INHERITANCE OF RESISTANCE IN WHEAT

TO STEM RUST - RACE 15B

by

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INTRODUCTION

For the areas where wheat stem rust (*Puccinia graminis tritici*, Erikss. and Henn.) has been, and may be, prevalent, the importance of rust resistant varieties cannot be over-emphasized. Although severe epidemics have occurred only periodically, yet the disease has been present every year with varying amounts of damage. According to Greaney (9) the average annual loss in wheat between 1925 and 1935 for Manitoba and Saskatchewan was calculated to be 35.5 million bushels, constituting a cash loss through reduction in yield alone of 30.8 million dollars for each year of this period. Losses for specific years have at times reached gigantic proportions: Craigie (4) stated that in Western Canada in 1916 there was a loss of 170 million dollars from reduction in wheat production and of 64 million dollars from reduction in grade, making a total monetary loss of 234 million dollars.

The development of rust resistant varieties has been invaluable in decreasing losses. In the development of these varieties, the plant breeder has to take into consideration, among other factors, physiologic specialization of rust and physiologic resistance of parent material.

There are many known physiologic races of stem rust. Recently, biotypes in some of these races have been identified. New physiologic races or biotypes may arise on the barberry through hybridization between existing races (Garcia-Rada *et al.* (6)).

Biotype B of Race 15 has recently been identified in several stem rust collections from different parts of the United States, but has not as yet been isolated in Canada. Hart (14) reports Race 15B as being virulent under Minnesota conditions and many of the varieties used there as rust resistant parents are moderately to highly susceptible to it. She emphasizes the possible economic danger of this Race:

> "If biotype B of race 15 once becomes established in the Mississippi Valley, which is not at all improbable, it may be very destructive to many of the new winter-wheat hybrids, to all spring-wheat varieties now grown commercially, to most of the newer varieties and hybrids of hard red spring wheat, and to the new durum varieties. Susceptible hosts would be well distributed over the entire central and northern parts of the Mississippi Valley. With an increase in inoculum of race 15B and with a wide distribution of susceptible wheats, it would be necessary to rely chiefly on enviromental factors for the prevention of future stem-rust epidemics until resistance to race 15B could be incorporated into other desirable wheats."

Craigie (5) points out that there is a similarity year by year in the amount of infection and in the physiologic races present in Western Canada and in the Northern Mississippi Valley. This, as he states, indicates strongly that the bulk of the wind-borne inoculum originates in the latter area.

In view of the situation as discussed above, the present study was undertaken to determine the mode of inheritance of resistance in the seedling stage to Race 15B of some of the parental varieties currently used by the Dominion Laboratory of Cereal Breeding and the Dominion Laboratory of Plant Pathology, Winnipeg, Manitoba.

REVIEW OF LITERATURE

Owing to its recent discovery, very little information is available concerning biotype B of Race 15.

Stakman *et al.* (28) mention that two biotypes of Race 15 have been found, one of which, differentiated by Rival, attacks certain Kenya wheats and Thatcher. Loegering and Stakman (19) refer to the two biotypes as Races 15A and 15B. Race 15A has been found in Japan and the United States while 15B commonly occurs in South America and is not uncommon in the United States.

Literature from South America indicates that the South American Race 15 differs from Race 15 described by Stakman and Levine (27), but biotypes are not mentioned.

Sixty varieties of wheat were sent to Peru from the United States and studied under field conditions by Abbott (1), and all were found to be very susceptible to stem rust. The physiologic form mainly responsible for infection fitted the description of Race 15 except that the infection on Khapli was heavy instead of light and it therefore was not considered as identical with Race 15.

Garcia-Rada *et al.* (6) isolated Race 189 in South America, describing it as the most virulent of all races. They suggest that it might have been the Race described by Abbott (1). However, Yadlin (34) and Vallega (29) report Race 15 as being the most prevalent Race in South America.

Watson (32) using inoculum of Race 15 from three sources (Brazil, Japan, and the United States) found differences in infection type. The inoculum from Japan and the United States produced one type of reaction whereas the inoculum from Brazil, more virulent, produced a different reaction.

Hart (13) found Triticum timopheevi, Zhuk., susceptible in the seedling stage to 15B which, in view of the findings of Newton et al. (24), indicates that 15B is different from the Canadian Race 15.

The problem confronting plant breeders with the advent of 15B is discussed by several authors. Hart (14, 15) working with recently developed rust resistant varieties and hybrids which include Apex, Renown, Regent, McMurachy, H-44-24 derivatives and Iumillo derivatives, found that no variety in this group had seedling resistance to 15B. In the mature plant stage, most of the varieties and hybrids were moderately to highly susceptible.

Ausemus (2) reports that Hope, Thatcher, some Kenya varieties and T. timopheevi are susceptible to 15B in both the seedling and mature plant stage. Red Egyptian, on the other hand, has moderate resistance. Loegering (20) also mentions Red Egyptian as showing some resistance to 15B.

The resistance or susceptibility of varieties to Race 15B, as reviewed above, need not be considered as an indication of what will happen under the climatic conditions of Manitoba. Johnson and Newton (18) have pointed out occasional differences in results obtained at St. Paul, Minnesota, and at Winnipeg, Manitoba. In the same paper they showed that mature plant resistance may break down under conditions of high temperature (about 80 degrees F.). The response of seedlings in most cases resembled that of the mature plants with respect to the effect of temperature.

Breakdown in resistance due to high temperature was also reported by Newton et al. (24) and Peterson et al. (25).

That a variety may vary somewhat from time to time in its reaction to a particular physiologic race, due to changes in enviromental conditions such as light, temperature, and humidity, was shown by Newton et al. (23), Hart and Forbes (11), Hart and Zaleski (12), and Watson (31).

The work of Cassell (3) as reported by Watson (33) has demonstrated very clearly that certain races of stem rust are aggressive at high temperatures, others thrive on their hosts at low temperatures, while still others seem to be adapted to a wide range of temperature conditions.

The effect of enviroment on the percentage of infection may be of considerable importance. Under greenhouse conditions, even with artificial illumination, Neatby (21) found that infection sometimes failed to take place on all seedlings. Hart and Forbes (11) obtained a higher degree of infection in light than in darkness but in no case did they obtain 100 per cent infection. They used seven varieties of wheat and two races of stem rust, obtaining a range in percentage of infection from 54.8 per cent to 90.1 per cent under light.

Watson (32) was able to obtain satisfactory segregation for resistant, segregating, and susceptible F_3 lines under greenhouse conditions.

Reference to resistance or susceptibility of the varieties used in this thesis (as listed under "Materials and Methods") will now be briefly reviewed.

Newton et al. (24) and Peterson et al. (25) describe McMurachy and Kenya as practically immune, except when grown under abnormally high temperatures, to all physiologic races of stem rust to which the two varieties had been exposed (about 20 races). This applied to both seedling and mature plants.

Yadlin (34), testing a number of varieties of wheat with a mixture of Chilean physiologic races in which the South American Race 15 was predominant, found Red Egyptian and McMurachy to be immune while Kenya and Hope were susceptible. H-44-24 was not included in the test but the reaction of Hope may be taken as indicative of that of H-44-24.

Johnson and Newton (18), in a greenhouse study, found McMurachy, Kenya, Red Egyptian, N.A. 95, and Iumillo either immune or resistant to Races 15, 29, and 56 in both seedling and the mature plant stage. Minor was found to be more susceptible in the seedling stage than in the mature plant stage. Marquis was susceptible in every test.

Goulden *et al*. (7), in a study of an H-44-24 x Marquis cross, showed that mature plant resistance was inherited independantly of seedling resistance. H-44-24 was susceptible in the seedling stage and resistant in the mature plant stage.

In general, seedling resistance is normally indicative of resistance in the fully grown plant. The correlation between the two is borne out by the findings of Harrington and Smith (10), Neatby (22), Waddell (30), and Peterson *et al*. (25). On the other hand, seedling susceptibility may not necessarily be indicative of mature plant reaction. Mature plant resistance has been demonstrated by Goulden *et al*. (7), Hayes and Aamodt (16), Hayes *et al*. (17), and Neatby (21).

MATERIALS AND METHODS

Varieties and Hybrids

The varieties of wheat (*Triticum vulgare*, Vill.) and the hybrids used were a part of material grown at the Dominion Laboratory of Cereal Breeding, Winnipeg, by Peterson *et al** in a study on the inheritance of resistance to races of stem rust commonly occurring in Canada.

The varieties selected as parents are listed with their Canadian Accession Numbers and the Accession Numbers of the Dominion Laboratory of Cereal Breeding.

Variety 'Thesis designation'	C.A.N.**	R.L.No.***
Kenya	1961	1373
McMurachy	1913	1313
Marquis	1396	84
Red Egyptian	3533	2061
Minor	3534	2058
N.A. 95	3532	2063
H-44-24	1352	229
R.L. 1544	3539	1544

Kenya is one of five Kenya varieties received in 1934 from the Department of Agriculture at Nairobi, Kenya Colony. It is described as rust resistant. McMurachy was received in 1935 from Mr. M. S. J. McMurachy,

* Unpublished data by R. F. Peterson, A. B. Masson and L. H. J. Shebeski, a brief review of which is given under the section "Previous Studies".

** Canadian Accession Number.

*** Dominion Laboratory of Cereal Breeding Accession Number.

a farmer near Strathclair, Manitoba. Mr. McMurachy discovered it about the year 1930 as a single rust-free plant in a field of Garnet wheat. He increased it, and when he found that it withstood the rust epidemic of 1935 he brought it to the attention of the staff of the Dominion Laboratory of Cereal Breeding, Winnipeg. Marquis was originated by cerealists of the Dominion Department of Agriculture at the Central Experimental Farm, Ottawa, from a cross between Hard Red Calcutta and Red Fife. It is susceptible to the common races of stem rust. Red Egyptian, Minor, and N.A. 95 were part of S. L. Macindoe's collection of rust resistant varieties brought to this continent from New South Wales and received at the Dominion Laboratory of Cereal Breeding in 1940. H-44-24 was selected by E. S. McFadden from a cross between Yaraslov Emmer and Marquis. It is generally susceptible in the seedling stage but has mature plant resistance to the races of stem rust commonly found in Canada. R.L. 1544 was developed at the Dominion Laboratory of Cereal Breeding, Winnipeg, as a product of a Marquis x Iumillo cross wherein an attempt was made to transfer the Iumillo resistance to vulgare wheats. Peterson and Love (26) reported that the immunity of Iumillo was closely approximated though not fully achieved.

Excluding Kenya, diallel crosses of the remaining parent varieties were studied in the F_2 generation with respect to their resistance to Race 15B.

The choice of crosses used in the F_3 generation study was governed by the results of the preliminary study of parents and F_2 hybrids. The crosses actually studied may be divided into groups in the order in which they were studied:

1. Marquis x McMurachy
   Marquis x Kenya
   McMurachy x Kenya

2. Marquis x Red Egyptian
   McMurachy x Red Egyptian

3. Marquis x Minor
   McMurachy x Minor

4. Marquis x R.L. 1544
   McMurachy x R.L. 1544

Forty random lines of each of the crosses listed were tested for their reaction to 15B and to a mixture of inoculum of common races. Parental varieties concerned were included in the tests.

Varieties and hybrids were grown under normal greenhouse conditions. Seed was sown in six inch porous earthenware pots, which had been filled with a soil mixture composed of three parts local black loam and one part sand. The amount of seed sown was 30 seeds for each of the parents, 120 for each of the F_2 crosses, and approximately 32 for each of the F_3 lines. These amounts are in excess of what was deemed sufficient by Neatby (21).

The various tests were made over a period of time extending from the 29th of September, 1945, to the 16th of February, 1946. The range in temperature for each of the tests varied slightly, but in no case reached the point where a breakdown of resistance could be expected. Artificial light was not used.

Inoculum

As mentioned previously, Race 15B has not been isolated in Canada. However, the Dominion Laboratory of Plant Pathology obtained a culture from St. Paul, Minnesota, and made available a supply of urediospores. The inoculum of a mixture of common races was also made available. This mixture consisted of the following races: 2, 3, 9, 11, 14, 15, 17, 19, 21, 29, 30, 32, 36, 38, 39, 46, 49, 52, 56, 59, 63, 73, 78, 80, 81, 83, 90, 96, 98, 102, 113, 125, 139, 151, 152, 155, 157, 171, 173, 192 and 193.

Method of Inoculating

Seedlings were inoculated five days to one week after emergence by the finger method. Upon inoculation the pots were placed in incubation chambers (see Figure 1.) for 24 hours. The temperature was then dropped 15 to 20 degrees F. This resulted in condensation of moisture or production of an artificial dew within the chambers. The temperature was then allowed to return to normal greenhouse temperatures.

The finger method of inoculating may be described as follows: Moistened thumb and forefinger were dipped into a 1 : 10 mixture of urediospores and talc. Urediospores were transferred to individual seedlings by passing the first seedling leaf between thumb and forefinger. Talc was used as a base for rust spores to prevent a too heavy use of the limited supply of inoculum.

Method of Classifying

Seedlings were classified approximately two to three weeks after inoculation. By that time the various types of rust reactions were well developed. Types of infection were classified using the symbols of Stakman and Levine (26) as described by Johnson and Newton (18).

Types of Infection

0 Indicates that plants are immune; no uredinia are developed and hypersensitive flecks are usually not present.

0; Plants are immune, no uredinia are developed, but hypersensitive flecks occur. The rust organism has entered the host tissues but the host is so uncongenial that development soon ceases.

1 Plants are very resistant. Uredinia are very small and surrounded by sharp, hypersensitive, necrotic areas.

2 Plants are moderately resistant. The uredinia are small to medium in size; hypersensitive areas present in the form of necrotic halos, surrounding green islands in the centre of which the uredinia are usually located.

3 Plants are moderately susceptible. The uredinia are of medium size, sometimes, but infrequently coalescing. Necrosis and hypersensitiveness are absent but chlorotic areas may surround the uredinia.

4 Plants are very susceptible. The uredinia are large and usually coalesce to form large irregular pustules. Hypersensitive and necrotic areas are absent but chlorotic areas may surround the pustules.

x Plants are heterogeneous in their reaction. All the above reactions may occur together on the same leaf. Certain physiologic forms produce this reaction on some varieties, especially on some of the durum wheats.

Types 0, 0;, 1, and 2 were grouped as resistant whereas types 3 and 4 were grouped as susceptible, as has been done by Stakman and Levine (26). Type-x was not used since the mixture of common races invariably gave type-x reaction. The seedlings that normally would be classified as type-x were classified as the type represented by the largest size pustule present.

Statistical Methods

The Chi-square test for goodness of fit as described by Goulden (8) was used to compare actual ratios obtained with theoretical Mendelian ratios.

Figure 1. Incubation Chambers

PREVIOUS STUDIES

The parental varieties and crosses described in the preceeding section had already been employed by Peterson, Masson and Shebeski to investigate the inheritance of reactions to the various races of stem rust which occur naturally in Canada. Their main findings as shown by unpublished data will now be described.

Random samples of F_1, F_2 and, in some cases, F_3 progeny of the crosses described above were grown along with plots of the parental varieties in the field at Winnipeg for several years under artificially induced epidemics of stem rust involving a large number of physiologic races which had been collected in Canada.

Rust Reaction of Parental Varieties

The typical stem rust reactions of the parental varieties were as follows:

Variety	Reaction
Marquis	susceptible
Kenya	no rust pustules, or a trace
McMurachy	" " " " " "
Red Egyptian	" " " " " "
H-44-24	" " " " " "
Minor	trace to 10%
R.L. 1544	" " "
N.A. 95	trace to 20%, variable

Under exceptional conditions of prolonged high temperatures there was a partial loss of resistance in Kenya and McMurachy.

Crosses Between Resistant Wheats and Marquis

In the crosses Kenya x Marquis, McMurachy x Marquis, and Red Egyptian x Marquis, or reciprocal crosses, the F_1 gave a reaction intermediate between those of the parents but usually resembling more closely the Marquis reaction, so that susceptibility appeared partially dominant. In F_2 approximately one quarter of the plants were as resistant as the resistant parent and Chi-square tests indicated a good agreement with the theoretical 1 : 3 ratio. In F_3 the lines classified as resistant, segregating and susceptible gave satisfactory fits to a 1 : 2 : 1 ratio. It was concluded that there was a main factor pair for resistance in each of these crosses. In exceptional seasons, with prolonged periods of temperature above normal, the partial breakdown of resistance in the F_2 and F_3 derivatives of Kenya and McMurachy made it impossible to classify plants or lines on a Mendelian basis.

Variations in F_3 lines indicated minor factors for resistance in all three crosses and the F_2 distributions supported this hypothesis. Evidence was obtained that the minor factors were not the same in the three resistant parents. They showed the greatest effect in the Red Egyptian crosses and the least in the Kenya crosses.

In the cross H-44-24 x Marquis, mature plant resistance appeared almost completely dominant in F_1 and good 3 : 1 ratios of resistant and susceptible plants were obtained in F_2 showing a single main factor pair for resistance as in earlier studies.

In the crosses Minor x Marquis, N.A. 95 x Marquis, and R.L. 1544 x Marquis, or reciprocal crosses, the F_1 gave rust reactions intermediate between those of the parental varieties. In F_2 no plants were obtained as resistant as the resistant parent; all were intermediate or susceptible in rust reaction. Inheritance of rust reaction appeared more complex than in the crosses involving Kenya, McMurachy, Red Egyptian, or H-44-24, and no outstanding main factor for resistance was indicated. There was evidence that the variety Minor has one or more factors for resistance complementary to one or more so-called minor resistance factors in McMurachy and Red Egyptian or to the main factor when in the heterozygous condition.

Crosses Between Resistant Varieties

In the crosses Kenya x McMurachy and McMurachy x Red Egyptian, F_1, F_2, and F_3 studies showed all progeny to be resistant apart from rare susceptible plants attributed to natural crossing. It was concluded that the main factor for resistance is allelic in the three varieties Kenya, McMurachy and Red Egyptian. In some populations no rust pustules were found, and in others where lines, though resistant, carried some rust, the segregation of minor factors was evident showing that no two of the three varieties have identical sets of minor factors.

Crosses between McMurachy or Red Egyptian as one parent, and Minor, N.A. 95, R.L. 1544, or H-44-24 as the other indicated that none of the four last-named varieties has the main gene for resistance possessed by McMurachy, Red Egyptian, or Kenya since the F_2 populations contained a considerable proportion of susceptible plants.

Crosses between H-44-24 and the various other resistant varieties showed that the main factor of H-44-24 is not possessed by the other varieties.

Diallel crosses of the varieties Minor, N.A. 95, and R.L. 1544 resulted in F_2 populations containing many susceptible plants indicating different sets of genes for resistance in these three varieties.

Greenhouse Tests

F_3 lines of Kenya x Marquis, McMurachy x Marquis, and McMurachy x Kenya, tested in the seedling stage in the greenhouse with the inoculum of mixed physiologic races, gave results in conformity with reactions of mature plants in the field. It was therefore concluded that the main allelic gene for resistance in Kenya, McMurachy, and Red Egyptian is effective at all stages of plant growth.

RESULTS AND DISCUSSION

Rust Reaction of Parental Varieties and F_2 Seedlings.

Table 1 shows the reactions to Race 15B of the parental varieties in the seedling stage. The reactions indicated were typical of the results obtained when parental varieties were used as checks in the F_3 studies.

Table 1. Reaction of Parental Varieties to Race 15B.

Variety	Resistant				Susceptible	
	0	0;	1	2	3	4
Kenya	28					
McMurachy	24					
Red Egyptian	25					
H-44-24						26
Minor	3				24	
R.L. 1544	4					25
Marquis	2					25
N.A. 95	8			18		2

Three varieties, Kenya, McMurachy, and Red Egyptian, were found to be immune under the conditions of this test. H-44-24, Minor, R.L. 1544, and Marquis were susceptible, although Minor only moderately so. The apparently immune seedlings of Minor, Marquis, and R.L. 1544 may be considered as escapes. N.A. 95 appeared to be segregating for rust reaction, showing moderately resistant seedlings, susceptible seedlings, and either a greater percentage of escapes than the susceptible varieties or a few seedlings immune. It was therefore decided to test N.A. 95 for heterogeneity of rust reaction at a later date.

The reason for escapes is not known. All seedlings were inoculated in the same manner and were in the same inoculating chambers. The difficulty of obtaining 100 per cent infection in susceptible varieties has been pointed out in the review of literature (Hart and Forbes (11) and Neatby (21)).

Table 2 lists the crosses studied in F_2 and their reactions in the seedling stage to Race 15B.

Table 2. Reactions of F_2 Seedlings to Race 15B.

Crosses	Resistant	Susceptible
Marquis x McMurachy	27	77
" x Red Egyptian	32	79
" x Minor	10	99
" x R.L. 1544	3	98
" x H-44-24	0	93
" x N.A. 95	64	47
McMurachy x Red Egyptian	112	0
" x Minor	89	23
" x R.L. 1544	66	32
" x H-44-24	34	68
" x N.A. 95	69	31
Red Egyptian x Minor	74	17
" " x R.L. 1544	55	45
" " x H-44-24	31	72
" " x N.A. 95	94	19
Minor x R.L. 1544	22	96
" x H-44-24	10	99
" x N.A. 95	85	30
R.L. 1544 x H-44-24	0	102
" " x N.A. 95	63	43
H-44-24 x N.A. 95	70	38

From the reactions as shown in Table 2, Marquis and H-44-24 may be considered as susceptible varieties with no minor factors for resistance, for when crossed with each other, all F_2 seedlings were susceptible. Likewise, when crossed with Minor or R.L. 1544, and allowing up to 10 per cent for escapes, all seedlings were considered as susceptible.

Minor and R.L. 1544 may be considered susceptible varieties carrying minor factors for resistance which are complementary to each other and which are complementary either to minor factors or to the main factor, in heterozygous condition, in McMurachy or Red Egyptian. The presence of complementary minor factors was indicated when 18.6 per cent resistant F_2 seedlings were observed in the Minor x R.L. 1544 cross, and clearly demonstrated by a comparison of the percentages listed in Table 3.

Table 3. The Percentages of F_2 Seedlings Resistant to Race 15B in Crosses of Susceptible with Resistant Varieties.

Parental Varieties Susceptible x Resistant	Resistant Seedlings Percentage
Minor x McMurachy	79.5
R.L. 1544 x McMurachy	67.5
Marquis x McMurachy	26.0
Minor x Red Egyptian	81.5
R.L. 1544 x Red Egyptian	55.0
Marquis x Red Egyptian	29.0

The data in Table 3 show not only the presence of complementary minor factors in Minor and R.L. 1544 but also that the minor factors of the variety Minor have a greater effect than the minor factors of R.L. 1544.

Reactions of McMurachy or Red Egyptian crossed with the susceptible parents, Marquis and H-44-24, indicate that each of the two resistant parents have one main recessive factor pair for resistance, the reactions approximating very closely the theoretical 1 : 3 ratio. In the McMurachy x Red Egyptian cross, all F_2 seedlings were resistant, indicating that the gene for resistance is allelic in the two varieties.

The resistance of N.A. 95 seemed dominant but the ratio of resistant to susceptible seedlings in the crosses N.A. 95 x Marquis and N.A. 95 x H-44-24 did not conform with the theoretical 3 : 1 ratio expected, considering one dominant main factor pair responsible for resistance. Reactions of N.A. 95 x Minor and N.A. 95 x R.L. 1544 substantiate the previous evidence as to presence of and relative effect of minor factors for resistance in Minor and R.L. 1544.

To study N.A. 95 for heterogeneity of rust reaction, half the seedlings of twenty random lines were inoculated with Race 15B and the other half inoculated with a mixture of common races. The majority of the seedlings showed moderate resistance (type-2 reaction) to Race 15B and to the mixture of common races. Three of the twenty lines were classified as segregating in their reactions to both Race 15B and the mixture of common races. Each of seven additional lines had at least one seedling susceptible to Race 15B. These were also classified as segregating. Therefore, N.A. 95 was considered as heterogeneous in rust reaction.

Since N.A. 95 has only moderate resistance to Race 15B in comparison with the high resistance of McMurachy, Red Egyptian, and Kenya, crosses involving this variety were not studied in F_3.

Rust Reactions of F_3 Lines

In the study of rust reactions of F_3 lines, Marquis was used as the susceptible parent. H-44-24, the other variety found to be fully susceptible in the seedling stage, was omitted from further study.

In classifying F_3 lines as resistant, segregating, or susceptible, a preponderance of segregating lines with a corresponding reduction in number of susceptible lines, was found. This was to be expected, since every susceptible line containing escapes was classified as segregating. Therefore, segregating and susceptible lines were grouped as one infection class. This class will hereafter be referred to, in this thesis, as "Segregating or Susceptible". With the new classification, the expected 1 : 2 : 1 ratio if one main factor pair is involved is changed to a 1 : 3 ratio. Likewise, the expected 7 : 8 : 1 ratio if two main factor pairs are involved is changed to a 7 : 9 ratio.

The first group of crosses listed under "Materials and Methods" for study in F_3 are the diallel crosses of Marquis, Kenya, and McMurachy. Reactions in the seedling stage are summarized in three tables, the Marquis x Kenya cross in Table 4, the Marquis x McMurachy cross in Table 5, and the McMurachy x Kenya cross in Table 6. The data in each of these tables illustrate not only the reactions of the F_3 lines to Race 15B but also the relationship between the reactions to Race 15B and the reactions to a mixture of common races.

Table 4. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross Marquis x Kenya.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	12	-
	Seg. or Susc.	-	28

The approximate 1 : 3 ratio of resistant to segregating or susceptible F_3 lines indicates that the resistance of Kenya either to Race 15B or to the common races is governed by one main recessive factor pair. Test for goodness of fit is given in Table 13. That the resistance of Kenya to Race 15B and to the common races is governed by the same gene is indicated by the identical reactions in each infection class.

Table 5. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross Marquis x McMurachy.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	11	2
	Seg. or Susc.	-	27

The resistance of McMurachy to Race 15B, as shown in the F_2 study, is governed by one main recessive factor pair. The data in Table 5 substantiate the previous findings. Test for goodness of fit of the 11 : 29 ratio obtained to the theoretical 1 : 3 ratio is given in Table 13. The relationship between the reactions to Race 15B and the reactions to the common races, though not perfect as in the Marquis x Kenya cross, indicates strongly that the resistance of McMurachy either to 15B or to the common races is governed by the same gene. There was an insufficient supply of seed to repeat the test on the two lines that were segregating or susceptible to Race 15B and resistant to the common races. The reason for the discrepancy is not known.

Table 6. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross McMurachy x Kenya.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	39	-
	Seg. or Susc.	-	1

In the section "Previous Studies" it was concluded that the main factor pair for resistance to the common races is allelic in McMurachy and in Kenya. The data in Tables 4 and 5 indicate that the gene responsible for resistance to the common races in either resistant parent is the gene responsible for resistance to Race 15B. It could therefore be expected that the main factor pair for resistance in McMurachy and the main factor pair for resistance in Kenya to Race 15B are allelic. The data in Table 6 demonstrate that such is the case. The difference between the 39 : 1 ratio of resistant to segregating or susceptible lines obtained and the 40 : 0 ratio expected may be considered insignificant, for if the main gene for resistance to Race 15B in Kenya were complementary to the main gene for resistance to Race 15B in McMurachy, an approximate 7 : 9 ratio of resistant to segregating or susceptible lines would have resulted.

The line that was classified as segregating or susceptible was probably the result of a natural cross -- a floret of the F_1 McMurachy x Kenya cross being pollinated by a susceptible variety.

The complete agreement between the reactions of the F_3 lines to Race 15B and to the common races substantiates the evidence that in

Kenya or McMurachy the same gene is responsible for resistance both to Race 15B and to the common races.

Reactions of the F_3 lines in the second group of crosses (as listed under "Materials and Methods") are summarized in two tables, the Marquis x Red Egyptian cross in Table 7, and the McMurachy x Red Egyptian cross in Table 8. The data in both tables illustrate the reactions of the F_3 lines in the seedling stage to Race 15B and also the relationship between the reactions to Race 15B and the reactions to the common races.

Table 7. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross Marquis x Red Egyptian.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	9	-
	Seg. or Susc.	-	31

The data in Table 7 indicate that the resistance of Red Egyptian to either Race 15B or to the common races is governed by the one and same gene. The test for goodness of fit between the observed ratio and the theoretical 1 : 3 ratio is given in Table 13.

Table 8. Number of F_3 Lines in the Seedling Stage in each Infection Class of Race 15B and the Common Races in the Cross McMurachy x Red Egyptian.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	40	-
	Seg. or Susc.	-	-

The data in Table 8 substantiate the former observation that the main gene for resistance is allelic in McMurachy and Red Egyptian, and is responsible for resistance both to Race 15B and the common races.

The last two groups of crosses, as listed under "Materials and Methods", are tested in the same manner as the first two groups were. Marquis is used as the known susceptible variety and McMurachy as the known resistant variety in crosses with Minor and R.L. 1544. The data for each of the crosses illustrate the reactions of the F_3 lines in the seedling stage to Race 15B and also the relationship between the reactions to Race 15B and the reactions to the common races.

Table 9. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross Marquis x Minor.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	-	8
	Seg. or Susc.	-	32

In the Marquis x Minor cross, no F_3 lines were resistant to Race 15B. This supports the results of the study of parental varieties and F_2 seedlings.

Minor is resistant to the common races under the enviromental conditions of this test. This was indicated by the resistance of the seedlings in the check pots of Minor and also by the approximate 1 : 3 ratio of resistant to segregating or susceptible F_3 lines.

Table 10. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross McMurachy x Minor.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	10	11
	Seg. or Susc.	-	19

The ten F_3 lines that are resistant to Race 15B may be considered as having obtained their resistance from McMurachy, although it is possible that the complementary minor factors of Minor and McMurachy may have had a slight effect. The test for goodness of fit, assuming the monofactorial hypothesis, is given in Table 13.

In each of the thirty lines, segregating or susceptible to Race 15B, there was a great deal of variation among the individual seedlings as to type of infection. A typical example is as follows:

Line No. 33:

Infection Type -	0	0;	1	2	3	4
No. of Seedlings -	7	5	2	1	8	10

The variation in infection types indicates the presence of minor factors that are complementary to each other in the two varieties, or minor factors of Minor complementary to the main factor of McMurachy when heterozygous for resistance. This substantiates the findings in the study of F_2 seedlings.

The eleven F_3 lines that were resistant to the common races and segregating or susceptible to Race 15B may be considered as having obtained most of their resistance from Minor, and possibly a small percentage of the resistance from the effect of the complementary minor factors of McMurachy and Minor.

Table 11. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross Marquis x R.L. 1544.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	-	1
	Seg. or Susc.	-	39

All F_3 lines of the Marquis x R.L. 1544 cross were susceptible to Race 15B, which was to be expected since both parents were known to be susceptible to this race.

The seedlings of R.L. 1544, used as a check in this test, were resistant to the common races. However, only one F_3 line was found to be resistant to the common races. It may be assumed that there is no main gene for resistance in R.L. 1544, and that the inheritance of rust reaction to the common races is complex.

Table 12. Number of F_3 Lines in each Infection Class of Race 15B and the Common Races in the Cross McMurachy x R.L. 1544.

		Race 15B	
		Resistant	Seg. or Susc.
Common Races	Resistant	8	7
	Seg. or Susc.	-	25

An approximate 1 : 3 ratio of resistant to segregating or susceptible F_3 lines to Race 15B was obtained. The resistant lines may be considered as having obtained their resistance from McMurachy. Test for goodness of fit is shown in Table 13. In each of the thirty-two F_3 lines segregating or susceptible to Race 15B, there was a considerable amount of variation among the seedlings as to infection type. This was interpreted as further evidence of the presence of complementary minor factors for resistance in McMurachy and R.L. 1544. The variation among the seedlings of the McMurachy x R.L. 1544 cross was not as pronounced as the variation among the seedlings of the McMurachy x Minor cross, indicating fewer or less important modifying genes in R.L. 1544 as compared with Minor.

There were seven F_3 lines segregating or susceptible to Race 15B and resistant to the common races. This may seem high in comparison with the single F_3 line that was resistant to the common races in the Marquis x R.L. 1544 cross. Taking into consideration the presence of complementary minor factors for resistance in McMurachy and R.L. 1544, it is highly probable that the resistance of the seven F_3 lines may, to a great extent, be due to the effect of the complementary minor factors in the two varieties.

It has been pointed out that for each of the crosses, Marquis x Red Egyptian, Marquis x Kenya, Marquis x McMurachy, McMurachy x Minor, and McMurachy x R.L. 1544, the F_3 data indicate that resistance to Race 15B is governed by one main recessive factor pair, the observed frequencies closely approximating the theoretical 1 : 3 ratio. The monofactorial hypothesis is tested by the Chi-square test for goodness of fit as shown in Table 13.

Table 13. Test for Goodness of Fit of Observed and Theoretical Frequencies, Assuming Resistance to Race 15B to be Governed by a Single Recessive Factor Pair.

Cross	Observed		Calculated		Chi-square	P
	Res.	Seg. or Susc.	Res.	Seg. or Susc.		
Marquis x Kenya	12	28	10	30	0.533	0.48
Marquis x McMurachy	11	29	10	30	0.133	0.73
Marquis x Red Egyptian	9	31	10	30	0.133	0.73
McMurachy x Minor	10	30	10	30	0.000	1.00
McMurachy x R.L. 1544	8	32	10	30	0.533	0.48

The fit in each of the five tests is quite good, the evidence supporting the single recessive factor pair hypothesis.

SUMMARY AND CONCLUSIONS

F_2 and F_3 progeny of various wheat crosses involving eight parental varieties were studied to investigate the inheritance of resistance in the seedling stage to Race 15B.

The typical seedling reactions of the parental varieties were found to be as follows:

Variety	Reaction
Kenya	Resistant
McMurachy	"
Red Egyptian	"
Minor	Moderately susceptible
H-44-24	Susceptible
R.L. 1544	"
Marquis	"
N.A. 95	Moderately resistant, variable

In the crosses Marquis x McMurachy, McMurachy x H-44-24, Marquis x Red Egyptian, and Red Egyptian x H-44-24, approximately one quarter of the seedlings were resistant. In the F_3 study of the crosses Marquis x McMurachy, McMurachy x Minor, McMurachy x R.L. 1544, Marquis x Red Egyptian, and Marquis x Kenya, the ratio of resistant to segregating or susceptible lines gave satisfactory fits to the theoretical 1 : 3 ratio. It was concluded that the resistance of each of the three varieties, Kenya, McMurachy and Red Egyptian, to Race 15B is governed by one main recessive factor pair.

The agreement between the reactions to Race 15B and the reactions to the common races in the F_3 lines of the crosses Marquis x McMurachy, Marquis x Red Egyptian, Marquis x Kenya, McMurachy x Red Egyptian, and McMurachy x Kenya, indicates that in each of the varieties, Kenya, McMurachy and Red Egyptian, one gene governs the resistance both to Race 15B and to the common races.

In the crosses McMurachy x Kenya and McMurachy x Red Egyptian, all progeny were resistant apart from the few susceptible seedlings of one F_3 line attributed to natural crossing. It was concluded that the gene for resistance is allelic, and could quite possibly be identical, in the three varieties, Kenya, McMurachy and Red Egyptian.

The F_2 study of crosses involving N.A. 95 indicates that in this variety moderate resistance is partially dominant. Since N.A. 95 has only moderate resistance to Race 15B in comparison with the simply inherited high resistance of McMurachy, Kenya or Red Egyptian, F_3 studies involving this variety were not made.

Minor and R.L. 1544, although susceptible to Race 15B, were found to have minor factors for resistance complementary to each other and complementary to minor factors in McMurachy and Red Egyptian. This was demonstrated in the F_2 studies and the evidence supported by the observations made in F_3. The results indicated that R.L. 1544 has fewer or less important modifying genes than Minor.

F_2 studies of the crosses involving the susceptible varieties, Marquis and H-44-24, indicated that these varieties have no appreciable major or minor factors for resistance complementary to factors for resistance in the other parental varieties studied.

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