the changeable behavior of Brevit in different environmental conditions might be the cause. A mutation might have occurred in the Brevit parent used in the cross. The results obtained when the F_4 progenies of the cross Wichita X Brevit were tested to the four races of leaf rust, and the hypotheses forwarded are merely speculations. Brevit appeared to have two complementary genes for resistance to race 9 of leaf rust. All the tested lines showed susceptible reaction to race 105 like their parents and no transgressive segregation was observed.

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REACTION OF F_4 LINES OF WICHITA X LOROS AND WICHITA X BREVIT TO SEVERAL RACES OF LEAF RUST

by

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Leaf rust is potentialy one of the most dangerous diseases of wheat in Kansas. The most important solution to solving this problem lies in breeding resistant varieties. This solution is complicated by the continual appearance of new races of leaf rust, which at the present time is composed of 163 physiologic races as differentiated on eight wheat varieties.

To carry out a sound breeding program for leaf rust resistance, the knowledge of the inheritance of reaction of varieties of wheat and the manner of transferring the factors for resistance to adapted wheat varieties is essential for rapid progress. Such research has been conducted at Kansas State College and a portion of that study is reported in this thesis.

Previous studies indicated that resistance to leaf rust in wheat is usually controlled by one or two factors which are inherited in a simple manner.

In the experiments reported here, F_4 lines of the two crosses Wichita X Loros and Wichita X Brevit were studied for their seedling reaction to four leaf rust races. Each F_4 line represented an F_2 plant. The races used in the experiments included physiologic races 15, 9, 5, and 105 because of their prevelance in the wheat growing region of the Great Plains and each race is an important component of a separate race group.

There were 297 hybrid lines from the cross Wichita X Loros and 91 lines from the cross Wichita X Brevit tested to race 15 and the homozygous resistant and susceptible lines were tested to the other three races. Plants were inoculated approximately 10 days after planting by wetting them thoroughly with water spray, dusting the seedlings with urediospores of a pure culture of each race separately and placing them in a moist chamber for 12 hours. Plant response was determined approximately 10 days after inoculation. The classification of the reaction of the rust was made according to the standard reaction types described by Mains and Jackson in which the most resistant response was designated by 0, and the most susceptible response was designated by 4.

A random sample of the hybrid population was not available so the data could not be analysed satisfactorily for genetic ratios. The main objective was to determine the reaction of one line to several races. The Wichita parent had a known 4-type response to all races studied. Loros had 0-type reaction to race 15. The data obtained suggested that Loros had a major factor pair and a minor gene for the inheritance of resistance to race 15 and that these same gene or genes were ones that governed the reaction of leaf rust to race 5.

Both parents were susceptible to races 9 and 105 and all their F_4 progenies tested to both races gave the same response. No transgressive segregation for resistance was obtained.

The Brevit parent had a 0-1 type reaction to races 15 and 5. The lack of more than one resistant line out of 91 tested lines to race 15 and two resistant lines out of 48 tested lines to race 5 indicated that some one or several of the following possibilities might account for the unexpected responses obtained: It was possible that the Brevit used in the original cross was not an actual Brevit plant; non-randomness of the sample studied; the hypersensitivity of Brevit to changes in environmental conditions might change the reaction type; or a mutation might have occurred in the Brevit plant used in the original cross. Because of these factors, the analysis of the results obtained with races 9 and 105 and the hypothesis advanced were merely speculation.

F_4 progenies of the cross Wichita X Brevit tested for their reaction to race 9 suggested that perhaps two complementary genes were involved. Both parents were susceptible to race 105 of leaf rust, and also their F_4 progenies gave the same susceptible reaction. No transgressive segregation for resistance was obtained.

The various phases and nature of leaf rust resistance in wheat were discussed.