THE INHERITANCE OF RESISTANCE TO LEAF RUST AMONG CERTAIN DIFFERENTIAL CROSSES OF WHEAT

by

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B. S., Kansas State College
of Agriculture and Applied Science, 1951

A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1955

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INTRODUCTION

Wheat leaf rust, Puccinia rubigo-vera tritici (Eriks.) Carl., has been present in cultivated wheat since the beginning of recorded history. The economic significance of leaf rust was not clearly recognized until about 1920, and upon occasion it was considered beneficial by preventing excessive foliage development of the wheat plant. Research on leaf rust since 1926 has shown this disease to be detrimental to the normal development of the wheat plant.

Some control measures for leaf rust include certain cultural practices such as varying the time of seeding, limiting the use of fertilizers that tend to produce an excess of vegetative growth, and dusting with certain chemicals such as sulphur. These methods have proved to be only partially effective. The most effective means of control is the breeding of wheat varieties resistant to the disease. It is of much concern, therefore, that the nature of inheritance of this resistance to leaf rust be understood as well as the physiology of the pathogen.

A study is underway at Kansas State College concerning the inheritance of resistance to the various physiologic races of leaf rust among the eight differential varieties of wheat used to separate the races and Pawnee, and this thesis is based upon a portion of the study.

REVIEW OF LITERATURE

The breeding of wheat for resistance to leaf rust is complicated by numerous physiologic races of the pathogen, the response of leaf rust to a change in environment, and the change of resistance due to age in the wheat plant.

Wheat varieties may show different reactions to a given race under different conditions. Mains (1926) and Mains and Jackson (1926) reported that Hussar's reaction to a given race of rust varied considerably in the greenhouse because of modifying environmental conditions such as light intensity and temperature. Melchers and Parker (1922) reported that the susceptible reaction of seedlings could be quite different from that of the mature plant and that if the rust reaction on seedlings were used as the only basis for determining resistance, many lines with adult plant resistance would be discarded. Johnston and Melchers (1929) also found certain varieties were susceptible to race 9 in the seedling stage but were resistant at heading. They found that the varieties that change their reaction to leaf rust as they grow older show higher resistance in the upper leaves. Newton and Johnson (1943) stated that seedling reactions are not reliable indices to adult plant reaction when the seedling is susceptible. They found the mature plant resistant if the seedling was resistant.

Mains and Jackson (1926) reported mixtures of rust in the field as differentiated by their reactions on various varieties of wheat. They found no morphological basis for distinction between races, and they stated that the rust was best identified by its effect on certain varieties of wheat. Mains, et al. (1926) reported that accurate determination of the mode of inheritance was difficult under field conditions because of soil, climate, time of maturity, and mixtures of races. In hybrids with Malakof as the resistant parent, they found resistance was dominant. With Fulcaster as the resistant parent in a cross with Kanred, resistance was recessive with the heterozygous plants being susceptible in the early stages of growth and showing more or less resistance in the later stages. They concluded that various factors were

responsible for resistance to different races of rust.

Leighty (1926-a) reported segregation in the F_2 generation of 3 resistant to 1 susceptible when Malakof was used as the resistant parent in greenhouse tests. When Malakof was used as the susceptible parent in greenhouse tests, segregation occurred in the ratio of 1:2:1. The factors involved were found to be inherited independently. Leighty (1926-b) found that the cross Fulcaster (resistant to race 9) X Kanred (susceptible to race 9) resulted in the F_1 generation being somewhat more resistant than Kanred in the seedling stage but intermediate in the shooting and heading stage. The F_2 generation segregated 1:2:1. He also found that the cross Malakof X CI 3778 when tested with race 12 resulted in a 3:1 ratio with the resistance of Malakof as dominant. The same plants were tested with race 5, and a 3:1 ratio was again obtained with the resistance of CI 3778 as dominant. The combined data then gave a typical 9:3:3:1 ratio, indicating two independent factors for resistance to the different races of rust.

Wismer (1934) obtained resistant lines from a cross between Oro and Tenmarq, highly susceptible and moderately susceptible respectively. He concluded that multiple factors were involved with each parent contributing some. Wells and Swenson (1944) found a single gene for resistance to four races of rust in the cross (H44-Reward x Baringa) X (Hard Federation x Dicklow). Swenson, et al. (1947) postulated complementary factors for resistance in a cross between two susceptible varieties, Thatcher and Triunfo, which resulted in a mature type of resistance. Wu and Ausemus (1953), in a study of adult plant reaction to a collection of leaf rust in the field, concluded that Lee, a resistant variety, was differentiated from Mida, a susceptible variety, by two pairs of independently inherited recessive factors that were additive in

their action.

Heyne and Livers (1953), in a study on monosomic analysis of Pawnee wheat for leaf rust reaction, concluded that at least two partially dominant factors were involved in resistance to race 9. Heyne and Johnston (1954), in a study of crosses among Timstein, Pawnee, and Red Chief using races 5, 9, 15, 44, and 126, concluded that Timstein had one major recessive factor and one or more modifying factors for adult plant resistance. Pawnee's resistance to race 9 in the seedling stage was non-allelic to and partially epistatic to the Timstein factor.

Woodward (1950), in a study of the cross Malakof X Democrat, concluded that Democrat carried two recessive factors for resistance to race 9. Malakof carried one dominant factor for resistance to races 15 and 58. The resistance to races 15 and 58 was probably due to the same factor which was not associated with the factor for resistance to race 9. The cross Democrat X Mediterranean resulted in no segregation when tested with races 9, 15, and 58, according to Woodward, indicating the same factor or factors were responsible for resistance or susceptibility in both.

Mode (1953) used several crosses involving the leaf rust differential varieties and Pawnee in testing for reaction to races 5, 9, 15, and 58. He found that Webster had one dominant factor for resistance to races 5, 15, and 58. Mediterranean had one incompletely dominant factor for resistance to race 9 with the resistance to race 9 being inherited independently of that to races 5, 15, and 58. Webster also had one dominant factor for resistance to race 5 in the cross Webster X Pawnee. He found the behavior of Carina inconsistent in the crosses tested; however, he concluded that Carina and Hussar have different factors for resistance to races 5, 9, 15, and 58 with the Carina factors,

when homozygous, epistatic to the Hussar factors to races 5 and 15. Carina and Pawnee were differentiated by linked duplicate factors in their reaction to races 5, 15, and 58. Brevit and Hussar carried different factors for resistance to races 9 and 15, but the reactions were associated. Loros had one incompletely dominant factor for resistance to race 5 in a cross with Pawnee.

MATERIALS AND METHODS

The seedling reaction of F_3 plants of the crosses Hussar X Democrat and Mediterranean X Hussar were tested in the greenhouse to races 5, 9, 11, and 35 of leaf rust. Two hundred lines of each cross were used and each line represented the seed from one F_2 plant which had been grown in the field. The tests were conducted in an isolated section of the greenhouse with one race of rust at a time. After completing a test with a given race, the greenhouse section was cleaned of contaminating material before a new race was introduced.

The pure cultures of races 5, 9, 11, 35, and 126 of leaf rust used in the experiments were obtained from Mr. C. O. Johnston, Pathologist, U. S. Dept. of Agriculture, stationed at Kansas State College. The rust was propagated on the susceptible variety Cheyenne, which was planted in six three-inch pots with about 25-50 seeds per pot. About ten days after planting the Cheyenne, the seedlings were innoculated by placing the pots containing them in a metal moist chamber which had several inches of sand in the bottom to retain moisture. They were sprayed with a fine mist of tap water until droplets started to coalesce and then the rust spores were dusted on the plants. A glass cover was placed on the moist chamber and the plants were allowed to remain undisturbed at least twelve hours. One hundred pots of the F_3 lines were

planted at the same time the Cheyenne was innoculated. This allowed the rust to develop on the Cheyenne to the desired stage by the time the seedlings were large enough to innoculate. In addition to the 100 pots of F_3 seed, at least six of the differential varieties were planted at the same time to serve as a check on the purity of the race of rust that was used.

The pots were all placed on a bench in the greenhouse and about ten days after planting, a large cloth moist chamber was placed over them. They were sprayed with tap water and the cloth chamber was wet thoroughly before the spores from the sporolating seedlings of Cheyenne were dusted on the F_3 seedlings. The top of the moist chamber was then put in place and left undisturbed until the following day.

About ten days after innoculating when the material was sporolating freely, the pots were classified as homozygous resistant, homozygous susceptible, or segregating. The pots that contained segregating material were classified on an individual plant basis according to the standard reaction types described by Johnston and Mains (1932). These types are as follows:

0; Highly resistant; no uredinia formed; flecked.

1 Very resistant; more or less flecked, accompanied by a few small uredinia.

2 Moderately resistant; uredinia fairly abundant and of moderate size, accompanied by necrosis.

3 Moderately susceptible; uredinia fairly abundant and of moderate size; sometimes chlorosis.

4 Very susceptible; uredinia abundant, sometimes in more or less pronounced green islands.

The crosses Brevit X Mediterranean, Brevit X Carina, Webster X Brevit,

and Loros X Webster were studied in the F_2 generation in the greenhouse and the study was made on an individual plant basis. One F_2 plant was grown in a small pot and tested with race 5 in a manner similar to that described for the F_3 material. After the completion of the test with race 5, the plants were transplanted to large five-inch pots in which they were grown to maturity. The adult plants were tested with races 9 and 126 of leaf rust by making an aqueous spore suspension of a given race and injecting this into the leaf whorl at the top of a tiller. An attempt was made to infect the flag leaf, but often the second or third leaf from the top was the one infected. A colored tag was placed on the tiller that received an injection, thus making it possible to test with two races simultaneously by using tags of two colors to identify the race of rust. Readings on the mature plants were made about ten days after they were innoculated.

The parental varieties and their seedling reaction to the races of rust used in this study are presented in Table 1 which was condensed from Johnston and Rodenhiser (1951).

Table 1. Differential varieties of wheat and their reaction to physiologic races of leaf rust used.

Variety and CI No.		Physiologic race				
		5	9	11	35	126
Malakof	4898	4	4	0	4	4
Hussar	3756	0-2$^+$	1-2$^+$	0-2	1	2$^-$
Democrat	3778	4	0-1	0-2$^+$	4	4
Mediterranean	3780	4	0-1	1-2	4	4
Brevit	3779	0-1	1-2	3-4	2$^+$	2
Carina	3332	0	1-2	2$^-$	2$^+$	1
Webster	4843	0-1	4	1-2$^+$	4	1
Loros	3384	0-1	4	3-4	4	4

EXPERIMENTAL RESULTS

Inheritance Studies in F_2 Progeny

The breeding behavior of the F_2 plants tested is presented in Table 2. In the cross Brevit X Mediterranean, Brevit appeared to have one dominant factor for resistance to race 5. Brevit and Mediterranean were both resistant to race 9, but the F_2 generation segregated approximately 15 resistant: 1 susceptible, indicating two factors for resistance. The original data gave a X^2 value of 4.69, suggesting that the hypothesis might be questionable. However when the plants classified as 2^{++} were included with the susceptible group, a X^2 of 2.49 was obtained indicating that these plants may have been susceptible genotypes. Brevit was resistant to race 126 and in a cross with Mediterranean the F_2 plants were classified into 7 resistant:192 susceptible. Brevit apparently had two recessive factors for resistance to race 126. This hypothesis was supported by a X^2 of 2.54.

Carina was susceptible to race 9 in the adult stage but is normally resistant in the seedling stage, giving a type 1-2 reaction. Reversal from resistant in the seedling to susceptible in the adult plant is uncommon. As observed in the literature, resistance of a plant may increase from the seedling to a mature stage but it had never been reported to decrease with the age of the plant.

In the cross Carina X Brevit for reaction to race 9 in the adult stage it appeared that Carina had two complementary factors for susceptibility. This would give a ratio of 7 resistant:9 susceptible, which was supported by a X^2 of 1.29.

The reaction of Brevit to race 126 was similar to that of Carina for

Table 2. Manner of segregation in F_2 plants among crosses of differential varieties of wheat.

Cross	Physiologic race	Reaction		Hypothesis	X^2	Probability lies between
		Resistant	Susceptible			
Brevit	5	156	44	3:1	0.96	0.30-0.50
X	9	193	5	15:1	4.69	0.02-0.05
Mediterranean	9**	191	7	15:1	2.49	0.10-0.20
	126	7	192	1:15	2.54	0.10-0.20
Brevit	5	all		identical factors		
X	9	95	104	7:9	1.29	0.20-0.30
Carina	126	125	72	9:7	4.63*	0.02-0.05
Webster	5	all		identical factors		
X	9	71	128	7:9	5.22*	0.02-0.05
Brevit	126	141	50	3:1	0.15	0.50-0.70
Loros	5	all		identical factors		
X	9		all	identical factors		
Webster	126	94	27	3:1	0.46	0.30-0.50

* Significant at the 5 per cent level.

** The classification was altered by including as susceptible those plants that were classified 2++.

reaction to race 9 in that Brevit was susceptible as an adult plant while the seedling was resistant. In the cross Carina X Brevit for reaction to race 126 in the adult stage, it appeared that Carina may have two complementary dominant factors for resistance. The ratio of 9 resistant:7 susceptible gave a X^2 of 4.63 which is not significant at the 1 per cent level. Further testing in the F_3 generation will be necessary to verify this hypothesis.

Webster and Brevit were both resistant to race 5. No segregation occurred in the F_2 progeny and it was assumed that both parents carried the same factor or factors for resistance. Brevit was resistant to race 9 and Webster was susceptible. Segregation in the cross Webster X Brevit indicated that two factors were involved in the resistance to race 9. Brevit may have had two complementary recessive factors for resistance as indicated by a X^2 of 5.22. This is not significant at the 1 per cent level; however, the hypothesis might be questioned since the X^2 is significant at the 5 per cent level. Further studies on this cross will be necessary to clarify the manner of segregation.

In the cross Webster X Brevit for reaction to race 126 in the adult stage, it appeared that Webster had one dominant factor for resistance. A X^2 of 0.15 supported the single factor hypothesis.

The Loros X Webster cross did not segregate when tested with races 5 and 9, indicating that the same factor or factors were responsible for resistance in both parents. In the cross Webster X Loros, Webster apparently contributed one factor for resistance to race 126 which behaved as a simple dominant. A X^2 of 0.46 supported the single factor ratio.

The reaction of all these crosses was determined on F_2 plants. Further study in the F_3 generation will be necessary to verify the results.

Inheritance Studies in F_3 Progeny of the Cross Mediterranean X Hussar

The data for the cross Mediterranean X Hussar are recorded in Table 3. Hussar contributed the resistance to race 5 in the Mediterranean X Hussar cross. It is obvious from the data that a single factor difference will not explain the reaction to race 5 in this cross. The hypothesis that two factors were involved resulted in a 3 resistant:13 susceptible ratio in the F_2. The F_3 segregating lines indicated that the F_2 genotype may have been 1 resistant: 8 segregating:7 susceptible. This two-factor hypothesis gave a X^2 of 28.61 which is a highly significant deviation from the expected, indicating that the chances were less than 0.01 that the plants segregated according to the hypothesis. A X^2 of 7.14 was obtained by reclassifying the data to include as homozygous susceptible those pots that contained only one or two resistant plants. These data admittedly do not give conclusive results concerning segregation in this cross. Hussar is known to give different reactions under varying conditions of environment, and it is possible that under different environmental conditions many of the lines that were classed as segregating would be found to be homozygous susceptible. The 3:13 ratio in the cross Mediterranean X Hussar for reaction to race 5 is explained as follows:

F_2 genotype	F_3 reaction to race 5
AABB	breeds true susceptible
AABb	segregates 1R:3S
AAbb*	breeds true resistant

* Parental genotype.

Table 3. Manner of segregation of the F_3 lines in the cross Mediterranean X Hussar.

Physiologic race	Reaction: Resistant	Segregating	Susceptible	Hypothesis	X^2	Probability lies between
5	16	134	50	1:8:7	28.61	< 0.01
5*	16	115	69	1:8:7	7.14	0.02-0.05
9	87	104	9	7:8:1	1.14	0.50-0.70
11	32	145	23	2:12:2	2.29	0.30-0.50

	Reaction Type: 1	1-2	1-4	2-4	1-2-4	4			
35	16	7	12	23	99	43	1:8:7	40.4	< 0.01
35	16	7	12	23	99	43	1:15	1.12	0.50-0.70

* Those pots that had two or less resistant plants were considered homozygous susceptible.

AaBB	breeds true susceptible
AaBb	segregates 3R:13S
Aabb	segregates 3R:1S
aaBB*	breeds true susceptible
aaBb	breeds true susceptible
aabb	breeds true susceptible

This would give 1 resistant:8 segregating:7 susceptible lines in the F_3. The manner of segregation in the segregating F_3 lines would be 1 resistant: 3 susceptible, 3 resistant:13 susceptible, and 3 resistant:1 susceptible. This approximated the manner of segregation of the F_3 segregating lines.

Mediterranean and Hussar were both resistant to race 9 but the progeny of their cross showed transgressive segregation for susceptibility, indicating that different factors were responsible for resistance in this cross. The hypothesis for duplicate dominant factors for resistance resulted in a ratio of 15 resistant:1 susceptible in the F_2. The F_3 lines should segregate 7:8:1. This hypothesis was supported by a X^2 of 1.14. The proposed breeding behavior of the segregating genotype is as follows:

F_2 genotype	F_3 reaction to race 9
AABB	breeds true resistant
AABb	breeds true resistant
AAbb*	breeds true resistant
AaBB	breeds true resistant
AaBb	segregates 15R:1S
Aabb	segregates 3R:1S
aaBB*	breeds true resistant

* Parental genotypes.

aaBb	segregates 3R:1S
aabb	breeds true susceptible

The segregating F_3 lines fit the above manner of segregation with a few exceptions which might be accounted for by chance variation or seed contamination.

Mediterranean and Hussar were both resistant to race 11, but the cross resulted in transgressive segregation for susceptibility, indicating that at least two factors for resistance were involved in the cross. One parent was assumed to have two factors for resistance, one dominant and one recessive, and the other parent was assumed to have two factors for resistance that were the reciprocal of the first. This resulted in a 6:10 ratio in the F_2. Segregation in the F_3 would be 2 resistant:12 segregating:2 susceptible. This hypothesis was supported by a χ^2 value of 2.29. The reaction of the expected F_2 genotypes in the F_3 generation may be as follows:

F_2 genotype	F_3 reaction to race 11
AABB	breeds true susceptible
AABb	segregates 1R:3S
AAbb*	breeds true resistant
AaBB	segregates 1R:3S
AaBb	segregates 6R:10S
Aabb	segregates 3R:1S
aaBB*	breeds true resistant
aaBb	segregates 3R:1S
aabb	breeds true susceptible

Mediterranean was susceptible to race 35 and Hussar was resistant. In

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* Parental genotypes.

this cross, erratic results were obtained. Resistant plants varied from a type 1 reaction like Hussar to a type 2 reaction. The data did not fit any common ratio; consequently the manner of segregation was altered to include classes of plants that were homozygous type 1, segregating types 1-2, 1-4, 2-4, 1-2-4, and homozygous type 4. The data were tested for a two-factor ratio in which the type 1 class was considered homozygous resistant and the type 1-2 group was placed with the segregating types 1-4, 2-4, and 1-2-4. This resulted in a X^2 value of 40.42, indicating that the factors probably did not segregate according to this hypothesis. If all the lines that were resistant like Hussar are placed in the resistant class and all other classes are grouped together, the resulting X^2 value of 1.12 for a 1:15 ratio is a good fit, indicating that there are at least two main factors for resistance. As stated previously, Hussar gave variable reactions which made it difficult to classify and especially to compare data from different tests. Apparently the factor or factors responsible for resistance to race 5 and 35 in Hussar are more responsive to environmental changes than are those factors for resistance to races 9 and 11.

The factors for resistance to races 5, 9, 11, and 35 from Hussar were all associated in the cross Mediterranean X Hussar, as shown in Table 4.

Table 4. Association between leaf rust reactions in the cross Mediterranean X Hussar to races 5, 9, 11, and 35.

Association	Degrees of freedom	X^2	Probability
5 and 9	4	47.78	< 0.001
5 and 11	4	31.86	< 0.001
5 and 35	4	123.17	< 0.001
9 and 11	4	111.93	< 0.001
9 and 35	4	59.51	< 0.001
11 and 35	4	33.45	< 0.001

Inheritance Studies in the F_3 Progeny of the Cross Hussar X Democrat

Data are presented in Table 5 for the Hussar X Democrat cross. Hussar contributed the resistance to race 5 for this cross. The data suggested that at least two factors were responsible for the resistance to race 5. A X^2 of 26.14 indicated that the probability of obtaining the data as recorded was less than one in one hundred for a two-factor ratio. It is possible that several pots classified as segregating would be classed as susceptible under different environmental conditions. This hypothesis was given additional support by the X^2 of 0.19 for a 1:15 ratio. This ratio was obtained by placing the resistant lines in one group and all the others in another group. The Hussar reaction to race 5 apparently was variable and consequently gave a larger proportion of segregating lines than would be found with stable reaction types.

The reaction of F_3 plants in the segregating lines closely followed the expected behavior for a two-factor relationship in which one dominant factor and one recessive factor were necessary for resistance. The proposed breeding behavior is the same as that for the cross Mediterranean X Hussar when tested with race 5.

Hussar and Democrat were both resistant to race 9, but transgressive segregation for susceptibility occurred in the cross Hussar X Democrat. Three independent dominant factors were apparently involved in the cross as indicated by a X^2 of 1.64 based upon this hypothesis. The reaction of the segregating lines in the F_3 should be 3 resistant:1 susceptible, 15 resistant: 1 susceptible, and 63 resistant: 1 susceptible. Testing the F_2 in the F_3 generation gave a 37:26:1 ratio. The segregating lines fit the expected

Table 5. Manner of segregation of the F_3 lines in the cross Hussar X Democrat.

Physiologic race	Reaction: Resistant	Segregating	Susceptible	Hypothesis	χ^2	Probability lies between
5	14	134	52	1:8:7	26.14	< 0.01
5	14	134	52	1:15	0.19	0.50-0.70
9	111	84	5	37:26:1	1.64	0.30-0.50
11	58	126	16	19:38:7	2.05	0.10-0.20

	Reaction Type: 1	1-2	1-4	2-4	1-2-4	4			
35	12	8	18	13	110	39	1:8:7	50.91	< 0.01
35	12	8	18	13	110	39	1:15*	0.02	0.80-0.90

* The type 1 class was considered homozygous resistant and the other classes were combined.

ratios closely except for one pot which may have been grown from mixed seed.

Transgressive segregation for susceptibility to race 11 occurred in the cross Hussar X Democrat although both parents were resistant. Three factors apparently were involved in the resistance to this race. The reaction of the F_3 plants from the segregating lines should be 3 resistant:1 susceptible, 15 resistant:1 susceptible, 1 resistant:3 susceptible, 3 resistant:13 susceptible, and 51 resistant:13 susceptible if one parent had one dominant factor for resistance and the other parent had two complementary factors for resistance. Testing the F_2 in the F_3 generation should give a 19:38:7 ratio. The reaction of the segregating lines followed the expected closely. A X^2 of 2.05 for the above hypothesis indicated that the data agreed with the number expected. The proposed breeding behavior of progeny of F_2 plants is as follows:

F_2 genotype	F_3 reaction to race 11
AABBCC	breeds true resistant
AABbCC	breeds true resistant
AAbbCC*	breeds true resistant
AaBBCC	segregates 3R:1S
AaBbCC	segregates 3R:1S
AabbCC	segregates 3R:1S
aaBBCC	breeds true susceptible
aaBbCC	breeds true susceptible
aabbCC	breeds true susceptible
AABBCc	breeds true resistant
AABbCc	breeds true resistant

* Parental genotype.

AAbbCc	breeds true resistant
AaBBCc	segregates 15R:1S
AaBbCc	segregates 51R:13S
AabbCc	segregates 3R:1S
aaBBCc	segregates 1R:3S
aaBbCc	segregates 3R:13S
aabbCc	breeds true susceptible
AABBcc	breeds true resistant
AABbcc	breeds true resistant
AAbbcc	breeds true resistant
AaBBcc	breeds true resistant
AaBbcc	segregates 15R:1S
Aabbcc	segregates 3R:1S
aaBBcc*	breeds true resistant
aaBbcc	segregates 3R:1S
aabbcc	breeds true susceptible

It was assumed that A and B were factors for resistance and C was a factor for susceptibility. It was further assumed that the resistance of A was epistatic over the susceptibility of C and C was epistatic over the resistance of B.

Hussar was resistant to race 35 and Democrat was susceptible. The cross between these two varieties gave erratic results, apparently due to the same variable reaction types from Hussar that gave inconclusive results in the cross Mediterranean X Hussar. The data from this cross were classified into parental reaction types. The type 4 reaction was considered homozygous

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* Parental genotype.

susceptible, the type 1 reaction was considered homozygous resistant, and the reaction types 1-2, 1-4, 1-2-4, and 2-4 were considered to be segregating. A X^2 of 50.9 suggested that the hypothesis for a two-factor ratio was questionable; however when the homozygous resistant lines were considered as one group and all other reactions were grouped together, a good fit to a 1:15 ratio was obtained. The variable reaction of Hussar to race 35 in this cross resulted in a number of lines being classified as segregating while under different environmental conditions they might be classified as homozygous susceptible. Further work with Hussar is needed to clarify its reaction to leaf rust. The manner of segregation in the segregating lines indicated that the factors for resistance to race 35 in Hussar were complementary in action. The proposed breeding behavior is the same as that given for Mediterranean X Hussar to race 5.

The factors for resistance to races 5, 9, 11, and 35 from Hussar are associated as shown by the data in Table 6. This agreed with the results obtained in the cross Mediterranean X Hussar.

Table 6. Association between leaf rust reactions in the cross Hussar X Democrat to races 5, 9, 11, and 35.

Association	Degrees of freedom	X^2	Probability
5 and 9	4	27.38	<0.001
5 and 11	4	13.57	<0.01
5 and 35	4	154.11	<0.001
9 and 11	4	110.67	<0.001
9 and 35	4	26.40	<0.001
11 and 35	4	16.75	<0.01

DISCUSSION

The resistance of a plant to a given physiologic race of leaf rust is dependent upon one or more genetic factors in the host and an unknown number of factors in the pathogen. These factors act under the conditions of a certain environment to produce the resistance of that plant. Previous workers found that the seedling reaction of a plant to a specific race, if resistant, was a good indication of the adult reaction of that plant to the same race. Often the degree of resistance increased with age, but it had not been reported to decrease with age. The adult plants of Carina gave a susceptible reaction to race 9 when tested in the greenhouse, as compared to a resistant seedling reaction. Brevit also gave a susceptible mature plant reading to race 126 in contrast with its resistant seedling reaction. In view of the variable results obtained by various workers with the three differential varieties Brevit, Carina, and Hussar, further work will be of interest in determining possible correlation among these wheats that give varying reactions to a given race of rust and the reversal of resistance noted for Carina and Brevit.

In the F_3 lines involving Hussar, it is evident that Hussar is responsible for the variable reaction of the plants and lines to races 5 and 35 in the seedling stage as shown by the inability of the data in either cross to fit a common hypothesis in a convincing way. This variability may be due to factors that react differently under varying environmental conditions, to modifying factors which affect the resistance displayed by Hussar, or to an interaction between the host and the pathogen. It may be possible under a controlled environment to classify definitely the reaction types involving Hussar to races 5 and 35; as this experiment was conducted over a period of

several months, the temperature, intensity of light, and length of day varied considerably during that time. This may have caused the erratic results obtained. The factors responsible for resistance to races 5 and 35 in the cross Hussar X Democrat gave variable reactions like the factors involved in the Mediterranean X Hussar cross, thus supporting the theory that environment plays a large role in determining the resistance or susceptibility of Hussar to certain races of rust.

Three factors were responsible for resistance to race 9 in the Hussar X Democrat cross as compared to two factors found in the Mediterranean X Hussar cross. Each acted independently of the others and it was probable that one of the factors in Democrat was the same one found in Mediterranean since Woodward (1950) reported no segregation for resistance to race 9 in the cross Democrat X Mediterranean.

The manner of segregation of crosses tested by Woodward (1950), Mode (1953), and the author indicates that different factors may be responsible for resistance in the differential varieties used. The following genotype is proposed for the factors for resistance to race 5:

Webster	Abcde
Mediterranean	abCde
Hussar	aBcde
Democrat	aBCDe
Carina	AbcdE
Pawnee	abcde
Loros	Abcde

Mode reported one dominant factor A for resistance in the crosses Webster X Mediterranean and Webster X Pawnee. Carina was found to have one dominant

factor A for resistance that differed from the single Hussar factor for resistance B. Carina had two linked duplicate factors A and E that differed from those of Pawnee. Loros and Pawnee differed by the one factor A for resistance in Loros. The author found Hussar had two complementary factors B and c for resistance in the cross Mediterranean X Hussar and two complementary recessive factors for resistance c and d in the cross Hussar X Democrat. The above genotype was based on the assumptions that the resistance of A is epistatic over the susceptibility shown by other factors, that the resistance shown by Hussar is due to three factors B, c, and d, and that the duplicate factors for resistance in Carina, A and E, are closely linked. If the above hypothesis is correct, no segregation should occur between crosses of Webster, Carina, and Loros.

Conflicting results were obtained by Woodward and by the author concerning the factors for resistance to race 9 in crosses involving Democrat. Woodward's data indicated that Democrat had two recessive factors for resistance to race 9, but the author's data indicated that two dominate duplicate factors were involved. This discrepancy cannot be explained with assurance; however, the parents of the crosses involved were grown with the F_3 progeny by the author and it was noted that the seed color of the Democrat parent was a light red. This was in contrast to pure Democrat which had white seed. The seed appeared like Democrat in every way except color and all the readings taken on the Democrat parent corresponded with those for Democrat. The seed was definitely not Mediterranean which had nearly the same reaction as Democrat. Possibly this off-type Democrat had some factors that did not correspond with those of pure Democrat, and the factors for resistance to race 9 may have been different than those in pure Democrat.

The following genotype for reaction to race 9 is presented in accordance with the results obtained in this study:

Mediterranean	Abcd
Hussar	aBcd
Democrat	AbCD
Webster	abcd
Carina	Abcd
Brevit	Abcd

Mode reported that Mediterranean had one factor A for resistance to race 9 in the Webster X Mediterranean cross. Carina had one factor A for resistance to race 9 which differed from the Hussar factor B for resistance to race 9. Brevit also had one factor A for resistance that differed from the factor B in Hussar. The author found that Hussar had two complementary factors, B and c, for resistance to race 9. The Hussar X Democrat cross indicated that three independent dominant factors for resistance were present, one from Hussar, B, and two from Democrat, A and D.

The above does not explain the two-factor recessive ratio obtained by Woodward in his studies. The following alternative genotype is proposed in accordance with his data for resistance to race 9:

Mediterranean	AbCD
Hussar	aBCD
Democrat	abcd
Malakof	abCD
Webster	abCD
Carina	AbCD
Brevit	AbCD

It was assumed that the resistance of A or B was epistatic to the susceptibility of C or D. According to Woodward's data, C and D were dominant factors for susceptibility shown by Malakof. Mediterranean had one dominant factor A for resistance that differed from the dominant factor B of Hussar, according to Mode. Mediterranean had one incompletely dominant factor A for resistance in the cross Webster X Mediterranean which may be the same factor for resistance as was found in the Mediterranean X Hussar cross. Carina had one dominant factor A for resistance which could be the same as the one in Mediterranean but which was different from the factor B in Hussar. Brevit had a factor A for resistance which was different from the factor B in Hussar but which might be the same one found in Carina and Mediterranean.

Mode reported an association between the Brevit and Hussar factors to races 9 and 15. This was possible as the two factors A and B for resistance to race 9 were on the same chromosome as the factors for resistance to race 15. Woodward reported independent segregation for the Democrat resistance to race 9 and susceptibility to race 15. This may also be explained by the above genotype if it is assumed that factors c and d which Democrat possessed were on a different chromosome than the Democrat factors for susceptibility to race 15.

Data from Woodward and Mode indicated that there were at least three dominant factors for resistance to race 15. The following genotype is presented in accordance with their data:

Malakof	Abc
Democrat	abc
Webster	Abc
Mediterranean	abc

Carina	AbC
Hussar	aBc
Brevit	Abc
Pawnee	abc

Woodward reported that Malakof carried one dominant factor A for resistance and Democrat carried the susceptible allele a. Mode reported Webster carried one dominant factor A for resistance in a cross with susceptible Mediterranean. He also reported one factor A for resistance in Carina which was different than the factor B for resistance in Hussar. In the cross of Carina X Pawnee, Carina was differentiated by two duplicate dominate linked factors A and C for resistance as compared to the susceptibility of Pawnee. Brevit was reported to have a single factor A for resistance that differed from the factor B possessed by Hussar. If the genotypes are as proposed, crosses involving Malakof, Webster, Carina, and Brevit would result in no segregation for susceptibility to race 15, and crosses involving Democrat, Mediterranean, and Pawnee would be completely susceptible.

There are at least three factors for resistance to race 58 as indicated in the following proposed genotype:

Webster	Abc
Mediterranean	abc
Carina	ABc
Hussar	abC
Pawnee	abc
Malakof	Abc
Democrat	abc

Mode reported that Webster carried one dominant factor A for resistance in

the cross with Mediterranean. Carina had one resistant factor A which was different from the factor B for resistance in Hussar but which was one of the duplicate factors A and B for resistance found in the cross Carina X Pawnee. Woodward reported that Malakof carried one dominant factor A for resistance in the cross with Democrat.

The foregoing genotypes presented may be used to explain the breeding behavior of the varieties involved, but it is likely that further work will modify these genotypes as more knowledge of the breeding behavior is obtained.

SUMMARY OF RESULTS

The crosses Brevit X Mediterranean, Carina X Brevit, Webster X Brevit, and Loros X Webster were tested in the F_2 generation with leaf rust races 5, 9, and 126. The resulting data could be explained by assuming that the resistant parent carried one or two factors for resistance. Carina was susceptible to race 9 and Brevit to race 126 in the adult stage. These are in contrast to a resistant seedling reaction for each to their respective races. Reversal of reaction from resistant to susceptible as the plant matured had not been reported previously but was consistent in the foregoing experiment.

Inconclusive results were obtained in the crosses involving Hussar when tested with races 5 and 35 in the F_3 generation, but it is probable that environment contributed to the erratic results obtained since Hussar is known to give varying reactions depending upon 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. The factors for resistance to races 5, 9, 11, and 35 were all associated in the crosses Mediterranean X Hussar and Hussar X Democrat.

ACKNOWLEDGMENT

Appreciation is expressed to Dr. E. G. Heyne, under whose guidance this work was done, for his excellent advice and helpful criticisms throughout the experiment and the preparation of this manuscript; to Mr. C. O. Johnston for supplying the pure cultures of rust used and for his help during the experiment; and to the Kansas Crop Improvement Association for supplying the financial assistance needed to conduct this study.

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THE INHERITANCE OF RESISTANCE TO LEAF RUST AMONG CERTAIN DIFFERENTIAL CROSSES OF WHEAT

by

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B. S., Kansas State College
of Agriculture and Applied Science, 1951

ABSTRACT OF THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1955

ABSTRACT OF THESIS

Leaf rust is a major disease of wheat, one of the world's most important cereal crops. Control of this disease is effective only through the breeding of resistant varieties, and a knowledge of the nature of inheritance of resistance to this disease is useful in wheat breeding.

The F_2 generation of the crosses, Brevit X Mediterranean, Brevit X Carina, Webster X Brevit, and Loros X Webster were grown to maturity in individual pots in the greenhouse. They were tested to race 5 of leaf rust in the seedling stage by placing the seedlings in a moist chamber and dusting with the rust spores. A humid atmosphere was maintained for at least twelve hours to promote germination of the rust spores. The same plants were tested with races 9 and 126 in the adult stage by injecting an aqueous spore suspension of the desired race into the whorl of leaves prior to the emergence of the flag leaf. All readings were taken about ten days after innoculation.

The results obtained indicated that Brevit had one dominant factor for resistance to race 5 that was identical to a factor for resistance found in Carina, Webster, and Loros. Brevit and Mediterranean each carried a dominant factor for resistance to race 9; however, the Brevit factor appeared recessive to the complementary dominant factors for susceptibility carried by Carina in the adult stage. Carina was susceptible to race 9 in the adult plant in contrast with a resistant seedling reaction. Reversal of resistance as a plant matures is uncommon and the reversal from resistance to susceptible had not been reported previously. Webster and Loros apparently had the same factors for susceptibility to race 9, as all the F_2 progeny were

susceptible. Brevit was susceptible to race 126 in the adult plant in contrast with a resistant seedling reaction. Carina had two complementary factors for resistance to race 126 and Webster had one.

Inconclusive results were obtained in crosses involving Hussar in the F_3 generation when tested with races 5 and 35. This was probably due to the effect of environmental conditions. Mediterranean, Hussar, and Democrat all were resistant to races 9 and 11 but segregation occurred in their crosses, indicating each had different factors for resistance. Mediterranean and Hussar had one dominant factor each for resistance to race 9 and Democrat had two, one of which may have been the same as the factor in Mediterranean. Mediterranean and Hussar had two factors each for resistance to race 11 and Democrat had one.

Tests for independence of inheritance of resistance indicated that the factors for resistance in Hussar to races 5, 9, 11, and 35 were associated in the crosses Mediterranean X Hussar and Hussar X Democrat.