INHERITANCE OF RESISTANCE TO RACES OF LEAF RUST, *PUCCINIA TRITICINA* ERIKSSON, IN CROSSES OF HARD RED WINTER WHEAT

INHERITANCE OF RESISTANCE TO RACES OF LEAF RUST, PUCCINIA TRITICINA ERIKSSON, IN CROSSES OF HARD RED WINTER WHEAT

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INTRODUCTION

The need for wheat varieties, Triticum vulgare Vill., resistant to leaf rust, Puccinia triticina Erikss., has been realized for some time. Annual losses due to leaf rust in the United States have caused the disease to be recognized as important and in some states, the most destructive disease of wheat. Leaf rust does not cause violent yield fluctuation from year to year as does stem rust, Puccinia graminis tritici Erikss. Leaf rust more often causes a fairly regular drain on wheat yields, with only occasional exceptions of either rust-free or epiphytotic seasons. One severe epiphytotic occurred in 1938 when losses due to leaf rust amounted to over 100,000,000 bushels in the United States (11).[1]

The importance of breeding rust-resistant varieties of wheat was recognized as early as 1886 by Farrer (3) in Australia. By 1894 the use of rust-resistant varieties was well established in Australia as a means of rust control. Later in England, Biffen (1) applied the newly rediscovered Mendel's laws to the breeding of wheat for resistance to stripe rust, Puccinia glumarum (Schmidt) Erikss. and Henn. In the United States in 1915, breeding of wheats resistant to stem rust got underway when McFadden (10) crossed Yaroslav Emmer, Triticum dicoccum Schrank, and Marquis wheat T. vulgare (C. I. 3641) to produce the variety Hope (C. I. 8178). Hope, being highly resistant to stem and leaf rust, has been used extensively in producing rust resistant, commercial wheats.

In a breeding program where rust resistance is of importance, the preliminary phases may be carried out more easily in the greenhouse than in the field. Greenhouse culture has certain advantages over field culture as

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[1] Figures in parenthesis refer to "Literature Cited", p. 30.

follows: (1) early generations of hybrid material can be protected from adverse weather conditions; (2) the hybrid plant material may be grown under optimum conditions of moisture, light, temperature, and soil for rust infection and for seed increase; (3) the plants can be inoculated with pure rust race cultures and thus can be exposed to a greater number of rust races than might be present in the field; (4) the reaction to each physiologic race can be determined; and (5) there is less chance for plants to escape infection.

Leaf rust of wheat exhibits physiologic specialization, that is, the leaf rust that attacks wheat will not attack rye, Secale cereale L., while the morphologically similar rye leaf rust, Puccinia dispersa Erikss., will not attack wheat. Stakman (13) showed that the stem rust of wheat could be further subdivided into a large number of physiologic races, similar and identical morphologically and all attacking wheat, but each differing from the other in its capacity to attack certain wheat varieties but not others. Later, Gains and Jackson (8) reported similar findings with the leaf rust of wheat, being able to differentiate 12 physiologic races. These 12 physiologic races were differentiated by their reaction on the following host varieties: Malakof (C. I. 4098), Webster (C. I. 3780), Loros (C. I. 3779), Mediterranean (C. I. 3332), Democrat (C. I. 3388), Brevit (C. I. 3778), Hussar (C. I. 4843), and Carina (C. I. 3756). These same differential varieties are in general use for race determination throughout the United States today. Chester (2) has deleted the varieties Brevit, Hussar, and Carina from this list of differentials because of their inconsistent reactions and has constructed a key for race group determinations based on the use of the varieties Malakof, Webster, Loros, Mediterranean, and Democrat. Physiologic races with similar reactions on these 5 differential varieties have been placed into the same race group. By this procedure, Chester (2) designated 44 race groups

comprising the 129 individual physiologic races.

Data with regard to the inheritance of resistance to races or race groups of leaf rust are needed by the breeder so that he may know what to expect in the progeny when wheat crosses are made. Such information should facilitate the development of superior varieties from the standpoint of disease resistance.

The primary objective of this investigation has been to determine the mode of inheritance of reaction to race groups of leaf rust in crosses of winter wheat.

REVIEW OF LITERATURE

A limited amount of research has been conducted on the genetics of resistance to leaf rust in crosses of winter wheat in the seedling stage.

It was reported by Scheibe (12), that if a variety is very resistant or very susceptible to leaf rust in the seedling stage, there is no change in reaction as the plant ages. The change from seedling susceptibility to mature plant resistance is found only in varieties that exhibit either a moderate degree of susceptibility or an intermediate reaction to leaf rust.

The heritability of resistance of wheat varieties to given races or race groups of leaf rust has been demonstrated and the literature pertaining thereto has been summarized by Chester (2). The resistant reaction is readily transferred from parent to hybrid progeny, and is usually governed by a single Mendelian factor. This factor in any given case may be dominant, recessive, or intermediate, and it is often conditioned by the developmental stage or metabolic stage of the host plant.

The first published study on the inheritance of resistance was a rather comprehensive one by Mains, Leighty, and Johnston (9). They found the resistance of Malakof to physiologic races 1 and 12 to be dependent upon a single dominant genetic factor. In a cross, between Malakof as the susceptible parent and Webster as the resistant parent, studied for reaction to physiologic race 5 in the seedling stage in the greenhouse, heterozygous F_1 plants were exhibited intermediate in susceptibility but approached Malakof so closely that in some cases they were difficult to distinguish from the homozygous-susceptible plants. Apparently in this cross, resistance is dependent upon a single main-factor difference with a segregation of 1 resistant: 2 intermediate: 1 susceptible. In another cross, between Fulcaster (C. I. 4062)

as the resistant parent and Konred (C. I. 5146) as the susceptible parent, studied for reaction to physiologic race 9 in the greenhouse, the ratio of segregation was 3:1; this time, however, resistance was recessive. In a cross between Kalaf, resistant to race 12 and susceptible to race 5, and Brevit, susceptible to race 12 and resistant to race 5, it was found that the resistance to each race was inherited independently of the other. A 9:3:3:1 ratio was obtained from a study of the material, indicating the inheritance to be controlled by two independent factors.

In a study of the cross Webster (C. I. 10003) X Brimro (P. P. I. No. 104130), Swenson, Buchholtz and Grafius (14) found that plants classed as resistant in the field proved to be highly susceptible when later generations were inoculated in the seedling stage in the greenhouse. Results from this experiment indicate rather clearly that the genes responsible for mature plant resistance are not necessarily the same as those genes that govern the seedling stage resistance.

In the F_3 of the cross, Normandie X Ringens r. Schlanstedter, studied for reaction to physiologic race 15, Isenbeck (6) obtained 31 resistant, 103 heterozygous, and 36 susceptible lines. He concluded that resistance was dependent upon a single dominant factor pair. In another cross, Blauesntiger Kolben X Normandie, studied for reaction to physiologic race 15 by Hubert (5), 23 resistant, 42 heterozygous, and 19 susceptible lines were obtained in the F_3. Again, it was concluded that resistance to physiologic race 15 was dependent upon a single dominant gene.

A study of the interspecific cross, Chinese Wheat (C. I. 6223) X Vernal Emmer for reaction to physiologic race 65 was made by Guard (4). The F_1 of this cross was intermediate in reaction to race 65. Cytological studies in the F_2 showed that all lines identified as tetraploids were resistant to race 65 of leaf rust as was the Vernal Emmer parent.

MATERIALS AND METHODS

This study was conducted in the greenhouses of the Botany and Agronomy Departments, Oklahoma Agricultural and Mechanical College, Stillwater, Oklahoma in 1947 and 1948. Seeds of the winter wheat hybrids used in this study were furnished by A. M. Schlehuber.[2] These hybrids resulted from crosses made by personnel of the Small Grain Section, Agronomy Department during the spring of 1946. The F_1 was grown at the Experiment Station Agronomy Farm during the 1946-1947 growing season.

Inoculum of the race groups of leaf rust was furnished by K. S. Chester[3] for the F_2 study. Inoculum of the race groups used in the F_3 study was furnished by C. O. Johnston[4] who also furnished seed of 5 differential varieties of wheat as follows: Malakof, Webster, Loros, Mediterranean, and Democrat.

F_2 Progenies

The F_2 study was carried out in the Botany Department greenhouse. The parents of hybrids used in this study were inoculated with leaf rust race groups 2, 5, 6, 9, 12, 45, and 65. These race groups of rust were tested for identity and purity on the 5 differential wheats, Malakof, Webster, Loros, Mediterranean, and Democrat. The parents were inoculated by the scalpel method and incubated in a moist chamber of approximately 100% relative

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humidity for 24 hours as described by Chester (2). After 10 days the reactions of the parent and differential varieties to the 8 race groups of rust were determined and recorded. These reactions are presented in Table 1.

After reactions were determined for the parent varieties to the 8 race groups of rust, crosses were selected for the inheritance study on the basis of differential reaction of the parents of each cross to at least one race group of rust. These crosses, cross numbers, selection numbers assigned to the F_1 plants, and the race group of rust to which the parents showed differential reaction are presented in Table 2.

On November 22, 1947, 250 seeds of each selection were planted in 6-inch flower pots, 50 seeds to the pot. The F_2 plants were inoculated 10 days after seeding by a method of mass inoculation. Spores of the physiologic race groups 9, 12, and 45 were collected separately for several days prior to inoculation and on the day of inoculation each race was mixed with a 0.1% agar solution. This solution was then applied to the plants by stripping the leaves with the fingers. The plants were then incubated in a moist chamber (100% relative humidity) for 24 hours.

The reactions of the F_2 populations were determined and recorded on December 18, 1947. Counts of the number of susceptible and resistant plants were made for each selection. The following classes of reaction as recognized by Mains and Jackson (8) were used in classifying the hybrid plant material:

Table 1.--Reactions of 5 differential and 7 parent varieties of wheat to 8 race groups of leaf rust at Stillwater, Oklahoma in 1947.

Variety	C. I. No.	Race Group							
		2	5	6	9	12	21	45	65
Differential Varieties									
Malakof	4898	R*	S**	S	S	R	S	R	S
Webster	3780	R	R	R	S	R	S	S	X***
Loros	3779	S	R	S	S	S	S	S	S
Mediterranean	3332	S**	S	S	R	S	S	S	X
Democrat	3382	S	S	S	R	S	S	S	X
Parent Varieties									
Mediterranean-Hope x Pawnee	12141	S	S	S	R	S	S	S	X
Triumph	12132	S	S	S	S	S	S	S	S
Comanche	11673	S	S	S	S	S	S	S	S
Loros x Mediterranean-Hope	12140	S	S	S	R	S	S	S	X
Cimarron	12120	S	S	X***	X	R	S	R	S
Kawvale-Marquille x Kawvale-Tenmarq	12123	S	S	S	R	S	S	S	X
Cheyenne	8385	S	S	S	S	S	S	S	S

* R = resistant; ** S = susceptible; and *** X = intermediate, showing both susceptible and resistant reactions on the same leaf.

Table 2.--Cross, cross number, and F_1 plant selection number of the selections used in the F_2 and the race group of rust to which the parents showed differential reaction.

Cross	Cross No.	F_1 Plant Selection No.	Race Group
(Mediterranean-Hope x Pawnee) X Triumph	1C	3602-2	9
(Mediterranean-Hope x Pawnee) X Triumph	1C	3602-4	9
(Mediterranean-Hope x Pawnee) X Comanche	3B	3609-2	9
(Mediterranean-Hope x Pawnee) X Comanche	3B	3609-5	9
(Mediterranean-Hope x Pawnee) X Cimarron	6B	3620-2	12, 45
(Mediterranean-Hope x Pawnee) X Cimarron	6C	3621-2	12, 45
(Mediterranean-Hope x Pawnee) X Cimarron	6D	3622-2	12, 45
(Oro x Mediterranean-Hope) X Comanche	2	3605-1	9
(Oro x Mediterranean-Hope) X Comanche	2	3605-2	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne	8B	3630-1	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne	8B	3630-2	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche	9A	3633-1	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche	9B	3634-1	9

Class of host reaction	Type of rust infection
0 - Highly resistant	No uredinia formed; small flecks, chlorotic or necrotic areas more or less prevalent.
1 - Very resistant	Uredinia few, small, always in small necrotic spots. Also more or less necrotic areas produced without development of uredinia.
2 - Moderately resistant	Uredinia fairly abundant, of moderate size, always in necrotic or very chlorotic spots. Necrotic spots seldom without uredinia.
3 - Moderately susceptible	Uredinia fairly abundant, of moderate size. No necrosis produced, but sometimes slight chlorosis immediately surrounding the uredinia.
4 - Very susceptible	Uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occurring as green islands surrounded in each case by a chlorotic ring.

Johnston and Mains (7) added these types:

X - Heterogeneous or indeterminate	Uredinia very variable, apparently including all types and degrees of infection on the same blade; no mechanical separation possible; on reinoculation small uredia produce large ones and vice versa.
Intermediate or variable	Varying from moderately resistant ("2") to moderately susceptible ("3") at different times, but consistent on a given leaf.

In classifying the hybrid material in this study, plants showing a type "0" and "1" reactions were classed as resistant, those showing reactions "2", "3", and "4" were classed as susceptible.

F_3 Progenies

The F_3 study was carried out in the Agronomy Farm greenhouse during the period November 4, 1948 to February 4, 1949. The following materials were chosen for study in the F_3:

Cross	F_1 Plant Selection No.	F_2 Row No.	Race Group
(Mediterranean-Hope x Pawnee) X Comanche	3609-1	4005	9
(Oro-Mediterranean-Hope) X Comanche	3605-3	4019	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne	3629-1	4030	9
(Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche	3634-1	4034	9
(Mediterranean-Hope x Pawnee) X Cimarron	3620-1	4013	12, 45
(Mediterranean-Hope x Pawnee) X Cimarron	3621-1	4014	12, 45
(Mediterranean-Hope x Pawnee) X Cimarron	3622-1	4015	12, 45

Fifty lines of each selection were studied in the F_3. Approximately 50 seeds of each line were planted in 4-inch flower pots, 25 seeds to the pot. In November 1948, optimum infection was obtained in 14 days, 7 days from seeding to date of inoculation and 7 days from the date of inoculation to the date the rust reactions were determined. In January 1949, with lower temperatures and shorter days, optimum infection was obtained in 24 days, 10 days from seeding to inoculation and 14 days from inoculation to the reading of the rust reactions. The plantings of the crosses were staggered; that is, when a line reached the stage of inoculation, another was planted. Following this procedure, an abundant supply of rust inoculum was available for the subsequent study.

The method of inoculation used in the F_3 was a mass method, somewhat different from the one used in the F_2. Spores of the race to be used on a

particular selection were collected each day for several days prior to inoculation and on the day of inoculation these spores were mixed with water in a 1000 ml. beaker that measured 4 inches in diameter. The 4-inch flower pots containing the wheat plants were then inverted onto the 1000 ml. beaker containing the inoculum. In this manner the leaves of the wheat plants came in contact with the rust spores in suspension. The leaves remained in the suspension for 15 to 20 seconds. The plants were then incubated in a moist chamber of approximately 100% relative humidity for 24 hours. Infection resulting from this type of inoculation was very uniform and the time consumed in performing it was only a fraction of the time consumed in the mass method used in the F_2.

RESULTS AND DISCUSSION

F_2 Reactions

A summary of the data on the mode of inheritance of reaction to race groups of leaf rust in the F_2 progenies is presented in Table 3, 4, and 5.

Seven of the ten selections studied for reaction to race group 9 of leaf rust segregated (Table 3), giving Chi-square values ranging from 0.003 to 3.542 (df = 1) and corresponding values of probability ranging from 5 to 10% to 95 to 98% for goodness of fit to the 3:1 ratio. The combined Chi-square value for these 7 selections was 8.086 (df = 7) with a probability of 30 to 50%. This indicates that in these 7 selections the inheritance of the resistant reaction to race group 9 of leaf rust can be explained by a single recessive gene.

The 2 selections, 3602-2 and 3602-4 of the cross (Mediterranean-Hope x Pawnee) X Triumph and 3633-1 of the cross (Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche did not exhibit any segregation to race group 9 of leaf rust. In these 3 selections the susceptible parent was the male parent, and according to the mode of inheritance demonstrated in the other 7 selections, there should have been an abundance of susceptible plants in the F_2. Since the reactions were similar to those of the female parent, it is assumed these selections were the results of self-fertilization.

In the 3 selections of (Mediterranean-Hope x Pawnee) X Cimarron studied for reaction to race group 12 (Table 4), Chi-square values for goodness of fit to the 3:1 ratio gave probabilities of less than 1%. In every selection, the number of resistant wheat plants observed was less than the expected. The best fitting ratios for these selections are as follows: for 3620-2, the dihybrid ratio of 13:3, with a Chi-square value of 0.504 and a probability

Table 3.—Numbers of susceptible and resistant wheat plants in 7 F_2 hybrid progenies inoculated with race group 9 of leaf rust with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

Cross	F_1 Plant Selection No.	Total No. Plants	Observed		Expected		Chi-Square	P
			Susceptible	Resistant	Susceptible	Resistant		
(Mediterranean-Hope x Pawnee) X Comanche	3609-2	166	135	31	124.50	41.50	3.542	5-10%
(Mediterranean-Hope x Pawnee) X Comanche	3609-5	166	127	39	124.50	41.50	0.200	50-70%
(Oro x Mediterranean-Hope) X Comanche	3605-1	109	82	27	81.75	27.25	0.003	95-98%
(Oro x Mediterranean-Hope) X Comanche	3605-2	208	163	45	156.00	52.00	1.256	20-30%
(Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne	3630-1	173	137	36	129.75	43.25	1.620	20-30%
(Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne	3630-2	192	148	44	144.00	48.00	0.444	50-70%
(Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche	3634-1	188	135	53	141.00	47.00	1.021	30-50%
Total for all crosses . . . . df = 7, Chi-square = 8.086, P = 30-50%								

Table 4.—Numbers of susceptible and resistant wheat plants in 3 F_2 hybrid progenies inoculated with race group 12 of leaf rust, with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

Cross	F_1 Plant Selection No.	Total No. Plants	Observed		Expected		Chi-Square	P
			Susceptible	Resistant	Susceptible	Resistant		
(Mediterranean-Hope x Pawnee) X Cimarron	3620-2	210	175	35	157.50	52.50	7.777	<1%
(Mediterranean-Hope x Pawnee) X Cimarron	3621-2	208	173	35	156.00	52.00	7.410	<1%
(Mediterranean-Hope x Pawnee) X Cimarron	3622-2	237	211	26	177.75	59.25	24.879	<1%
Total for all progenies					df = 3, Chi-square = 40.066, P = <1%			

of 30 to 50%; for 3621-2, the dihybrid ratio of 13:3, with a Chi-square value of 0.502 and a probability of 30 to 50%; and for 3622-2, the dihybrid of 15:1, with a Chi-square value of 0.801 and a probability of 30 to 50%. The combined Chi-square values for these 3 selections gave probabilities of less than 1% for goodness of fit to the ratios of 3:1, 13:3, and 15:1. It is felt that further study is necessary to determine the mode of inheritance of resistance in this cross.

In the 3 selections of (Mediterranean-Hope x Burnse) x Simcrron studied for reaction to race group 45, Chi-square values for goodness of fit to the 3:1 ratio gave probabilities ranging from less than 1% to 90%. The number of resistant plants in each selection was less than expected. In considering the dihybrid ratio of 13:3 (Table 5), with the combined Chi-square value for the 3 selections equal to 5.461, a probability of 10 to 20% was obtained. Again, as was found with the reactions to race group 12, it is felt that more extensive work with this cross is needed before conclusions as to the mode of inheritance of reaction to race group 45 should be made.

Table 5.—Numbers of susceptible and resistant wheat plants in 3 F_2 hybrid progenies inoculated with race group 45 of leaf rust, with numbers expected under the 13:3 hypothesis and values of Chi-square and P.

Cross	F_1 Plant Selection No.	Total No. Plants	Observed		Expected		Chi-Square	P
			Susceptible	Resistant	Susceptible	Resistant		
(Mediterranean-Hope x Kanred) x Cimarron	3620-2	218	174	44	177.125	40.875	0.2941	50-70%
(Mediterranean-Hope x Kanred) x Cimarron	3621-2	187	141	46	151.9375	35.0625	4.1991	2-5%
(Mediterranean-Hope x Kanred) x Cimarron	3622-2	234	196	38	190.125	43.875	0.9681	30-50%

Total of all progenies . . . . . df = 3, Chi-square = 5.461, P = 10 -20%

F_3 Reactions

In the selection 3609-1 of the cross (Mediterranean-Hope x Pawnee) X Comanche, the line segregation in the F_3 was 13 susceptible, 24 heterozygous, and 13 resistant. The Chi-square value of 0.080 (df = 2) and a probability of 95 to 98% was obtained for the goodness of fit to the 1:2:1 ratio. The numbers of susceptible and resistant wheat plants in each of the 24 heterozygous lines are presented in Table 6. The total of 24 values of Chi-square 22.557 (df = 24) and a probability of 50 to 70% in the study of this cross indicate that the inheritance of the resistant reaction is dependent upon a single recessive factor pair.

The line segregation in the F_3 of the selection 3629-1 of the cross (Kawvale-Marquillo x Kawvale-Tennarq) X Cheyenne was 13 susceptible, 25 heterozygous, and 12 resistant. The Chi-square value of 0.040 (df = 2) and a probability of 99% was obtained for goodness of fit to the 1:2:1 ratio. The numbers of susceptible and resistant wheat plants in each of the 25 heterozygous lines are presented in Table 7. The total of 25 values of Chi-square 50.621 (df = 25) shows a probability of less than 1%. This large value of Chi-square can be attributed largely to the reactions of lines 3 and 22. Since the segregation of the lines shows a probability of 99%, it is assumed that the samples used in the heterozygous material were not representative and that the mode of inheritance of the resistant reaction can best be explained by a single recessive gene pair.

Table 6.—Numbers of susceptible and resistant wheat plants in 24 F_3 heterozygous lines of the cross (Mediterranean-Hope x Pawnee) x Comanche, inoculated with race group 9 of leaf rust, with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

F_2 Plant Selection No.	Total No. Plants	Observed: Suscept-ible	Observed: Resistant	Expected: Suscept-ible	Expected: Resistant	Chi-square	P
3609-1- 5	55	44	11	41.25	13.75	0.733	30-50%
- 6	37	31	6	27.75	9.25	1.522	20-30%
-10	59	46	13	44.25	14.75	0.276	50-70%
-11	23	19	4	17.25	5.75	0.710	30-50%
-16	54	41	13	40.50	13.50	0.024	80-90%
-18	49	39	10	36.75	12.25	0.551	30-50%
-21	50	36	14	37.50	12.50	0.240	50-70%
-22	46	36	10	34.50	11.50	0.240	50-70%
-23	52	39	13	39.00	13.00	0.000	100%
-27	58	40	18	43.50	14.50	1.126	20-30%
-28	58	38	20	43.50	14.50	2.781	5-10%
-29	53	43	10	39.75	13.25	1.062	30-50%
-32	43	33	10	32.25	10.75	0.069	70-80%
-35	30	20	10	22.50	7.50	1.111	20-30%
-36	36	28	8	27.00	9.00	0.148	70%
-40	40	25	15	30.00	10.00	3.333	5-10%
-41	30	24	6	22.50	7.50	0.400	50-70%
-42	64	46	18	48.00	16.00	0.333	50-70%
-43	45	36	9	33.75	11.25	0.600	30-50%
-44	20	14	6	15.00	5.00	0.266	50-70%
-45	56	37	19	42.00	14.00	2.380	10-20%
-47	40	25	15	30.00	10.00	3.333	5-10%
-50	65	45	20	48.75	16.25	1.153	20-30%
-51*	57	44	13	42.75	14.25	0.146	70-80%
Total of all lines				df = 24,	Chi-square = 22.557,		P = 50-70%

* Substituted for line 15 because of small amount of seed available.

Table 7.--Numbers of susceptible and resistant wheat plants in 25 F_3 heterozygous lines of the cross (Kanvale-Marquillo x Kanvale-Tenmarq) x Cheyenne, inoculated with race group 9 of leaf rust, with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

F_2 Plant Selection No.	Total No. Plants	Observed: Susceptible	Observed: Resistant	Expected: Susceptible	Expected: Resistant	Chi-square	P
3629-1- 3	58	27	31	43.50	14.50	25.034	<1%
- 4	40	26	14	30.00	10.00	2.133	10-20%
- 6	46	32	14	34.50	11.50	0.724	30-50%
- 7	44	34	10	33.00	11.00	0.121	70-80%
- 9	69	54	15	51.75	17.25	0.391	50-70%
-11	54	42	12	40.50	13.50	0.222	50-70%
-14	43	29	14	32.25	10.75	1.310	20-30%
-15	45	32	13	33.75	11.25	0.362	50-70%
-18	69	51	18	51.75	17.25	0.043	80-90%
-20	69	52	17	51.75	17.25	0.004	95%
-22	59	35	24	44.25	14.75	7.734	<1%
-23	69	50	19	51.75	17.25	0.236	50-70%
-25	53	44	9	39.75	13.25	1.817	50-70%
-26	54	45	9	40.50	13.50	2.000	10-20%
-29	61	47	14	45.75	15.25	0.136	70-80%
-30	78	61	17	58.50	19.50	0.427	50-70%
-33	72	56	16	54.00	18.00	0.296	50-70%
-39	59	38	21	44.25	14.75	3.531	5-10%
-41	68	54	14	51.00	17.00	0.705	30-50%
-43	54	42	12	40.50	13.50	0.222	50-70%
-45	62	48	14	46.50	15.50	0.193	50-70%
-46	49	33	16	36.75	12.25	1.530	20-30%
-47	58	44	14	43.50	14.50	0.022	80-90%
-48	61	49	12	45.75	15.25	0.923	30-50%
-49	66	47	19	49.50	16.50	0.505	30-50%

Total of all lines . . . . df = 25, Chi-square = 50.621, P = <1%

Segregation was 14 susceptible, 21 heterozygous, and 15 resistant in the selection 3605-3 of the cross (Oro x Mediterranean-Hope) X Comanche. The Chi-square value of 1.320 (df = 2) and probability of 50 to 70% was obtained for goodness of fit to the 1:2:1 ratio. Because of low infection, reactions were recorded for only 4 of the heterozygous F_3 lines. The number of susceptible and resistant wheat plants in these 4 heterozygous lines are presented in Table 8. For these 4 lines a Chi-square value of 6.568 (df = 4) and a probability of 10 to 20% for goodness of fit to the 1:2:1 ratio was obtained. Since only 4 lines were counted for segregation, it is felt that not too much emphasis should be placed on the F_3 study of the heterozygous material of this selection. However, since the 2 F_2 selections gave a Chi-square value of 0.884 (df = 1) and a probability of 30 to 50% for goodness of fit to the 3:1 ratio and since the probability of the line segregation fitting the 1:2:1 ratio was 50 to 70% in the F_3, it may be concluded that the inheritance of the resistant reaction to race group 9 of leaf rust is dependent upon a single recessive factor.

Table 8.—Numbers of susceptible and resistant wheat plants in 4* F_2 heterozygous lines of the cross (Ore x Mediterranean-Hope) x Comanche, inoculated with race group 9 of leaf rust, with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

F_2 Plant Selection No.	Total No. Plants	Observed: Susceptible	Observed: Resistant	Expected: Susceptible	Expected: Resistant	Chi-square	P
3605-3-24	43	35	8	32.25	10.75	0.938	30-50%
-36	40	30	10	30.00	10.00	0.000	100%
-49	27	15	12	20.25	6.75	5.440	1-2 %
-58	28	20	8	21.00	7.00	0.190	50-70%
Total of all lines							

df = 4, Chi-square = 6.568, P = 10-20%

* Counts were made of only 4 of the 21 heterozygous lines because of low infection.

In the selection 3634-1 of the cross (Kanvale-Marquillo x Kanvale-Kenaro) X Comanche, the line segregation in the F_3 was 8 susceptible, 22 heterozygous, and 20 resistant. The Chi-square value of 6.480 (df = 2) and a probability of 2 to 5% was obtained for goodness of fit to the 1:2:1 ratio. The numbers of susceptible and resistant F_3 wheat plants in the 22 heterozygous lines are presented in Table 9. The total of 22 values of Chi-square 91.445 (df = 22) gave a probability of less than 1% for goodness of fit to the 3:1 ratio. This large value of Chi-square may be attributed to the reactions of lines 4, 10, and 30. A possible explanation of these results might be that the samples used in this study were not representative of the population. It is felt that further study with this selection is needed to determine the inheritance of the resistant reaction. In both the F_2 and F_3 of this hybrid, there existed an excess of wheat plants with resistant reactions. There were 28.19% resistant plants in the F_2 and 28.73% resistant plants in the F_3. The Chi-square value of 1.020 (df = 1) obtained for goodness of fit to the 3:1 ratio in the F_2 indicates that between 30 and 50% of the time, resistant wheat plants in the amount of 28.19% of the population would be expected to occur. However, because of the large number of wheat plants classified in the F_3, the probability that 28.73% of the plants would be resistant is less than 1%. At this time no genetic hypothesis is suggested because it is felt that more work with larger numbers of plants is needed before any satisfactory conclusions can be drawn.

Table 9.—Numbers of susceptible and resistant wheat plants in 22 F_3 heterozygous lines of the cross (Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche, inoculated with race group 9 of leaf rust, with numbers expected under the 3:1 hypothesis and values of Chi-square and P.

F_2 Plant Selection No.	Total No. Plants	Observed: Susceptible	Observed: Resistant	Expected: Susceptible	Expected: Resistant	Chi-square	P
3634-1- 4	97	50	47	72.75	24.25	28.457	<1%
- 5	51	39	12	38.25	12.75	0.059	80-90%
-10	53	23	30	39.75	13.25	28.232	<1%
-13	59	45	14	44.25	14.75	0.050	80-90%
-14	55	41	14	41.25	13.75	0.006	90-95%
-16	53	40	13	39.75	13.25	0.006	90-95%
-19	52	38	14	39.00	13.00	0.102	70-80%
-21	48	32	16	36.00	12.00	1.777	10-20%
-22	45	27	18	33.75	11.25	5.400	2-5 %
-24	56	47	9	42.00	14.00	2.380	10-20%
-26	55	39	16	41.25	13.75	0.491	30-50%
-27	53	38	15	39.75	13.25	0.308	50-70%
-29	60	47	13	45.00	15.00	0.355	30-50%
-30	51	30	21	38.25	12.75	7.117	<1%
-33	45	30	15	33.75	11.25	1.666	10-20%
-34	54	38	16	40.50	13.50	0.617	30-50%
-36	57	46	11	42.75	14.25	0.988	30-50%
-39	59	48	11	44.25	14.75	1.271	20-30%
-40	62	41	21	46.50	15.50	2.602	10-20%
-42	72	59	13	54.00	18.00	1.851	10-20%
-45	70	46	24	52.50	17.50	3.219	5-10%
-47	76	49	27	57.00	19.00	4.491	2-5 %

Total for all lines . . . . df = 22, Chi-square = 91.445, P = <1%

A summary of the data on line segregation of the 4 crosses studied in the F_3 for reaction to race group 9 of leaf rust is presented in Table 10. Of the 200 lines studied, 48 were susceptible, 92 heterozygous, and 60 resistant. The Chi-square value of 7.920 (df = 8) and a probability of 30 to 50% were obtained for the goodness of fit to the 1:2:1 ratio. The low probability may be accounted for in the selection 3634-1 as it is the only selection of the 4 studied whose probability of fit to the 1:2:1 ratio was low.

A summary of all segregating material studied in the F_2 and F_3 for reaction to race group 9 of leaf rust shows that of a total of 5164 plants, 3850 were susceptible and 1314 were resistant. The Chi-square value of 0.546 (df = 1) and a probability of 40 to 50% for goodness of fit to the 3:1 ratio was obtained. This offers additional evidence that the inheritance of the resistant reaction to race group 9 of leaf rust is dependent upon a single recessive factor pair.

In the F_3, all progenies and the two parents studied for reaction to race groups 12 and 45 of leaf rust were susceptible. As a result of these reactions, the inheritance study with regard to race groups 12 and 45 was terminated. An explanation for the complete susceptible reactions of the F_3 material that definitely segregated in the F_2 for reactions to race groups 12 and 45 might be that of the "X" type reaction. Previous unpublished work at the Oklahoma Agricultural Experiment Station shows that the resistant parent, Cimarron, has exhibited susceptible and "X" type reactions to race groups 12 and 45. When studying the F_2, Cimarron exhibited resistant reactions to race groups 12 and 45. Chester (2) states, "The type 'X' reaction has 3 possible interpretations: (a) that it is an environmentally-conditioned irregularity; (b) that it is due to genetic instability of fungus or host, not primarily conditioned by environment; and (c) that in some cases it may

Table 10.—Numbers of susceptible and resistant lines of wheat in 4 F_3 hybrid progenies, inoculated with group 9 of leaf rust, with numbers expected under the 1:2:1 hypothesis and values of Chi-square and P.

Selection No.	Total No. Lines	Observed: Susceptible	Observed: Heterozygous	Observed: Resistant	Expected: Susceptible	Expected: Heterozygous	Expected: Resistant	Chi-square	P
3609-1	50	13	24	13	12.50	25	12.50	0.080	95-98%
3629-1	50	13	25	12	12.50	25	12.50	0.040	99%
3605-3	50	14	21	15	12.50	25	12.50	1.320	50-70%
3634-1	50	8	22	20	12.50	25	12.50	6.480	2-5 %
Total	200	48	92	60	50	100	50		

Total for all selections . . . . df = 8, Chi-square = 7.920, P = 30-50%

be merely the result of an unrecognized mixture of 2 or more races in what was supposed to be a pure race culture." Another explanation might be that the source of rust used in the two studies was different. The reactions on the differential varieties of the rust used for race groups 12 and 45 in the F_2 were the same as the reactions of race groups 12 and 45 of Chester (2). The same was true for the race groups of rust used in the F_3, however, the physiologic races used in the F_2 and F_3 were not the same. It might be concluded that the gene or genes responsible for the resistance to one physiologic race are not necessarily responsible for resistance to all physiologic races that have been placed in that race group. Since the amount of data on hand is limited, no conclusions are made as to the mode of inheritance of reaction to race groups 12 and 45.

SUMMARY

An experiment to determine the mode of inheritance of reaction in certain crosses of winter wheat to race groups of leaf rust was conducted in the greenhouse at the Oklahoma Agricultural and Mechanical College in 1947 and 1948.

Segregation to race group 9 of leaf rust was exhibited by the following 7 selections: 3609-2 and 3609-5 of the cross (Mediterranean-Hope x Pawnee) X Comanche; 3605-1 and 3605-2 of the cross (Oro x Mediterranean-Hope) X Comanche; 3630-1 and 3630-2 of the cross (Kawvale-Marquillo x Kawvale-Tenmarq) X Cheyenne; and 3634-1 (Kawvale-Marquillo x Kawvale-Tenmarq) X Comanche. A combined Chi-square value of 8.086 (df = 7) and a probability of 30 to 50% for goodness of fit to a 3:1 ratio was obtained for these 7 selections. This indicates that in these 7 selections the mode of inheritance for the resistant reaction is dependent upon a single recessive factor pair.

In the 3 selections of the cross (Mediterranean-Hope x Pawnee) X Cimarron studied for reaction to race groups 12 and 45 of leaf rust, Chi-square values for goodness of fit to the 3:1 ratio showed probabilities of less than 1%. Since the numbers obtained did not fit any known genetic ratio, and only one year's data are available, no conclusions are made as to the mode of inheritance of reaction to race groups 12 and 45.

Fifty lines of each of 4 crosses were studied in the F_3 to determine the mode of inheritance of reaction to race group 9 of leaf rust. The Chi-square value and probability for goodness of fit to the 1:2:1 ratio for the 4 selections are as follows:

Cross	Selection No.	Chi-square	P
(Mediterranean-Hope x Pawnee) X Comanche	3609-1	0.080	95-98%
(Kanvale-Marquillo x Kanvale-Tenmarq) X Cheyenne	3629-1	0.040	99%
(Ore x Mediterranean-Hope) X Comanche	3605-3	1.320	50-70%
(Kanvale-Marquillo x Kanvale-Tenmarq) X Comanche	3634-1	6.480	2-5 %
Total for all crosses . . . . df = 8.		7.920	30-50%

The combined Chi-square value of 7.920 and a probability of 30 to 50% for all crosses indicate a fair fit to the 3:1 ratio. It may be concluded that in these 4 crosses the mode of inheritance of the resistant reaction to race group 9 of leaf rust is dependent upon a single recessive factor pair.

All selections of the cross (Mediterranean-Hope x Pawnee) X Cimarron studied for reactions to race groups 12 and 45 of leaf rust were completely susceptible in the F_3. These same selections did, however, segregate in the F_2 for reactions to race groups 12 and 45. Two explanations are offered for these results; (a) that the reactions exhibited by this cross to race groups 12 and 45 was the "T" type and (b) that the source of rust used in the 2 studies was different. Since segregation did not appear in the F_3, no conclusions are made as to the mode of inheritance of reaction to race groups 12 and 45 of leaf rust.

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