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CONTENTS

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LEAF RUST OF WHEAT is a disease caused by the fungus *Puccinia rubigo-vera tritici* (Erikss.) Carleton, which may cause heavy losses from year to year. In 1938 the estimated total loss in the United States from leaf rust of wheat was more than 100,000,000 bushels *(6)*[3], which represents nearly 11 per cent of the wheat production for that year.

Thatcher wheat has been grown widely in the spring wheat area of the United States and Canada since it was released in 1934. In 1939 Thatcher occupied 41.6 per cent of the total hard red spring wheat acreage of this country, being grown on 5,524,631 acres [see Clark and Bayles *(7)*]. By 1949 its acreage had decreased to 3,370,823 acres or only 19.1 per cent of the hard red spring wheat acreage, due to its susceptibility to leaf rust. Apparently, where leaf rust has not been a problem, as in Montana, Colorado, Wyoming, and Canada, the acreage of Thatcher wheat increased. In 1949 the total estimated acreage for Thatcher in the United States and Canada was 18,708,000 acres.

The only practical way of controlling leaf rust today is by the use of resistant varieties.

Inheritance studies of disease reaction provide fundamental information for scientific breeding for disease resistance. The purpose of the present study was to determine the mode of inheritance of leaf rust reaction in a cross of Thatcher, which is susceptible to most of the prevalent races, with Premier x Bobin-Gaza-Bobin Nursery Stock No. II-39-2. The latter is resistant in the seedling stages to 33 of the prevalent races and is susceptible, so far as tested, only to race 129.

[1] From a thesis submitted by the senior author to the faculty of the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writers express appreciation to Dr. H. K. Hayes, former head, Department of Agronomy and Plant Genetics, University of Minnesota, for his suggestions during the course of the investigation and in preparation of the manuscript; to Dr. E. C. Stakman, head of the Department of Plant Pathology and Agricultural Botany, and to Dr. M. N. Levine, pathologist of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture, for providing the rust races and for aid in reading the rust reactions.

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[3] Numbers in parentheses refer to Literature Cited, page 34.

Review of Literature

INHERITANCE OF LEAF RUST REACTION

Mature Plant Reaction in the Field

EXTENSIVE STUDIES on the inheritance of leaf rust reaction using Kanred and Malakof wheats as resistant parents crossed to a number of susceptible varieties were conducted by Mains *et al. (21).*

They found in the F_1 generation of various crosses that susceptibility behaved as a dominant, intermediate, or recessive character in different crosses. In the F_2 generation of certain crosses it was impossible to determine the number of genetic factors involved in the segregation. This was explained by the fact that the material was grown at several locations where different leaf rust races and environmental conditions occurred. No attempt was made to formulate a factorial analysis of these results because of the many factors involved. However, they stated that it seemed possible that strains of wheat may be developed in which the various factors could be combined and thus provide resistance to all physiologic races of rust.

Adams *(2)* used Hope wheat as a resistant parent in crosses with three susceptible varieties. His F_3 generation field data showed that a one factor pair hypothesis could be used to explain the results in two of the crosses. However, the number of F_6 lines was very small. He did not explain his results on a factorial basis because of complicated conditions of soil, climate, time of maturity, and mixture of physiologic races. He concluded that segregation had occurred and that leaf rust reaction was inherited.

Hayes, *et al. (11)* studied F_3 lines of H44 x (Marquis x Kota N.S. No. II-19-167) and H44 x Double Cross N.S. No. II-21-28 or Thatcher. It appeared rather easy to recover the type of resistance of the H-44 parent, but no definite conclusion was drawn regarding the number of genetic factors involved.

Wismer *(28)* studied F_4 lines of Oro x Tenmarq wheats. Oro was highly susceptible, while Tenmarq was only moderately susceptible. Transgressive segregation was observed since some of the F_4 lines were more resistant than the Tenmarq parent. He concluded that both parents carried factors for resistance and that inheritance of leaf rust resistance in this cross can probably be best explained on a multiple factor basis.

Gorlatch *(8)* in crosses of line 037, a resistant Ukraine line, with certain susceptible lines found that susceptibility was dominant, recessive, or intermediate in the F_1 generation, depending on the cross involved. One and two factor pair segregations were observed in the F_2 generations of different crosses.

Macindoe *(18)* found the F_1 generation of Kenya-Gular x Argentine wheat crosses to be intermediate in field reaction with a one factor pair segregation in the F_2 population. Kenya-Gular was resistant and Argentine was susceptible. The same segregation was obtained in crosses of Kenya-Gular with Uruguay and K33 wheats.

Wells and Swenson *(27)* studied F_2, F_3, and F_4 progenies of the cross of H44-Reward-Baring with Hard Federation-Dicklow wheat under artificial epidemics produced with four prevalent races. H44-Reward-Baring was the resistant parent. They concluded that a single gene pair appeared to govern the reaction to leaf rust in this cross.

Abbasi *(1)* found a one factor pair segregation in the F_3 progeny of Premier x Kenya Rust Laboratory No. 1373. The F_1 plants were like the moderately resistant Premier parent, indicating dominance of resistance. The Kenya parent was susceptible.

Swenson *et al. (23)* obtained resistant F_2 plants and F_3 lines from the cross of two susceptible parents, Thatcher and Triunfo. Their results were explained by two complementary dominant genes, one from each parent.

Koo and Ausemus *(16)* studied F_3 lines of the Timstein x Thatcher, Timstein x Newthatch, and Timstein x Mida crosses in two consecutive years. They found a one factor pair segregation for each of the three crosses. Timstein was the resistant parent, and the behavior of parents and progeny was the same in both years.

Wu *(29)* studied the F_1, F_2, and F_3 generations of a Lee x Mida cross, the mature plants being inoculated with a collection of leaf rust races in the field. He found that the resistance of Lee was differentiated from the susceptibility of Mida by two pairs of independently inherited genes. These genes were additive in effect, and susceptibility was partially dominant.

Unrau *(24)* reported a one factor pair segregation for leaf rust reaction in crosses of Federation 41 with 17 different monosomic lines of Chinese Spring, indicating that none of these carried the gene under study. The chromosomes not tested by him were XII, XIII, XIV, and XXI.

Hashim *(9)* found that the resistance of Frontana was differentiated from the susceptibility of Thatcher by a single factor pair, resistance being dominant. In the Frontana x Newthatch cross, he explained the resistance of Frontana as being due to duplicate factors. The different results from these two crosses were explained by assuming that Thatcher carries a factor for resistance that is closely linked with a specific dominant inhibitor for that resistance, the linkage being so close that the crossovers do not seriously disturb the 3:1 ratio.

Seedling Reaction to Individual Races

Mains *et al. (21)* found single factor pair segregations in crosses involving Malakof, Kanred, Webster, Norka, and other wheats. They used leaf rust races 1, 3, 5, 9, 11, and 12. Resistance was dominant, intermediate, or recessive, depending upon the parents and races involved. The resistance of Malakof to race 12 and that of Norka to race 5 were determined by simple independent genetic factors. The authors emphasized the significance of obtaining segregates that were resistant to more races than was either parent.

Mains *(19)* obtained a one factor pair segregation in the F_2 progeny of a Norka x Ceres cross inoculated with race 3 of leaf rust. The resistance of the Norka parent was dominant.

Waterhouse *(25)* used the Australian leaf rust race 1 to study progenies of resistant Thew crossed to susceptible Canberra, Federation, Riverina, and Gluyas wheats. In all cases he obtained single factor pair segregation with resistance dominant.

Caldwell and Compton *(5)* used races 9, 31, 65, 78, 79, 80, 101, and 110 to test F_3 lines and bulk F_4 progenies of the cross Wabash x Michigan Amber. Wabash was resistant and Michigan Amber was susceptible. Their data indicated a monogenic inheritance of reaction to these leaf rust races with susceptibility dominant. Each line gave the same reaction to all eight races used. These results showed that the same gene controlled the resistance, or type *X* reaction, of the Wabash parent.

Wu *(29)* studied F_4 progenies from randomly selected F_3 lines of the cross Lee x Mida. Two linked factors with a recombination value of 21 ± 2.7 were found to govern the resistance of Lee to races 126 and 5. One factor behaved as a recessive and the other as a dominant. The parents were highly resistant to race 9. In the progeny of the cross there were moderately resistant segregates which were explained on the basis of different factors for resistance being carried by each parent.

Hashim *(9)* studied the F_2 and F_3 generations of Thatcher x Frontana and Newthatch x Frontana. Using race 126 from Kansas, he obtained a 13:3 segregation in the F_2 generation and a 7:8:1 breeding behavior in the F_3 lines. These ratios were explained as the result of the interaction of a dominant factor for resistance from Frontana with a dominant factor for susceptibility from Thatcher, the latter being epistatic to the factor for resistance in Frontana. Duplicate factors for susceptibility were postulated for the Thatcher x Frontana cross, using races 9, 11, 15, and 126 from St. Paul, Minnesota. When race 9 was used on the Newthatch x Frontana cross, a three factor pair hypothesis was postulated, any four of these six dominant factors giving resistance. With race 126, the progeny of the latter cross gave a one factor pair segregation with susceptibility dominant.

Comparison of Seedling and Mature Plant Resistance

Mains *et al.* *(21)* studied the reaction to race 9 of F_1, F_2, and F_3 progenies of Fulcaster x Kanred in the seedling, shooting, and heading stages. The F_1 seedlings were somewhat more resistant than the susceptible Kanred parent, while in the shooting and heading stages they developed more resistance and were classified as intermediate in reaction. Heterozygous F_2 plants became progressively more resistant in successive stages of development to the point of changing the ratio from 3 susceptible:1 resistant in the seedling stage to almost 1:3 respectively in the shooting stage. The F_3 segregating lines also showed the apparent change of dominance from suceptibility toward resistance. Homozygous resistant and susceptible lines also showed a general tendency to become more resistant as they grew older, although the changes were less marked than in the heterozygous plants.

Swenson *et al.* *(23)* found that resistance in the field in certain F_3 lines of Thatcher x Triunfo was of the mature plant type. Seedlings of lines that were classified in the field as being either resistant, segregating, or susceptible were then tested in the greenhouse to races 6 and 20, which were found to be prevalent in the field. All lines were susceptible to these races in the greenhouse.

On the basis of reaction in the seedling and mature plant stages to a number of leaf rust races, Newton and Johnson *(22)* classified nine wheat varieties into three groups. In one group, they included Regent and Renown which showed only mature plant resistance to all races tested. Thatcher, Apex, Marquis, Reward, and Kenya R.L. 1373 made up group 2, which was characterized by mature plant resistance to only certain races. In the third group they listed McMurachy as susceptible and Warden-Hybrid-English as resistant in the seedling and mature plant stages.

In F_3 and F_4 progenies of a Lee x Mida cross, Wu *(29)* found association between seedling reaction to races 5, 9, and 126 and mature plant reaction to a collection of races in the field.

In the Thatcher x Frontana cross, Hashim *(9)* found association between seedling reaction to races 126, 11, and 15 and mature plant reaction to a collection of races in the field. In the same cross, seedling reaction and mature plant reaction to race 9 were inherited independently. Some lines were resistant to race 126 in the seedling stage but susceptible to it in the mature plant stage. Apparently different linked genes governed seedling and mature plant reaction.

INHERITANCE OF STEM RUST REACTION AND AWNEDNESS

Since the primary purpose of the present work was the study of inheritance of leaf rust reaction, no attempt is made to review the literature on the inheritance of stem rust reaction and of awnedness. The reader is referred to Ausemus *(3)* and Koo and Ausemus *(16)* for reviews of literature on stem rust reaction. Hayes and Immer *(12)* and Ausemus *et al.* *(4)* have summarized the literature on awnedness. In most crosses awnletted and bearded wheats are differentiated by a single factor pair, awnletted being dominant. Others have used two factor pairs to explain the segregation in crosses of awnless and bearded varieties.

Materials and Methods

PARENTS, F_1, AND F_2

THE PARENTS used in the present study were Thatcher, Minn. 2303, C.I. 10003, and a Minnesota selection from Premier x Bobin-Gaza-Bobin, N.S. No. II-39-2, C.I. 12821. Ten crossed seeds, seeds from 16 F_1 plants, and seeds from 109 F_2 plants were available.

Thatcher was developed by the Minnesota Agricultural Experiment Station in cooperation with the United States Department of Agriculture from the cross Marquis-Iumillo x Marquis-Kanred. It was described by Hayes *et al. (10)*. Thatcher is an awnletted spring wheat variety which is susceptible in the seedling stage to leaf rust races 1, 2, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 21, 26, 28, 31, 33, 35, 40, 43, 49, 50, 52, 60, 61, 64, 77, 90, 91, 93, 107, 126, and 128, and resistant to race 44 *(17)*. In the present study Thatcher was found to be susceptible also to races 3, 58, and 128a.

The II-39-2 parent was selected from a cross of Premier x Bobin-Gaza-Bobin, made at University Farm in 1939. Premier, developed at the North Dakota Agricultural Experiment Station, is bearded and similar to Hope under field conditions in stem and leaf rust reaction. Bobin-Gaza- Bobin was obtained by Waterhouse *(26)* as a result of backcrossing Gaza durum-Bobin to the *vulgare* parent Bobin. A bearded spring wheat, II-39-2, is resistant in the seedling stage to races 1, 2, 3, 5, 6, 7, 9, 11, 12, 13, 14, 15, 16, 17, 21, 28, 31, 35, 40, 43, 49, 50, 52, 58, 64, 77, 90, 91, 93, 106, 126, and 128 (*17* and unpublished). In the present study II-39-2 was found to be resistant also to race 128a and susceptible to race 129 in the seedling stage.

LEAF RUST RACES USED IN SEEDLING STUDIES

Race 126 was obtained from C. O. Johnston at Kansas State College, and races 1, 3, and 128a were obtained from the Canadian Rust Laboratory at Winnipeg, Manitoba. Races 2, 5, 15, 28, 58, and a collection of 18 races (2, 5, 6, 7, 9, 10, 11, 15, 17, 21, 28, 31, 33, 35, 40, 52, 77, and 126) were obtained through the courtesy of Dr. M. N. Levine of the United States Department of Agriculture, with headquarters at University Farm.

FIELD EXPERIMENTS

Rust Nursery

In the spring of 1950, 109 F_3 lines were seeded in the Rust Nursery at University Farm. A row of each parent was included at intervals of approximately every 10 rows. Also one row each of Ceres, Lee, and Marquis was included at intervals of about every 30 rows. Each line, parent, and standard variety was sown in 6-foot rows, 1 foot apart. The seeds were spaced 3 inches apart, thus giving 25 plants per row. Border rows of a mixture of susceptible wheat varieties were planted around the nursery and through all alleys. When the plants in these border rows were about 8 inches tall, they were inoculated by spraying with a water suspension of uredospores of 14 races of leaf rust. Stem rust inoculations with 41 races were made hypodermically in several plants at 2- or 3-yard intervals. The leaf rust races used were: 2, 5, 6, 9, 11, 15, 28, 31, 33, 35, 44, 49, 52, and 126. The stem rust races used were 1, 9, 11, 15, 16, 17, 18, 19, 20, 21, 32, 33, 38, 47, 49, 51, 53, 56, 57, 59, 59A, 70, 75, 80, 90, 98, 117, 139, 140, 147, 173, 176, 182, 184, 186, NR6, NR27, NR28, NR30, NR60, and NR75. All the leaf and stem rust races used in the Rust Nursery were made available by the Department of Plant Pathology and Agricultural Botany of the University of Minnesota.

The purpose of the nursery study was to determine the inheritance of leaf rust and stem rust reaction to collections of prevalent races under epidemic conditions in the field. A heavy leaf and stem rust epidemic was obtained. Readings on mature plant reaction to leaf rust were recorded at the time of maximum development of rust on the flag leaf. The notes were taken on individual plants. Three classes established by Mains and Jackson *(20)* were used to classify the materials.

- Class 1 included plants showing reaction type 1 and 2, i.e. small pustules surrounded by chlorotic or necrotic areas.
- Class 2 included plants showing the type 3 reaction, i.e. medium sized pustules usually with less chlorosis or necrosis than in class 1.
- Class 3 included plants showing the type 4 reaction, i.e. large confluent pustules with little or no chlorosis or necrosis.

Class 1 was considered as moderately resistant, while classes 2 and 3 were considered as susceptible.

Notes on field reaction to stem rust were taken on individual plants at harvest time. Five classes were established according to the per cent of infection as follows:

- Class 1—0 to 10 per cent, some pustules of susceptible type
- Class 2—11 to 20 per cent, some pustules of susceptible type
- Class 3—21 to 30 per cent, some pustules of susceptible type
- Class 4—31 to 40 per cent, pustules of susceptible type
- Class 5—41 per cent and more, pustules of susceptible type

Agronomy Nursery

In the spring of 1950, 81 of the 109 F_3 progenies planted in the Rust Nursery were sown also in the Agronomy Nursery along with the ten crossed seeds and seeds of 18 F_2 progenies in 6-foot rows, 1 foot apart. The seeds were spaced 3 inches apart in the row. One row of each parent was grown in every tenth row. The purpose of these plantings was to obtain F_2, F_3, and F_4 seed for seedling studies in the greenhouse. The seed of the F_1 plants was harvested and bulked, but the F_2 and F_3 plants were harvested individually. One head of each F_2 and of each F_3 progeny was bulked to provide seed for seedling studies.

Twenty-two of the 28 F_3 lines grown only in the Rust Nursery were harvested in the same manner. These 22 lines plus the 81 lines from the Agronomy Nursery provided the 103 F_4 bulked lines which were used in the seedling studies in the greenhouse. Six lines that were studied only in the Rust Nursery had insufficient seed for bulking.

A natural epidemic of leaf and stem rust developed in the Agronomy Nursery. Data on leaf and stem rust reaction of the F_1 and F_2 progenies were taken, as these were not grown in the Rust Nursery. Data also were taken on the parents. The same method of taking notes on leaf and stem rust reaction was used as has already been described for the Rust Nursery.

GREENHOUSE EXPERIMENTS

Determination of Races in the Field

In the summer of 1950, leaf rust infected leaves of Thatcher, II-39-2, and one of the F_3 susceptible lines of Thatcher x II-39-2 were collected separately, placed in glassine bags and stored in a refrigerator. Determination of leaf rust races from the samples collected was made under the direction of Dr. M. N. Levine during the winter of 1950-51. The procedure used included the following steps:

1. Seedlings of Little Club wheat about one week old were sprayed with water, rubbed with the fingers to take off some of the wax, and sprayed with water again.

2. Uredospores of each sample were placed on the Little Club leaves with a scalpel, using one greenhouse pot of Little Club seedlings for each sample of inoculum. Only a small amount of inoculum was used in order to permit single pustule isolations.

3. The inoculated pot was sprayed with water, covered with a lamp chimney to prevent contamination, and then placed in an incubator.

4. The inoculated plants were left in the incubator for 48 hours, and then the pots were placed in separate compartments on the greenhouse bench.

5. After about 10 days one or two plants having only a few isolated uredia were selected from each leaf rust culture, the other plants being pulled out. The selected plants were then trimmed with scissors until only one leaf with one uredium remained.

6. The inoculum was increased on Little Club as soon as each selected uredium had produced abundant uredospores.

7. A set of eight differential varieties for determination of leaf rust races was grown and inoculated for each monopustular culture. Thatcher and II-39-2 were included with each set of differentials.

8. Readings were made two weeks after inoculation, using the key of Johnston *et al.* *(15)* to determine the identity of the leaf rust races isolated.

Seedling Reaction to Leaf Rust Races

The material studied in the greenhouse experiments consisted of 103 F_4 bulked lines, one bulked F_3 progeny made up by combining a single head of many F_2 plants, the F_2, and the Thatcher and II-39-2 parents. This material was inoculated separately in the seedling stages with races 1, 2, 3, 5, 15, 28, 58, 126, 128a, and with a mixed collection of 18 races (2, 5, 6, 7, 9, 10, 11, 15, 17, 21, 28, 31, 33, 35, 40, 52, 77, and 126).

The inoculum of each race was increased on Little Club wheat. To avoid contamination each race was handled in a separate section of the greenhouse. The purity of each race was checked by inoculating the eight differential varieties with the race under study and comparing the results with the key of Johnston *et al.* *(15)*.

For the greenhouse studies the parents and segregating material were seeded in 4-inch pots. The parents, F_2, F_3, and F_4 progenies were seeded in individual pots, with approximately 25 seeds per pot. The seedlings were inoculated when the first foliage leaf was about 3 inches tall.

Seedling studies of reaction to races 58 and 126 were carried on during the winter of 1950-1951, under fairly constant temperatures, varying from 60 to 70° F. Reaction to races 2, 5, 15, 28, and the collection of 18 races was studied in the spring of 1951. The temperature in the greenhouse was around 70° F., although extremes of 55° and 90° F. were recorded. Reaction to race 1 was studied in the summer of 1951 with temperatures varying from 60° to 95° F. The greenhouse glass was whitewashed several times to keep the temperatures down. Reaction to races 3 and 128a was studied in the fall of 1951 when the temperatures varied around 70° F. with occasional recordings of from 52° to 94° F.

Infection types 0, 1, and 2 were considered resistant and types *X*, 3, and 4 were susceptible. No *X* types were observed on the resistant II-39-2 parent with races 1, 2, 5, 15, 28, 126, and 128a. Type *X*, with a preponderance of resistant reaction, was observed on II-39-2 when race 3 and the collection of 18 races were used, and in these cases the *X* type of reaction was considered resistant.

Comparative Reaction at Seedling and Six-Leaf Stage

In the spring of 1951, seedlings of parents and of F_4 progenies were inoculated with a collection of 18 leaf rust races. A considerable number of these seedlings were transplanted individually to 4-inch pots. Where possible, several plants were taken from each of the reaction classes—highly resistant, mesothetic, and highly susceptible. The pots and the soil used were sterilized to prevent seedling root rot. The plants were grown to the six-leaf stage and then inoculated with a mixture of inoculum from the 18 races. In this case the uredospores were mixed with talc and dusted on the plants with a dusting apparatus. The greenhouse temperatures varied from 60° to 95° F. during the time that the plants were in the six-leaf stage.

Experimental Results

LEAF RUST REACTION IN THE FIELD

LEAF RUST REACTION of F_1, F_2, and F_3 progenies was studied in the field in the summer of 1950. Table 1 presents the classification of the parents and the progenies of the cross for field reaction to leaf rust.

The II-39-2 parent was moderately resistant, showing an infection ranging from a trace to 25 per cent of small to large pustules. Thatcher was susceptible, with 40 per cent of midsized to large pustules. The six F_1 plants were susceptible. There were 14 moderately resistant and 511 susceptible F_2 plants. Two F_3 lines were moderately resistant, 25 were segregating, and 82 were susceptible. These results may be explained on a three factor pair basis assuming independent inheritance with any factor in the dominant condition

Table 1. Classification of Parental and F_3 Rows and of F_1 and F_2 Plants for Field Reaction to Leaf Rust

Parents or progenies	Number of parental rows, plants, or lines: Moderately resistant	Segregating	Susceptible	Total
Thatcher	......	......	17	17
II-39-2	17	......	......	17
Thatcher x II-39-2				
F_1 plants	......	......	6	6
F_2 plants	14	......	511	525
F_3 lines	2	25	82	109

causing susceptibility. The hypothesis used to explain the results may be illustrated on the following basis: Thatcher, SS, S2S2 S3S3, susceptible; II-39-2 (Premier x Bobin-Gaza-Bobin) ss s2s2 s3s3, moderately resistant; F_1, Ss S2s2 S3s3, susceptible. The expected F_2 phenotypic ratio would be 63 susceptible: 1 resistant. The chi-square tests for goodness of fit are presented in table 2. For the F_2 data the fit is poor, $P = .02 - .05$. For the F_3 data, the expected ratio must be corrected for the small numbers observed in each line.

For a total of 64 F_3 lines, on the above three factor pair hypothesis, the expected breeding behavior in F_3 would be 1 breeding true for resistance; 37 breeding true for susceptibility, and 26 segregating either 3:1, 15:1, or 63:1. The expected frequencies of these three latter types of segregation are 6, 12, and 8, respectively. The average number of plants classified per line was 20. With this number, no correction is necessary for the F_3 lines that were expected to segregate in a 3:1 ratio. Where a 15:1 segregation is expected, with only 20 plants classified, the probability of not getting at least one double recessive is $(\frac{15}{16})^{20}$ or .2751, i.e in 27.51 per cent of such lines all plants would be susceptible. For the same size of family where a 63:1 ratio is expected, a triple-recessive segregate will be missed with a frequency of $(\frac{63}{64})^{20}$ or .7298, i.e. 72.98 per cent of such lines. Therefore, without correction there would be a deficiency of the segregating group and an excess of the susceptible group.

Corrections were calculated for the lines that were expected to segregate in 15:1 and 63:1 ratios. For the 12 expected to segregate 15:1, the correction is $(12 \times .2751)$ or 3.30. Then $12 - 3.30 = 8.7$ which should be observed to segregate. For the eight expected to segregate 63:1 the correction is $(8 \times$

Table 2. Chi-Square Tests for Goodness of Fit of Leaf Rust Reaction Data in F_2 and F_3 Progenies from the Cross Thatcher x II-39-2

Generation	Class	Theoretical ratio	Observed	Calculated	Chi-square value	P values
F_2 plants	Moderately resistant	1	14	8.20	4.10	
	Susceptible	63	511	516.80	.07	
	Total	64	525		4.17	.02-.05
F_3 lines	Moderately resistant	1.00	2	1.70	.05	
	Susceptible	46.14	82	78.58	.15	
	Segregating	16.86	25	28.72	.48	
	Total	64.00	109		.68	.70-.80
Plants in F_3 lines assumed to segregate 3:1	Moderately resistant	1	51	53.5	.12	
	Susceptible	3	163	160.5	.04	
	Total	4	214		.16	.50-.70

.7298) or 5.84. Then $8 - 5.84 = 2.16$ which should be observed to segregate. The number of lines that appear to breed true for susceptibility is increased by the values of these correction factors. The corrected ratio for the 64 lines is:

1.00 breeding true for resistance: $6 + 8.7 + 2.16 = 16.86$ observed to segregate: $37 + 3.3 + 5.84 = 46.14$ breeding true for susceptibility (no segregation observed).

The observed numbers of F_3 lines and the expected numbers based on this corrected ratio are in table 2.

The chi-square test for goodness of fit of these F_3 data, also in table 2, shows a good fit to this hypothesis, $P = .70 - .80$.

On the basis of the corrections made for small numbers, the number of expected F_3 lines segregating 15:1 or 63:1 was 18.46. The number expected to segregate 3:1 was 10.22. Eleven lines had a higher ratio of resistant plants than the other lines and were assumed to be segregating 3 susceptible : 1 resistant leaving 14 with the other types of segregation. This is a reasonably close fit to the expected numbers. From the 11 lines considered to be segregating 3:1, a total of 51 resistant and 163 susceptible plants was obtained. The P value of $.50 - .70$ shown in table 2, is a satisfactory fit to a 3:1 ratio. These data provide more evidence supporting the three factor hypothesis.

Determination of Leaf Rust Races Found in the Field

The identification of races found on Thatcher, II-39-2, and their F_3 hybrid is given in table 3. This material was grown in the University Farm Rust Nursery (artificially inoculated) in the summer of 1950. Of the 14 races used to produce the leaf rust epidemic, only five were recovered from 16 isolations. Table 4 shows the race identification of each of 16 isolates and their reaction on the leaf rust differential wheat varieties and on Thatcher and II-39-2. Thirteen of the 16 isolates recovered were races 126 or 5.

INHERITANCE OF SEEDLING REACTION TO INDIVIDUAL RACES OF LEAF RUST

The parents, F_2, F_3, and F_4 progenies were tested to a number of individual races. Since the inheritance of the reaction to races 1, 2, 5, 15, 28, and 128a appeared to be of the monogenic type, while the inheritance of the reaction to races 3, 58, 126, and to a collection of 18 races bulked appeared to be more complex, they will be presented in two separate groups.

Seedling Reaction to Leaf Rust Races 1, 2, 5, 15, 28, and 128a

The seedling reactions of Thatcher, II-39-2, and F_4 bulked lines from

Table 3. Races of Leaf Rust Found on Thatcher, II-39-2, One F_3 Line (M213 Culture) Wheats Grown in the Rust Nursery at University Farm in the Summer of 1950

Number of isolates	Races found	Prevalence of races	Inoculum taken from leaves of		
			Thatcher	II-39-2	Thatcher x II-39-2 F_3 (M213)
		per cent			
8	126	50.00	4	2	2
5	5	31.25	......	2	3
1	28	6.25	1	......	......
1	35	6.25	......	1	......
1	21	6.25	......	......	1

Table 4. Reaction of Nine Differential Hosts, Thatcher, and II-39-2 to 16 Leaf Rust Monopustular Cultures Obtained from Leaves of Thatcher, II-39-2, or One of Their F_3 Hybrid Lines

Monopustular culture from rust on leaves of	Reactions of differential hosts and parents											Race number
	Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Hussar	Democrat	Thew	Thatcher	II-39-2	
Thatcher	S	R	R	R	S	S	R	S	S	S	R	126
Thatcher	S	R	R	R	S	S	R	S	S	S	R	126
Thatcher	S	R	R	R	S	S	R	S	S	S	R	126
Thatcher	S	R	R	R	S	S	S	S	S	S	R	28
Thatcher	S	R	R	R	S	S	R	S	S	S	R	126
II-39-2	S	R	R	R	R	S	R	S	S	S	R	5
II-39-2	S	R	R	R	R	S	R	S	S	S	R	126
II-39-2	S	R	R	R	R	S	R	S	S	S	R	5
II-39-2	S	R	R	R&S	S	S	R	S	S	S	R	126,35
M213	S	R	R	R	S&R	S	R	S	S	S	R	126,5
M213	S	R	R	R	R	S	R	S	S	S	R	5
M213	S	R	R	R	R	S	R	S	S	S	R	5
M213	S	R&S	R	R&S	S	S	R&S	S	S	S	R	126,21

R = resistant, S = susceptible.

Table 5. Classification and Chi-Square Tests for Goodness of Fit for 103 F_4 Lines Which Were Classified for Seedling Reaction to Leaf Rust Races 1, 2, 5, 15, 28, and 128a Tested Separately

Race	Parent or cross	Number of lines or pots: Resistant	Segregating	Susceptible	Total	Chi-square values*	P values
	Thatcher	......	......	18†	18	....	....
	II-39-2	19†	......	..	19	....	....
1	Thatcher x II-39-2, F_4	22	58	23	103	1.66	.30—.50
2	Thatcher x II-39-2, F_4	21	58	24	103	1.82	.30—.50
5	Thatcher x II-39-2, F_4	17	59	27	103	4.06	.10—.20
15	Thatcher x II-39-2, F_4	23	57	23	103	1.18	.50—.70
28	Thatcher x II-39-2, F_4	20	58	25	103	2.12	.30—.50
128a	Thatcher x II-39-2, F_4	21	60	22	103	2.73	.20—.30

* The calculated ratio is 1 resistant : 2 segregating : 1 susceptible.

† The same number of pots of the parents were used for tests to individual races 1, 2, 5, 15, 28, 128a, and a collection of 18 races bulked. In all cases Thatcher was susceptible and II-39-2 resistant.

Table 6. Classification of F_2 Plants for Reaction to Leaf Rust Races 1, 2, 5, 15, and 28

Races	Number of plants: Resistant	Susceptible	Total
1	7	23	30
2	2	15	17
5	3	9	12
15	5	16	21
28	7	22	29

Thatcher x II-39-2 to leaf rust races 1, 2, 5, 15, 28, and 128a are presented in table 5. Thatcher was susceptible and II-39-2 was resistant to each race. The F_4 bulked lines were classified into the following three types: those breeding true for resistance, those segregating, and those breeding true for susceptibility.

For reaction of the F_4 lines to each of the leaf rust races 1, 2, 5, 15, 28, and 128a, the observed numbers approach the ratio of 1 resistant : 2 segregating : 1 susceptible. This is the ratio expected from a one factor pair segregation. The chi-square tests for goodness of fit (table 5) are in good agreement with expectation.

Individual plants in F_2 (table 6), F_3 plants representing a bulk sample of seed from F_2 plants (table 7), and plants in the segregating F_4 lines (table 8) were then classified as resistant or susceptible and counted. The expected ratios are shown in table 9.

It will be noted that the expected ratio for bulked F_2 and bulked F_3 segregating lines is 10 susceptible : 6 resistant. The genotypes expected on a single factor pair basis and their ratios for plants in F_2, an F_3 progeny from bulked F_2 plants, F_3 lines (each from random F_2 selection), F_4 lines from

Table 7. Classification and Chi-Square Tests for Goodness of Fit for F_3 Plants, Which Were Classified for Seedling Reaction to Leaf Rust Races 1, 2, 5, 15, 28, and 128a

Race	Number of plants: Resistant	Susceptible	Total	Chi-square values*	P values
1	246	325	571	7.59	.01—.001
2	161	233	394	1.90	.10—.20
5	116	242	358	3.97	.02—.05
15	186	272	458	1.89	.10—.20
28	179	257	436	2.35	.10—.20
128a	130	233	363	.45	.50—.70
Total plants	1,018	1,562	2,580		

* The calculated ratio is 10 susceptible : 6 resistant.

Table 8. Classification and Chi-Square Tests for Goodness of Fit for Plants in Segregating F_4 Lines, Which Were Classified for Seedling Reaction to Leaf Rust Races 1, 2, 5, 15, 28, and 128a. The Chi-Square Test for Heterogeneity Is Shown Also

Race	Number of segregating lines	Number of plants: Resistant	Number of plants: Susceptible	Total plants	Chi-square values*	P values
1	58	778	1,282	2,060	0.06	.98
2	58	580	831	1,411	7.82	.01—.001
5	60	496	907	1,403	2.75	.05—.10
15	57	623	1,011	1,634	0.27	.70—.80
28	60	483	881	1,364	2.54	.10—.20
128a	57	566	1,185	1,751	20.01	<.001
Total number of plants		3,526	6,097	Summation X^2	=33.88	
				Total X^2	= 3.02	
				Heterogeneity X^2	=30.86	<.001

* The calculated ratio is 10 susceptible : 6 resistant.

bulked F_3 lines, and plants from F_4 lines showing segregation are given in table 9.

Although the observed numbers of F_2 plants were small (table 6), 3 susceptible : 1 resistant is the probable segregation for reaction to races 1, 2, 5, 15, and 28. Comparing the segregations in F_3 (table 7) and F_4 (table 8) with a ratio of 10 susceptible : 6 resistant, the reaction to race 1 gave a good fit in F_4 and a poor fit in F_3; to race 2, the fit was good in F_3, but poor in F_4; to race 5 the fit was poor in F_3 and fair in F_4; to race 15 the fit was good in F_3 and in F_4; to race 28 the fit was good in both tests; and to race 128a, the fit was good in F_3 and poor in F_4. The heterogeneity chi-square for F_4 plant reaction to races 1, 2, 5, 15, 28, and 128a, shown in table 8, is highly significant and is accounted for largely by the large deviations from expected shown by the reactions to races 2 and 128a. The deviations in the F_3 and F_4 were not consistent. It is concluded that the reaction to each race probably corresponds to segregation for a single factor pair.

Seedling Reaction to Leaf Rust Races 3, 58, 126, and to 18 Races Bulked

The seedling reactions of Thatcher, II-39-2, and F_4 lines of Thatcher x II-39-2 to leaf rust races 3, 58, 126, and to a collection of 18 races bulked are shown in table 10.

These F_4 lines each represent a bulked F_3 progeny. Thatcher was susceptible and II-39-2 was resistant to each of these races. For the reaction of the F_4 lines to the above mentioned leaf rust races, the observed numbers approach a ratio of 1 breeding true for resistance : 8 segregating : 7 breeding true

Table 9. Expected One Factor Pair Ratios for F_2 Plants, F_3 Plants from Bulked Seed of F_2 Plants, F_4 Bulked Lines and Plants from Segregating F_4 Lines

F_2 plants: Genotypes	F_2 plants: Phenotypes	Breeding behavior — F_3: F_3 plants (bulked F_2)	Breeding behavior — F_3: F_3 lines	Breeding behavior — F_4 (each F_3 line bulked): Plants from segregating F_4 lines	Breeding behavior — F_4 (each F_3 line bulked): F_4 lines
1 SS	S	4S	1S	4S	1S
2 Ss	S	6S : 2R	2 seg	6S : 2R	2 seg
1 ss	R	4R	1R	4R	1R
Ratios:	3S : 1R	10S : 6R	1R : 2 seg : 1S	10S : 6R	1R : 2 seg : 1S

R = resistant, Seg = segregating, and S = susceptible.

Table 10. Classification and Chi-Square Tests for Goodness of Fit for 103 F_4 Lines Which Were Classified for Seedling Reaction to Leaf Rust Races 3, 58, 126, and to a Collection of 18 Races Bulked

Race	Parent or cross	Number of lines or pots: Resistant	Segregating	Susceptible	Total	Chi-square values*	P values
3, 58, 126	Thatcher	.....	.....	18†	18	....	....
3, 58, 126	II-39-2	19†	.....	.....	19	....	....
3	Thatcher x II-39-2, F_4	5	55	43	103	.65	.70—.80
58	Thatcher x II-39-2, F_4	4	58	41	103	2.11	.30—.50
126	Thatcher x II 39-2, F_4	5	56	42	103	.92	.50—.70
18 races bulked	Thatcher x II-39-2, F_4	8	61	34	103	5.30	.05—.10

* The calculated ratio is 1 resistant : 8 segregating : 7 susceptible.

† The same number of pots of the parents were used for tests to individual races 3, 58, 126, and a collection of 18 races bulked. In all cases Thatcher was susceptible and II-39-2 resistant.

for susceptibility. This is the expected ratio for a two factor pair segregation. The chi-square tests for goodness of fit presented in table 10 show a good agreement of the observed to the calculated numbers. This ratio for F_4 lines may result from an F_2 factor interaction ratio of either 9 resistant : 7 susceptible, 13 susceptible : 3 resistant, or 15 susceptible : 1 resistant. Therefore, more information than was obtained from the breeding behavior of F_4 lines is needed in order to distinguish the type of interaction. The ratios in the segregating lines should distinguish between them.

These expected ratios are summarized in table 11. In each case they deviate greatly from the original segregation ratio in F_2.

The ratio of 1 resistant : 8 segregating : 7 susceptible F_3 or F_4 (bulked F_3) lines results from 13:3 and 15:1 F_2 interaction types in which susceptibility is the predominant class. The same ratio of F_3 or F_4 lines results from a 9:7 F_2 interaction only if resistance is dominant and the F_2 ratio is 9 resistant : 7 susceptible.

The F_3 individual plants from a bulk sample of the seed from F_2 plants and plants in the segregating F_4 lines were

Table 11. Expected Segregation for Interactions Which Give a Ratio of 1 Resistant : 8 Segregating : 7 Susceptible F_3 or F_4 (Bulked F_3 Lines)

Genotype of parents: Resistant		Susceptible		F_2 plants	F_3 plants from bulked F_2	Segregating lines: F_3 ratio	Number of lines	F_4 (bulked F_3)	Per cent resistance in F_4 lines
AA	BB	aa	bb	9R:7S	25R:39S	9R:7S	4	25R:39S	39.1
						3R:1S	4	40R:24S	62.5
					Total	21R:11S	8	65R:63S	49.2
cc	DD	CC	dd	13S:3R	49S:15R	13S:3R	4	49S:15R	23.4
						3S:1R	2	20S:12R	37.5
						1S:3R	2	12S:20R	62.5
					Total	21S:11R	8	81S:47R	36.7
ee	ff	EE	FF	15S:1R	55S:9R	15S:1R	4	55S:9R	14.1
						3S:1R	4	40S:24R	37.5
					Total	27S:5R	8	95S:33R	25.8

R = resistant, S = susceptible.

Table 12. Leaf Rust Reaction to Race 58 of F_3 Plants from a Bulk Sample of F_2 Plants, and of Segregating F_4 Lines to Races 58 and 3. The Chi-Square Test for Goodness of Fit to Expectations Is Based on a 15 Susceptible : 1 Resistant Type of F_2 Interaction. In F_3 the Expected Ratio Is 10 Susceptible : 6 Resistant; in F_4 It Is 55 Susceptible : 9 Resistant

Race		Susceptible	Resistant	Total	Chi-square values	P values
58	F_3 observed	234	45	279		
	calculated	239.77	39.23	279	0.99	.30—.50
58	F_4 observed	866	278	1,144		
	calculated	849.08	294.92	1,144	1.31	.20—.30
3	F_4 observed	315	99	414		
	calculated	307.27	106.73	414	0.75	.70—.80

classified as resistant or susceptible. The total numbers of resistant or susceptible plants in the F_3 and F_4 lines, for each leaf rust race tested, are shown in table 12, together with chi-square values for tests of goodness of fit to the expectations based on a 15 susceptible : 1 resistant type of two factor interaction.

The chi-square and the *P* values show good fits of observed to expected numbers. These results indicate that the reaction to each of the two races, 3 and 58, is determined by two independent factor pairs. Susceptibility was dominant over resistance and was determined by either or both factors in the dominant condition. Resistance occurs only when the two factors are homozygous recessive.

The reaction of the F_4 lines to race 126 also fits a ratio of 1 resistant : 8 segregating : 7 susceptible. Evidence in F_3 and F_4 should determine the type of two-factor interaction. The F_3 (bulk of F_2) population, 139 resistant : 261 susceptible shows a fair fit to the 25 resistant : 39 susceptible ratio expected from the 9 resistant : 7 susceptible F_2 interaction and a poor fit to the ratios expected from 13 susceptible : 3 resistant and 15 susceptible : 1 resistant. In the F_4, segregating lines from the 9 resistant : 7 susceptible and 13 susceptible : 3 resistant F_2 ratios (table 11), lines with high percentages of resistant plants, and lines with high percentages of susceptible plants are expected in ratios of 1:1 and 1:3 respectively; while from the 15 susceptible : 1 resistant only lines with high percentages of susceptible plants are expected. For the ratios expected correction factors are not needed even though the average number of plants per line is only 19.3. Five of the 56 F_3 lines had approximately equal numbers of resistant and susceptible and could not be placed in either group. Seven of the remaining lines had a high percentage of resistant plants and 44 had high percentages of susceptible plants. This ratio of 7:44 F_4 lines and the totals of resistant to susceptible plants in the two groups (table 13) show a close fit to the numbers expected from the 13:3 two factor type of interaction and poor fits to the other ratios.

On the basis of these results, it seems probable that the reaction to race 126, in the cross Thatcher x II-39-2, may be explained as the result of an interaction of two genetic factors, a dominant factor for resistance coming from II-39-2 and a dominant factor for susceptibility coming from Thatcher with the latter epistatic over the factor for resistance in II-39-2. An F_2 ratio of 13 susceptible : 3 resistant results from this interaction.

No plant counts were made in the study of the reaction to the collection of 18 leaf rust races. Hence the type of two factor pair interaction could not be determined.

Table 13. Summary of Plant Counts in F_4 Segregating Lines Tested for Reaction to Race 126 of Leaf Rust

	High percentage of resistant plants				Doubtful			High percentage of susceptible plants			
	Number of lines	Number of plants		Percentage of plants resistant	Number of lines	Number of plants		Number of lines	Number of plants		Percentage of plants resistant
		Resistant	Susceptible			Resistant	Susceptible		Resistant	Susceptible	
Observed	7	102	57	64.1	5	51	52	44	226	592	27.5
Expected from 13S : 3R	12.75	99	60	62.5	.....	.....	.....	38.25	230	588	28.1
Expected from 9R : 7S	25.5	99	60	62.5	.....	.....	.....	25.5	320	498	39.1
Expected from 15S : 1R	0	.....	.....	....	.....	.....	.....	51	211	607	25.8

R = resistant, S = susceptible.

Table 14. Comparison of the Seedling and Six-Leaf Stage Reaction of Plants of Thatcher, II-39-2, and F_4's Inoculated with a Collection of 18 Bulked Races of Leaf Rust

Seedling reaction		Number of plants	Sixth leaf reaction classication		
Parent or F_4	Classification		Resistant	Mesothetic	Susceptible
II-39-2	Resistant	20	15	......	5
F_4's	Resistant	57	53	1	3
II-39-2	Mesothetic	5	4	......	1
F_4's	Mesothetic	106	66	30	10
Thatcher	Susceptible	6	2	......	4
F_4's	Susceptible	141	24	8	109

COMPARISON OF SEEDLING AND SIX-LEAF-STAGE PLANT REACTION TO A COLLECTION OF 18 RACES BULKED

Table 14 shows the results obtained by comparing the seedling and six-leaf stage reactions of plants of Thatcher, II-39-2, and F_4's from Thatcher x II-39-2. These plants were inoculated at both stages with a collection of 18 races of leaf rust bulked.

Twenty plants of II-39-2 were classified as resistant in the seedling stage. In the six-leaf stage 15 of these plants remained in the resistant class, while the other five were classified as susceptible. Five plants of II-39-2 had a mesothetic reaction in the seedling stage and four of these were classified as resistant and one as susceptible in the six-leaf stage.

The six plants of Thatcher were susceptible in the seedling stage. In the six-leaf stage four of these plants were classified as susceptible, while the other two were classified as resistant.

Of the 304 F_4 plants tested, 63 per cent (192 plants) gave the same reaction in the seedling and six-leaf stages. Thirty-two per cent (98 plants) showed more resistance in the six-leaf stage than in the seedling stage, while 5 per cent (14 plants) showed less resistance in the six-leaf stage than in the seedling stage.

A chi-square test for independence between seedling and six-leaf stage reactions of F_4 plants to a collection of 18 races bulked gave a chi-square value of 179.24 with a *P* value of $<.001$ indicating high association. However, the association was not 100 per cent since 37 per cent of the F_4 plants gave a different reaction in the seedling and six-leaf stages. The parents themselves did not show uniform behavior in the two stages tested.

STEM RUST REACTION

Stem rust reaction was studied in the field during the summer of 1950. Thatcher was the more resistant parent with an average infection of 18 per cent. The II-39-2 parent had an average infection of more than 32 per cent. Table 15 shows the frequency distribu-

Table 15. Frequency Distributions of the Plants of Thatcher, II-39-2, and F_1 and F_2 Progenies for Per Cent of Stem Rust Infection

Parent or cross	Frequency distribution in per cent					Total
	0-10	11-20	21-30	31-40	41+	
Thatcher	50	105	77	20	......	252
II-39-2	7	13	62	103	59	244
Thatcher x II-39-2 F_1	1	......	......	1	3	5
Thatcher x II-39-2 F_2	32	35	75	157	242	541

Table 16. Range of Means and Standard Deviations Calculated for Stem Rust Per Cent in Rows of Thatcher and II-39-2

Parent	Range	
	Means in percentage of stem rust	Standard deviations
Thatcher	9.76-22.37	6.01-11.12
II-39-2	20.24-42.50	0.00-11.22

tions of the plants of Thatcher, II-39-2, and F_1 and F_2 progenies of Thatcher x II-39-2 for per cent of stem rust infection. These data show considerable overlapping for stem rust infection in Thatcher and II-39-2. The F_1 and F_2 frequencies show distributions skewed to the susceptible side, indicating dominance of susceptibility.

The F_3 plants of each F_3 line were also classified. The stem rust readings on individual rows as expressed in mean per cent and standard deviations for Thatcher, II-39-2, and F_3 lines of Thatcher x II-39-2, were calculated. The ranges of means and standard deviations for stem rust per cent in rows of Thatcher and II-39-2 are shown in table 16.

Each F_3 line was classified with respect to its standard deviation and mean per cent of stem rust in figure 1. Each of the 103 F_3 lines is represented by one dot in this figure. The areas on figure 1 covered by Thatcher and II-39-2 were determined by using the means and standard deviations in table 16.

Seventeen of the F_3 lines fall within the area of the Thatcher parent and outside the area of the II-39-2 parent. One F_3 line showed a lower mean per cent of stem rust and a lower standard deviation than Thatcher. Another F_3 line had less variability than Thatcher but fell within the limits of this parent for per cent of stem rust. Four lines fell in the area where Thatcher and II-39-2 overlap. The 41 lines that showed larger standard deviations than either parent apparently were segregating.

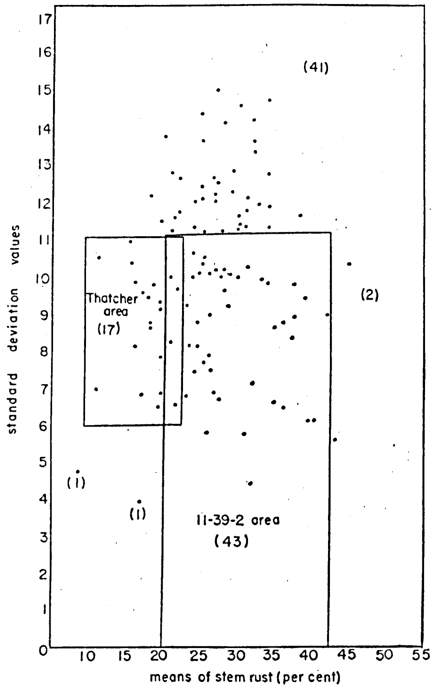

Fig. 1. Distribution of F_3 lines, with respect to the Thatcher and II-39-2 parents, for mean per cent of stem rust and standard deviation.

Forty-three lines fell within the area of II-39-2 and outside the area of Thatcher, while only two lines were more susceptible than this parent.

It is shown in figure 1 that about one-fourth of the F_3 lines were similar to Thatcher in both mean per cent of stem rust and standard deviation. This indicates that reaction to stem rust in the cross Thatcher x II-39-2 is probably determined by the action of one major genetic factor pair with susceptibility dominant.

INHERITANCE OF AWNEDNESS

Thatcher is awnletted and II-39-2 is bearded. The classification for awnedness of the parents, F_1, F_2, and F_3 progenies is shown in table 17. The F_1 plants were awnletted indicating the usual dominance of the awnletted condition.

Table 17. Classification and Chi-Square Tests for Goodness of Fit for Awnedness of Thatcher, II-39-2, and F_1, F_2, and F_3 Progenies

Parents or progeny	Number of rows, lines, or plants				Expected ratios	Chi-square values	P values
	Awnletted	Segregating	Bearded	Total			
Thatcher (rows)	17	......	....	....	....	....	....
II-39-2 (rows)	......	......	17	17	....	....	....
Thatcher x II-39-2							
F_1 plants	5	......	......	5	....	....	....
F_2 plants	381	......	141	522	3:1	1.12	.20-.30
F_3 lines	22	55	32	109	1:2:1	1.84	.30-.50
F_3 plants in 55 segregating F_3 lines	809	......	276	1,085	3:1	0.11	.50-.70

In the F_2 generation, 381 awnletted and 141 bearded plants were obtained. These observed numbers show good agreement with the numbers expected on the basis of a 3:1 segregation. The *P* value of .20-.30 for these data, shown in table 17, represents a good fit.

For the F_3 lines the expected breeding behavior would be as follows: 1 line breeding true for the awnletted condition, 2 lines segregating, and 1 line breeding true for the bearded condition. The *P* value of .30-.50 shows good agreement of F_3 observed numbers to expected numbers (table 17).

There were 809 awnletted and 276 bearded plants in the 55 segregating F_3 lines. The *P* value of .50-.70 (table 17) indicates a good fit of these observed numbers to the expected 3:1 segregation.

ASSOCIATION STUDIES

The chi-square tests for independent inheritance of the characters in the F_3 and F_4 lines are shown in table 18.

Seedling reactions to races 1, 2, 5, 15, 28, and 128a were each explained on a single factor pair basis with susceptibility dominant. There are high associations between seedling reactions to races 1, 2, 5, 15, 28, and 128a when they are compared two races at a time. The data for these comparisons, two at a time, are shown in table 19. In no case is there complete association.

The 103 F_4 lines were grouped according to their reaction to races 1, 2, 5, 15, 28, and 128a, i.e., the ones for which a one factor pair was indicated. This is summarized in table 20. Eighty-seven of these lines reacted similarly to all these races, i.e., forty-nine were segregating, 16 were resistant, and 22 were susceptible. The remaining 16 lines showed different combinations of reaction to these races. If only one factor controlled the reaction to these six races, each F_4 line should have reacted the same to each race. The occurrence of the 16 exceptional lines, plus the fact that perfect association was not found for any two of the races (table 19) suggests that there may be six different genetic factors conditioning the reactions to these six races. Since the reactions to these races are closely associated (table 19), close linkage of the six factors is indicated.

To measure recombination between the six genetic factors, the F_4 data from table 19 were substituted in Immer's formula *(13)* for calculating linkage intensities from F_3 data from the doubly dominant F_2 plants, i.e., the susceptible and segregating classes.

The F_4 lines from bulked F_3 progenies represent the genotypes present in F_3.

Table 18. Chi-Square Tests for Independence of Inheritance of the Characters in the F_3 and F_4 Generations

Generation	Number of lines	Characters compared	Degrees of freedom	Chi-square values	P values
F_4	103	Seedling reaction to races 1 and 2	4	166.85	<.001
F_4	103	Seedling reaction to races 1 and 3	4	7.92	.05-.10
F_4	103	Seedling reaction to races 1 and 5	4	134.57	<.001
F_4	103	Seedling reaction to races 1 and 15	4	154.25	<.001
F_4	103	Seedling reaction to races 1 and 28	4	176.35	<.001
F_4	103	Seedling reaction to races 1 and 58	4	27.00	<.001
F_4	103	Seedling reaction to races 1 and 126	4	11.89	.01-.02
F_4	103	Seedling reaction to races 1 and 128a	4	183.90	<.001
F_4	103	Seedling reaction to races 1 and bulk	4	101.79	<.001
F_4	103	Seedling reaction to races 2 and 3	4	7.80	.05-.10
F_4	103	Seedling reaction to races 2 and 5	4	169.04	<.001
F_4	103	Seedling reaction to races 2 and 15	4	176.40	<.001
F_4	103	Seedling reaction to races 2 and 28	4	180.21	<.001
F_4	103	Seedling reaction to races 2 and 58	4	24.26	<.001
F_4	103	Seedling reaction to races 2 and 126	4	24.12	<.001
F_4	103	Seedling reaction to races 2 and 128a	4	175.86	<.001
F_4	103	Seedling reaction to races 2 and bulk	4	108.26	<.001
F_4	103	Seedling reaction to races 3 and 5	4	4.24	.30-.50
F_4	103	Seedling reaction to races 3 and 15	4	11.44	.02-.05
F_4	103	Seedling reaction to races 3 and 15	1	1.34	.20-.30
F_4	103	Seedling reaction to races 3 and 28	4	9.06	1.05-.10
F_4	103	Seedling reaction to races 3 and 58	4	35.33	<.001
F_4	103	Seedling reaction to races 3 and 126	4	37.44	<.001
F_4	103	Seedling reaction to races 3 and 128a	4	7.89	.05-.10
F_4	103	Seedling reaction to races 3 and bulk	4	6.91	.05-.10
F_4	103	Seedling reaction to races 5 and 15	4	144.60	<.001
F_4	103	Seedling reaction to races 5 and 28	4	156.87	<.001
F_4	103	Seedling reaction to races 5 and 58	4	28.96	<.001
F_4	103	Seedling reaction to races 5 and 126	4	15.85	.01-.001
F_4	103	Seedling reaction to races 5 and 128a	4	165.04	<.001
F_4	103	Seedling reaction to races 5 and bulk	4	90.17	<.001
F_4	103	Seedling reaction to races 15 and 28	4	128.44	<.001
F_4	103	Seedling reaction to races 15 and 58	4	30.46	<.001

Table 18. Continued

Generation	Number of lines	Characters compared	Degrees of freedom	Chi-square values	P values
F_4	103	Seedling reaction to races 15 and 126	4	20.35	<.001
F_4	103	Seedling reaction to races 15 and 128a	4	159.46	<.001
F_4	103	Seedling reaction to races 15 and bulk	4	99.03	<.001
F_4	103	Seedling reaction to races 28 and 58	4	24.87	<.001
F_4	103	Seedling reaction to races 28 and 126	4	10.35	.02-.05
F_4	103	Seedling reaction to races 28 and 128a	4	164.54	<.001
F_4	103	Seedling reaction to races 28 and bulk	4	115.22	<.001
F_4	103	Seedling reaction to races 58 and 126	4	78.15	<.001
F_4	103	Seedling reaction to races 58 and 128a	4	25.31	<.001
F_4	103	Seedling reaction to races 58 and bulk	4	21.56	<.001
F_4	103	Seedling reaction to races 126 and 128a	4	12.69	.01-.02
F_4	103	Seedling reaction to races 126 and bulk	4	15.61	.01-.001
F_4	103	Seedling reaction to races 128a and bulk	4	65.15	<.001
F_4 and F_3	103	Seedling reaction to race 1 and awnedness	4	3.13	.50-.70
F_4 and F_3	103	Seedling reaction to race 2 and awnedness	4	2.60	.50-.70
F_4 and F_3	103	Seedling reaction to race 3 and awnedness	4	13.99	.01-.001
F_4 and F_3	103	Seedling reaction to race 3 and awnedness	1	1.37	.20-.30
F_4 and F_3	103	Seedling reaction to race 5 and awnedness	4	2.80	.50-.70
F_4 and F_3	103	Seedling reaction to race 15 and awnedness	4	3.34	.50-.70
F_4 and F_3	103	Seedling reaction to race 28 and awnedness	4	2.73	.50-.70
F_4 and F_3	103	Seedling reaction to race 58 and awnedness	4	1.35	.80-.90
F_4 and F_3	103	Seedling reaction to race 126 and awnedness	4	.85	.90-.95
F_4 and F_3	103	Seedling reaction to race 128a and awnedness	4	3.18	.50-.70
F_4 and F_3	103	Seedling reaction to race bulk and awnedness	4	3.21	.50-.70
F_3 and F_3	103	Field reaction to a collection of races and awnedness	4	6.74	.10-.20
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 1	4	8.67	.05-.10
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 2	4	6.16	.10-.20
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 3	4	12.24	.01-.02
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 5	4	6.37	.10-.20
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 15	4	7.53	.10-.20
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 28	4	5.94	.20-.30
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 58	4	19.00	<.001
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 126	4	20.72	<.001
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race 128a	4	3.70	.30-.50
F_3 and F_4	102	Field reaction to a collection of races and seedling reaction to race bulk	4	2.58	.50-.70

Table 19. Interrelationships of Seedling Reactions in the Greenhouse of F_4 Lines from Bulked F_3 Lines to Leaf Rust Races 1, 2, 3, 5, 15, 28, 58, 128a, and a Collection of 18 Races

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 1		Race 2		
R	20	2	......	22
Seg	1	55	2	58
S	.....	1	22	23
Total	21	58	24	103
		Race 3		
R	3	9	10	22
Seg	2	36	20	58
S	.....	10	13	23
Total	5	55	43	103
		Race 5		
R	17	5	......	22
Seg	.....	53	5	58
S	.....	1	22	23
Total	17	59	27	103
		Race 15		
R	19	3	......	22
Seg	4	53	1	58
S	.....	1	22	23
Total	23	57	23	103
		Race 28		
R	19	3	......	22
Seg	1	54	3	58
S	.....	1	22	23
Total	20	58	25	103
		Race 58		
R	3	15	4	22
Seg	1	38	19	58
S	.....	5	18	23
Total	4	58	41	103
		Race 126		
R	2	15	5	22
Seg	3	34	21	58
S	.....	7	16	23
Total	5	56	42	103
		Race 128a		
R	21	1	......	22
Seg	.....	58	......	58
S	.....	1	22	23
Total	21	60	22	103

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 1		Collection of 18 races		
R	8	13	1	22
Seg	.....	45	13	58
S	.....	3	20	23
Total	8	61	34	103
Race 2		Race 3		
R	3	9	9	21
Seg	2	35	21	58
S	.....	11	13	24
Total	5	55	43	103
		Race 5		
R	16	5	......	21
Seg	1	54	3	58
S	.....	......	24	24
Total	17	59	27	103
		Race 15		
R	20	1	......	21
Seg	3	55	......	58
S	.....	1	23	24
Total	23	57	23	103
		Race 28		
R	19	2	......	21
Seg	1	56	1	58
S	.....	......	24	24
Total	20	58	25	103
		Race 58		
R	3	13	5	21
Seg	1	39	18	58
S	.....	6	18	24
Total	4	58	41	103
		Race 126		
R	3	14	4	21
Seg	2	34	22	58
S	.....	8	16	24
Total	5	56	42	103
		Race 128a		
R	20	1	......	21
Seg	1	57	......	58
S	.....	2	22	24
Total	21	60	22	103

R = resistant, Seg = segregating, and S = susceptible.

Table 19. Continued

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 2	Collection of 18 races			
R	8	12	1	21
Seg	......	46	12	58
S	......	3	21	24
Total	8	61	34	103
Race 5	Race 3			
R	2	9	6	17
Seg	3	34	22	59
S	0	12	15	27
Total	5	55	43	103
Race 15	Race 3			
R	4	10	9	23
Seg	1	34	22	57
S	......	11	12	23
Total	5	55	43	103
Race 28	Race 3			
R	3	9	10	22
Seg	2	36	20	58
S	......	10	13	23
Total	5	55	43	103
Race 58	Race 3			
R	2	1	1	4
Seg	3	40	15	58
S	......	14	27	41
Total	5	55	43	103
Race 126	Race 3			
R	2	3	......	5
Seg	3	40	13	56
S	......	12	30	42
Total	5	55	43	103
Race 128a	Race 3			
R	3	9	9	21
Seg	2	36	22	60
S	......	10	12	22
Total	5	55	43	103
Race 3	Collection of 18 races			
R	1	3	1	5
Seg	5	36	14	55
S	2	22	19	43
Total	8	61	34	103

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 5	Race 15			
R	16	1	......	17
Seg	7	52		59
S	......	4	23	27
Total	23	57	23	103
	Race 28			
R	16	1	......	17
Seg	4	55	......	59
S	......	2	25	27
Total	20	58	25	103
	Race 58			
R	3	10	4	17
Seg	1	40	18	59
S	......	8	19	27
Total	4	58	41	103
	Race 126			
R	2	11	4	17
Seg	3	35	21	59
S	......	10	17	27
Total	5	56	42	103
	Race 128a			
R	17	......	......	17
Seg	4	55	......	59
S	......	5	22	27
Total	21	60	22	103
	Collection of 18 races			
R	5	10	2	17
Seg	3	46	10	59
S	......	5	22	27
Total	8	61	34	103
Race 15	Race 28			
R	20	3	......	23
Seg	......	56	1	57
S	......	1	22	23
Total	20	60	23	103
	Race 58			
R	4	15	4	23
Seg	......	38	19	57
S	......	6	17	23
Total	4	59	40	103

R = resistant, Seg = segregating, and S = susceptible.

Table 19. Continued

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 15	Race 126			
R	4	15	4	23
Seg	1	33	23	57
S	......	8	15	23
Total	5	56	42	103
	Race 128a			
R	19	4	......	23
Seg	2	55	......	57
S	......	1	22	23
Total	21	60	22	103
	Collection of 18 races			
R	8	14	1	23
Seg	......	44	13	57
S	......	3	20	23
Total	8	61	34	103
Race 28	Race 58			
R	3	13	4	20
Seg	1	38	19	58
S	......	7	18	25
Total	4	58	41	103
	Race 126			
R	2	14	4	20
Seg	3	33	22	58
S	......	9	16	25
Total	5	56	42	103
	Race 128a			
R	19	1	......	20
Seg	2	56	......	58
S	......	3	22	25
Total	21	60	22	103
	Collection of 18 races			
R	8	12	......	20
Seg	......	45	13	58
S	......	4	21	25
Total	8	61	34	103

Seedling reaction	Seedling reaction: Resistant	Segregating	Susceptible	Total
Race 58	Race 126			
R	3	1	......	4
Seg	1	45	12	58
S	1	10	30	41
Total	5	56	42	103
	Race 128a			
R	3	1	......	4
Seg	14	39	5	58
S	4	20	17	41
Total	21	60	22	103
	Collection of 18 races			
R	1	3	......	4
Seg	5	42	11	58
S	2	16	23	41
Total	8	61	34	103
Race 126	Race 128a			
R	2	3	......	5
Seg	15	34	7	56
S	4	23	15	42
Total	21	60	22	103
	Collection of 18 races			
R	1	4	......	5
Seg	5	37	14	56
S	2	20	20	42
Total	8	61	34	103
Race 128a	Collection of 18 races			
R	8	12	1	21
Seg	......	46	14	60
S	......	3	19	22
Total	8	61	34	103

R = resistant, Seg = segregating, and S = susceptible.

Table 20. Classification of 103 F_4 Lines According to Their Reaction to Leaf Rust Races 1, 2, 5, 15, 28, and 128a

Combination number	Reaction to races: 1	128a	15	2	28	5	Number of lines
1	Seg	Seg	Seg	Seg	Seg	Seg	49
2	R	R	R	R	R	R	16
3	S	S	S	S	S	S	22
4	R	R	R	R	R	Seg	3
5	Seg	Seg	R	Seg	R	Seg	1
6	Seg	Seg	Seg	Seg	Seg	S	2
7	Seg	Seg	Seg	Seg	S	S	1
8	Seg	Seg	R	Seg	Seg	Seg	2
9	R	R	Seg	R	Seg	Seg	1
10	Seg	Seg	R	R	Seg	Seg	1
11	R	R	Seg	Seg	Seg	R	1
12	R	Seg	Seg	Seg	Seg	Seg	1
13	Seg	Seg	Seg	S	S	S	1
14	Seg	Seg	S	S	S	S	1
15	S	Seg	Seg	Seg	Seg	Seg	1
						Total	103

R = resistant, Seg = segregating, and S = susceptible.

The data from table 19 were arranged as follows:

Reaction to one race:	Reaction to another race: Susceptible	Segregating
Susceptible	(e)	(f)
Segregating	(g)	(h and i)

Immer's formula for F_3 from doubly dominant F_2's in coupling is as follows:

$$-\frac{2e+f+g}{1-p}+\frac{f+g}{p}+\frac{2(h+i)\ (2p-1)}{1-2p+2p^2}+\frac{(2-2p)\ (e+f+g+h+i)}{3-2p+p^2}=0$$

where p is the crossover value, e, f, g, and $h+i$ are the observed numbers from the F_4 data as indicated in the preceding 2 x 2 table. The standard errors for the different p values were determined by the use of Immer's and Henderson's table 5 *(14)* which gives a factor to be divided by $\sqrt{N}$ (the number of lines) to obtain the standard error.

The calculated p values for recombination for each combination of two pairs of factors responsible for reaction to races 1, 2, 5, 15, 28, and 128a, and the corresponding standard errors, are given in table 21.

Table 21. Recombination *(p)* Values and Their Standard Errors for Genetic Factors Responsible for Reaction to F_4 Lines to Leaf Rust Races 1, 2, 5, 15, 28, and 128a

Races compared	p-value	Standard error	Races compared	p-value	Standard error
1-128a	.009	±.007	128a-5	.046	±.018
1-15	.020	±.012	15-2	.010	±.009
1-2	.028	±.014	15-28	.019	±.011
1-28	.042	±.017	15-5	.040	±.017
1-5	.057	±.020	2-28	.009	±.007
128a-15	.010	±.009	2-5	.028	±.014
128a-2	.019	±.011	28-5	.018	±.011
128a-28	.029	±.014			

Using the recombination values obtained between the reaction to race 1 and the reaction to each of the other races 2, 5, 15, 28, and 128a, the following genetic map is obtained:

1	128a	15	2	28	5
0	0.9	1.9	2.9	3.8	5.6

The observed recombination values may be summarized as follows:

	1	128a	15	2	28	5
1	......	.009	.020	.028	.042	.057
128a	......	....	.010	.019	.029	.046
15	......	....	....	.010	.019	.040
2	......	....	....	....	.009	.028
28	......	....	....	....	....	.018

As expected for this gene order, all values increase from left to right.

Under the hypothesis of linkage of six genes responsible for reaction to races 1, 2, 5, 15, 28, and 128a, combinations number 2 and 3 of table 20 would be parental combinations. The number 1 combination would be largely of the F_1 hybrid type between the parental combinations.

Combinations 4 and 6 may be explained as the result of crossing over in region 28-5 of the genetic map. Combinations 7, 12, 13, and 15 may result from single crossing over also. Combinations 8, 10, and 11, seemingly double crossovers, may result from the union of two gametes from the same F_1 plant, each carrying a different single crossover, e.g. combination 8 from the union of single crossovers in the 128a-15 and 15-2 regions.

Combination 9, an apparent triple crossover, may result from the union of a double crossover in the 128a-15 and 15-2 regions with a single crossover in 2-28. Combination 5 seemingly has crossed over in four regions. It can be accounted for by the union of two double crossover gametes. Multiple crossovers in such a short map distance should be extremely rare. It is not the result of single crossovers in successive generations, since each of the bulked 103 lines traces back to an individual F_2 plant. Its genotype was determined by the genes carried by the two F_1 gametes which united. This gene order may not be the correct one. If loci 15 and 2 are interchanged, only one exceptional combination requires a double crossover, but then there are other inconsistencies.

Based on this analysis the exceptions in table 20 may be accounted for by 2, 7, 5, 4, and 7 crossovers, respectively, in the five regions from left to right in the linkage map.

No combination was homozygous for resistance to certain races and for susceptibility to others (table 20).

As shown by the chi-square tests for independence (table 18), association was not indicated between seedling reaction to race 3 and seedling reaction to each of the races 1, 2, 5, 15, 28, 128a, or to the collection of 18 races. It has already been shown (table 5) that the reaction to each of the races 1, 2, 5, 15, 28, and 128a was determined by a single genetic factor, while the reaction to race 3 and to the collection of races was determined by two genetic factors. Therefore, neither of the two factors responsible for reaction to race 3 was responsible for the reaction to races 1, 2, 5, 15, 28, and 128a. Also there was no indication of association between the two factors controlling reaction to race 3 and the two factors controlling reaction to the collection of races. Therefore, the two factor pairs responsible for reaction to the collection of 18 races were not the same factors involved in the reaction to race 3.

The reaction to race 3 was associated with the reaction to race 58 and also with the reaction to race 126 (table 18). Even though the reaction to races 3 and 58 was the same type of two factor interaction (15:1 in F_2, tables 13 and 14) the two genetic factors involved were not the same. This was shown by the fact that 34 out of the 103 lines gave different reactions to race 3 than to race 58 (table 19). Assuming that genes S1 and S2 were responsible for reaction to race 3 and genes S3 and S4 were responsible for reaction to race 58, the association of reaction to race 3 with reaction to race 58 may be explained by either of four possibilities: linkage of S1 with S3 and S2 with S4; linkage of S1 with S3 and independent inheritance of S2 and S4; or linkage of S2 with S4 and independent inheritance of S1 and S3; or that two of the four genes, either S1 and S3 or S2 and S4, are the same gene and that the other two are either independently inherited or linked. The data are not sufficient to distinguish between these possibilities.

The reaction of races 3 and 126 or 58 and 126 are a combination of relations, where the two types of segregation concerned are 15:1 and 13:3, respectively. Considering races 3 and 126 (table 19), 31 out of 103 F_4 lines reacted differently to the two races. The association of reaction to race 3 with reaction to race 126 may be due to one of the following:

1. One of the dominant genetic factors responsible for reaction to race 3 was also the dominant epistatic factor in the 13:3 interaction.
2. Genes responsible for reaction to race 3 were linked with those responsible for reaction to race 126.
3. Only two of the four genes responsible for reactions to races 3 and 126 were linked.

Table 22. Interrelationship of Leaf Rust Reaction, under an Artificial Field Epidemic, and Seedling Reaction in the Greenhouse of F_3 and F_4 Lines to a Number of Leaf Rust Races

Field reaction of F_3 lines	Seedling reaction of F_4 lines: Resistant	Segregating	Susceptible	Total
	Race 1			
R	......	2	......	2
Seg	8	15	1	24
S	14	40	22	76
Total	22	57	23	102
	Race 2			
R	......	2	......	2
Seg	7	15	2	24
S	14	40	22	76
Total	21	57	24	102
	Race 3			
R	1	......	1	2
Seg	2	15	7	24
S	2	39	35	76
Total	5	54	43	102
	Race 5			
R	......	2	......	2
Seg	5	16	3	24
S	12	40	24	76
Total	17	58	27	102
	Race 15			
R	1	1	......	2
Seg	7	16	1	24
S	15	39	22	76
Total	23	56	23	102

Field reaction of F_3 lines	Seedling reaction of F_4 lines: Resistant	Segregating	Susceptible	Total
	Race 28			
R	......	2	......	2
Seg	8	15	1	24
S	12	40	24	76
Total	20	57	25	102
	Race 58			
R	1	1	......	2
Seg	1	22	1	24
S	2	34	40	76
Total	4	57	41	102
	Race 126			
R	1	1	......	2
Seg	1	20	3	24
S	3	34	39	76
Total	5	55	42	102
	Race 128a			
R	......	2	......	2
Seg	6	17	1	24
S	15	40	21	76
Total	21	59	22	102
	Collection of 18 races			
R	......	2	......	2
Seg	3	15	6	24
S	5	43	28	76
Total	8	60	34	102

R = resistant, Seg = segregating, and S = suscepible.

For races 58 and 126 (table 18), 25 of the 103 lines tested had different reactions to these races (table 19). This showed that the genes involved in the reaction to race 58 were not the same as those involved in the reaction to race 126. The association of the reactions to these two races may be due to the same possible relationships mentioned in explaining the observed associations for races 3 and 126.

The interrelationships between leaf rust reaction, under artificial field epidemics, and seedling reaction in the greenhouse of F_3 and F_4 lines from Thatcher x II-39-2 to a number of leaf rust races are shown in table 22. Field reaction was not associated with seedling reaction to races 1, 2, 5, 15, 28, and 128a or to the collection of 18 races bulked (table 18). Field reaction was associated with seedling reaction to races 3, 58, and 126. Since field reaction is explainable on the basis of three factors, while the seedling reaction to each of these three races is due to two factors, there are many possible linkages which would explain the observed associations. It was impossible to determine which best explains the data.

The association between awnedness and seedling reaction to race 3 indicated in table 18 requires closer examination. The data on which that *P* value is based are in table 23. The chi-square test for independence, calculated on the data in this 3×3 contingency table with four degrees of freedom, is not entirely satisfactory since the calculated values in the upper horizontal row of cells are all less than 5. If each of these observed numbers is added to the cell below, making it a 2×3 table, the chi-square test for independence indicates no association, $P = 0.5$. It is probable there is no association, the only evidence for it being in the class resistant to race 3 with a frequency of only 5.

Table 23. Relationship between Awnedness of F_3 Lines and Seedling Reaction of Corresponding F_4 Bulked Lines to Race 3 of Leaf Rust

		Awnedness			
		Awnletted	Segregating	Bearded	Total
Race 3	Resistant	4	1	......	5
	Segregating	8	27	20	55
	Susceptible	9	24	10	43
	Total	21	52	30	103

Discussion and Summary

THE INHERITANCE of leaf rust reaction and of certain other characters was studied in the Thatcher x (Premier x Bobin-Gaza-Bobin) N.S. No. II-39-2 cross. Thatcher is a spring wheat variety susceptible to a large number of leaf rust races in both seedling and mature plant stages.

It was grown on a large acreage in the hard red spring wheat area of the United States after it was released by the Minnesota Agricultural Experiment Station in 1934. However, it is now grown mainly where leaf rust is not a problem because of its susceptibility to prevalent races of the causal organism of leaf rust, *Puccinia rubigo-vera tritici* (Erikss.) Carleton.

Premier x Gaza-Bobin-Gaza, N.S. No. II-39-2 is a Minnesota selection that showed good leaf rust resistance in the field until 1950 when it showed only moderate resistance. It is resistant to several leaf rust races in the seedling stage in the greenhouse.

In order to determine the mode of inheritance of leaf rust reaction in the field to a collection of races, the F_1, F_2, and F_3 progenies from the Thatcher x II-39-2 cross were grown, together with the parents, in the Rust Nursery at University Farm in the summer of 1950. Readings of a trace to 25 per cent of small to large pustules were recorded on II-39-2. Thatcher was susceptible, with an infection of 40 per cent of mid-sized to large pustules. The inheritance of mature plant reaction to a collection of leaf rust races in the field in the Thatcher x II-39-2 cross is explained by the action of three genetic factor pairs independently inherited. Any factor in the dominant condition would cause susceptibility.

Hashim *(9)* studied a Thatcher x Frontana cross and concluded that the inheritance of mature plant reaction to a collection of races in the field could be explained on a single factor pair basis, with resistance dominant. Evidently the II-39-2 parent used in the present study does not carry the dominant factor for resistance that Hashim found in Frontana. The results of both studies can be explained by assuming the following parental genotypes:

Thatcher	S S	S2 S2	S3 S3	r r
II-39-2	s s	s2 s2	s3 s3	r r
Frontana	S S	S2 S2	S3 S3	R R

It seems desirable to use these symbols rather than those suggested by Ausemus *et al. (4)*, until further experiments prove the correctness of the genetic explanation given.

The *R* factor for resistance would be epistatic to the *S* factors for susceptibility. A 3 resistant : 1 susceptible segregation would be expected in F_2 from the Frontana x II-39-2 cross if *Rr* were independently inherited, although four factor pairs would be segregating.

To determine the races to which II-39-2 is susceptible, leaves with leaf rust uredia were collected from both parents and one of the F_3 hybrids. These leaves were stored until the winter of 1950-51 when 16 monopustular isolates were obtained from them. Race 126 was present in 50 per cent of the isolates. Races 5, 28, 35, and 21 represented 31.25, 6.25, 6.25, and 6.25 per cent, respectively, of the isolates. Even though some of the isolates came from susceptible pustules on II-39-2, this parent was highly resistant in the seedling stage to these same isolates. Therefore, no conclusion can be drawn regarding the race or races that attacked II-39-2 in the field.

The inheritance of reaction in the seedling stage to individual races of leaf rust was studied using F_2 and F_3 progenies and F_4 lines from Thatcher x II-39-2. The races tested were 1, 2, 3, 5, 15, 28, 58, 126, 128a, and a collection of 18 races. Thatcher was susceptible in the seedling stage to all these races, while II-39-2 was resistant.

The reaction to races 1, 2, 5, 15, 28, and 128a was found to be determined by six different genetic factors, one factor for each race. Susceptibility was dominant. The reactions to these races were highly but not completely associated, suggesting linkage of these six genes. On this assumption, a linkage map was set up that fits closely the observed recombination values. Designating the genes by the race number, the gene order was 1-128a-15-2-28-5 with recombination values or map distances in successive regions of 0.9 ± 0.7, 1.0 ± 0.9, 1.0 ± 0.9, 0.9 ± 0.7, and 1.8 ± 1.1, respectively. Although the data agreed well with the hypothesis of linked genes, more genetic and cytological data are needed to prove its correctness.

The reaction to each of the races 3, 58, 126, and to the collection of 18 races was shown to be determined by two genetic factors. The reaction to races 3 and 58 was shown to be of the 15 susceptible : 1 resistant F_2 interaction type, but at least one of the factors controlling reaction to race 3 and race 58 was different. The reaction to race 126 was probably of the 13 susceptible : 3 resistant F_2 interaction type. No plant counts were made in the study of reaction to the collection of 18 leaf rust races and, therefore, it was not possible to determine the type of two factor pair interaction responsible for the reaction to this group of races.

It is of interest to point out that five lines were resistant to the collection of 18 races, but when tested to race 126, they segregated for resistance and susceptibility. Race 126 supposedly was included in the collection of 18 races. Furthermore, lines M151 and M261 were resistant to the collection of races but susceptible to race 126. Races 2, 5, 15, and 28 were also included in the collection of 18 races. The eight lines resistant to the collection of races were also resistant to races 2, 5, 15, and 28 with two exceptions. Lines M151 and M241 segregated for susceptibility to race 5. No explanation can be offered for these observed differences in results when race 126 was used alone as compared with the results when it was one of a collection of races.

There was no association between the reaction to races 1, 2, 5, 15, 28, and 128a and reaction to race 3. This indicates that there are two additional factors for reaction to race 3 which makes a total of eight different genetic factors that control the reaction to these seven races, if the reaction to the six races is due to six closely linked but different genes.

The reactions to races 1, 2, 5, 15, 28, and 128a were each associated with the reactions to races 58 and 126. The reaction to race 58 and the reaction to race 126 were associated. However, at least one of the factors controlling reaction to race 58 and race 126 was different since the association was not complete. There must be then at least nine different genetic factors that control the reaction to these eight races of leaf rust.

The reaction to race 3 was associated with the reaction to race 58 and with the reaction to race 126. This means that at least four different genetic factors control the reaction to races 3, 58, and 126.

If the associations, exclusive of the six closely linked factors, are due to one gene in common in each of the segregations, a minimum of ten genetic factors appear to control the reaction to the nine races studied. If the associations are due to linkage, then 12 genetic factors would control the reaction to the nine races studied. If the reaction to races 1, 2, 5, 15, 28, and 128a were explained as due to one single gene, the total number of genes would be five and seven, respectively. These do not include the factors for reaction to the collection of 18 races.

The large number of genetic factors found responsible for reaction to a rather limited number of leaf rust races indicates that the inheritance of leaf rust reaction in the Thatcher x II-39-2 cross is rather complex. It also explains why no F_4 lines were found to be as resistant as the II-39-2 parent. Lines M206 and M238 approached the resistance of the II-39-2 parent more closely than did any of the other lines. Line M206 was resistant to races 1, 2, 5, 15, 28, 58, 126, 128a, and to the collection of 18 races, but was susceptible in the field and it segregated for reaction to race 3. Line M238 was resistant to races 1, 2, 3, 5, 15, 28, 58, 126, and 128a but was susceptible in the field and segregated for reaction to the collection of 18 races.

Association was found between the seedling and six-leaf stage reactions of F_4 plants to a collection of 18 races. However, only 63 per cent of the 304 F_4 plants tested gave the same reaction in the seedling and six-leaf stages. Thirty-two per cent showed more resistance in the six-leaf stage than in the seedling stage, while 5 per cent showed less resistance in the six-leaf stage than in the seedling stage.

The inheritance of stem rust reaction to a collection of races was studied in the field during the summer of 1950. Thatcher was the more resistant parent with an average infection of 18 per cent. The II-39-2 parent had an average infection of more than 32 per cent. One major genetic factor appeared to control the reaction to stem rust in the field. Susceptibility was dominant.

Thatcher is awnletted and II-39-2 is bearded. The difference was dependent on a single genetic factor with the awnletted condition dominant.

Conclusions

1. In a cross of Thatcher x (Premier x Bobin-Gaza-Bobin) N.S. No. II-39-2, the inheritance of mature plant reaction to a mixture of leaf rust races in the field is explained as due to the action of three genetic factor pairs independently inherited. Any factor in the dominant condition causes susceptibility.

2. Seedling reaction to races 1, 2, 5, 15, 28, and 128a appears to be determined by six different genetic factors, one for each race. Susceptibility is dominant. The reactions to these races were highly but not completely associated, suggesting linkage of these six genes. Assuming linkage, a gene order was set up that fits the observed recombination values closely.

Designating the genes by the race number, the gene order is 1-128a-15-2-28-5 with recombination values or map distances in successive regions of 0.9 ± 0.7, 1.0 ± 0.9, 1.0 ± 0.9, 0.9 ± 0.7, and 1.8 ± 1.1, respectively. Although the data agreed with the linkage hypothesis, more genetic and cytological data are needed to prove its correctness.

3. The reaction to each of the leaf rust races 3, 58, 126, and to a collection of 18 races bulked is determined by two genetic factors. The reaction to races 3 and 58 is of the 15 susceptible : 1 resistant F_2 interaction type. The reaction to race 126 probably is of the 13 susceptible : 3 resistant F_2 interaction type.

4. Association studies of seedling reactions to individual leaf rust races indicate that a minimum of 10 and possibly 12 genetic factors control the seedling reactions to races 1, 2, 3, 5, 15, 28, 58, 126, and 128a in the material studied. If the reactions to races 1, 2, 5, 15, 28, and 128a were explained as due to a single gene, the total number of genes would be five and seven, respectively.

5. Seedling and six-leaf stage reactions of F_4 plants to a collection of 18 races are associated. However, only 63 per cent of the 304 F_4 plants tested gave the same reaction in the seedling and six-leaf stages. Thirty-two per cent of these plants showed more resistance in the six-leaf stage than in the seedling stage, while 5 per cent showed less resistance in the six-leaf stage than in the seedling stage.

6. The relatively large number of genetic factors segregating in this cross may account for the difficulty in recovering lines equal in resistance to the original resistant II-39-2 parent.

7. One major genetic factor appears to control mature plant reaction in the Thatcher x II-39-2 cross to a number of stem rust races in the field.

8. A single factor pair controls the inheritance of awnedness. The awnletted condition of Thatcher is dominant over the bearded condition of II-39-2.

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