A STUDY OF THE INHERITANCE OF REACTION TO PUCCINIA GRAMINIS TRITICI IN THE DURUM WHEATS, MINDUM, CARLETON, GAZA AND IUMILLO UNDER FIELD CONDITIONS.

by

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INTRODUCTION

Stem rust of wheat, *Puccinia graminis tritici* Eriks. and Henn.,has been *the* major rust problem throughout the wheat growing areas of the world. For many years, seemingly cyclical epidemics threatened to wipe out the entire wheat crop on the Great Plains. The greatest of these epidemics, as reported by Clark (8), occurred in 1904, 1916, and 1935. In the 1935 epidemic, losses from stem rust in North Dakota alone, were estimated at $100,000,000. These epidemics resulted in a demand for rust resistant varieties of common and durum wheats.

Stakman and Piemiesel (26), 1917, reported the existence of physiologic specialization within the rust fungus, but the means by which the different races arose was not clearly understood until Craigie (10), 1927, discovered their mode of hybridization on the barberry. This information was of great value in the breeding of rust resistant varieties.

Unfortunately, when varieties resistant to prevalent races were produced, those races which had previously competed unsuccessfully with other races or those which were newly hybridized, became predominant. Such a race is 15B which, at the present time, is capable of attacking all commercially grown varieties of the Great Plains.

Many sources of resistance have been investigated with primary importance placed on their incorporation into commercial wheat varieties. Hayes et al. (13), in 1914, crossed Marquis × Iumillo, the latter a resistant durum variety, and selected the rust resistant common wheat variety Marquillo. This variety was found to be unsuitable for milling, but a sister selection was used in the double cross (Marquis × Iumillo) × (Marquis × Kanred), from which the high-quality rust-resistant variety Thatcher was selected.

In 1916, McFadden (17) succeeded in transferring the resistance of Yaroslav emmer to Marquis and selected the two rust resistant varieties Hope and H-44. These were selected for their near immunity to stem rust in the field. Goulden et al. (11), 1928, found that H-44 carried two types of resistance, namely mature plant resistance to many races and physiologic resistance to some.

Another excellent source of resistance was found in a group of highly resistant common wheats developed by Burton in Kenya Colony. The origin of the resistance in these varieties is unknown, but Macindoe (15), on the basis of the grain characters, considers that it may be of durum origin.

Pridham, as reported by Ausemus (2), transferred the resistance of Triticum timopheevi to the common wheat Steinwedel, and selected the variety Timstein which was resistant to races of stem rust prevalent in Australia.

A number of the factors for resistance, as may be seen, were of durum origin. The present investigation was designed to determine the mode of inheritance of reaction to stem rust of four of the durum varieties in the field. In addition, an attempt was made to explain a chlorophyll deficiency which was observed in the crosses involving Iumillo. Finally, Gaza, bright green, when crossed with Iumillo, blue green, showed a definite segregation in colour. A record was made of this segregation.

REVIEW OF LITERATURE

Stem rust of wheat, because of its major importance, has interested plant breeders and plant pathologists from a very early date. Biffen (5) noted that Thomas Knight, in 1815, suggested that rust-resistant wheat varieties might be produced. He also reported that Farrer, in 1899, took detailed notes of rust reaction on a number of wheat varieties in Australia and came to the conclusion that susceptibility to stem rust was hereditary. In 1905, Biffen (5) investigated the inheritance of the resistance to Puccinia glumarum (Schm.) Eriks. and Henn. in a cross between the susceptible variety Red King and the resistant variety Burt. It was found that the F_1 was susceptible and that the F_2 segregated 3 susceptible to 1 resistant. In a later paper, the same author (6) reported that relatively immune hybrid forms of wheat bred true and that immunity appeared to be independent of any discernible morphological character. He implied that definite characters for resistance to stem rust were inherited independently of other factors.

This early work indicated to plant breeders that rust resistant varieties could be produced through hybridization between susceptible but otherwise desirable varieties and others which carried the required resistance.

Ausemus (2) has published an extensive review of genetic studies dealing with durums, H-44-24, Hope, Kota, Kanred, the Kenya varieties and Timstein sources of resistance. Investigations reported, which did not include durums as a source of resistance, are not reviewed here, as they are not directly applicable to the present study.

Carleton (7), 1904, reported that early plant breeders recognized that some of the durums, emmers and spelts carried considerable resistance to stem rust. Of the durum varieties, Iumillo appeared to be practically immune. Hence, this variety was widely employed in early breeding work. The following extensive studies of the Iumillo resistance present an indication of its mode of inheritance.

In 1919, Waldron and Clark (as reported by Ausemus (2)) found that Iumillo, when crossed with common wheat varieties, produced a susceptible F_1, while the F_2 segregated in a complicated manner. In many cases, none of the plants were as resistant as the Iumillo parent. Peterson and Love (22), 1940, reported that they, also, had been unable to recover the full immunity of Iumillo in a variety of 42-chromosome wheat.

Hayes et al. (13), 1920, crossed a number of resistant varieties, including Iumillo, with a number of common wheat varieties. Where Iumillo was involved, the F_1 was found to be fully as susceptible as the common wheat parent. In the F_2 there appeared to be a close linkage between the durum characteristics and rust resistance, as it was relatively easy to select resistant "durum-like" lines, but was difficult to find resistant "vulgare-like" lines. The significant fact, however, was that some crossing over did occur, resulting in occasional common wheat lines which possessed the durum resistance. The resistance of this variety has been the object of several genetic studies. The variety Marquillo was selected from one of these crosses, Marquis × Iumillo.

Ausemus (1), 1934, reported the results from crosses of Hope × Marquillo and Marquillo × Supreme. In the first cross, Hope × Marquillo, it was noted that mature plant reaction appeared to depend on three or more factors. The mature plant semi-resistance of Marquillo, was apparently dependent on factors which were not allelomorphic to the Hope type factor for mature plant resistance. In the cross, Marquillo × Supreme, at least three genetic factors were indicated by the stem rust reaction. Ausemus observed that the Hope × Marquillo cross exhibited abnormal chromosome behaviour in F_3. This abnormality was believed to have originated in Iumillo. Similar results were obtained by Myers and Powers (18) in Marquillo,and by Peterson and Love (22) in Iumillo. The latter authors found chromosome numbers varying from 38 to 43 in "vulgare-like" lines.

Clark and Ausemus (9), 1928, in the cross Marquillo × Red Bobs, found that susceptibility to stem rust was dominant.

Neatby and Goulden (19), in a cross of Marquillo × H-44-24, found that two or more factors were contributed by Marquillo. In the three-way cross, Marquillo × (Marquis × Kanred), three or more factors were indicated. In addition, Marquillo, in crosses with Reward or Garnet, appeared to carry a number of factors governing resistance.

Waddell (27), 1940, in the cross Iumillo × Mindum, reported the presence of two types of resistance in Iumillo. One of these gave resistance from the seedling stage to maturity. The second type gave resistance only in the mature plant stage.

A sister selection of Marquillo was used by Hayes et al. (14), 1925, in the double cross (Marquis × Iumillo) × (Marquis × Kanred). Kanred, a winter wheat, was known to have physiologic resistance to several races. The Marquis × Kanred portion of the cross showed that resistance was governed by a single factor. In the Marquis × Iumillo portion, resistance appeared to be governed by two factors which were completely independent of the factor in the Marquis × Kanred portion. Thatcher was selected from this cross.

Ausemus and Koo (4), 1951, published a comprehensive study of crosses involving Thatcher, Newthatch and Timstein. In the cross Thatcher × Timstein, resistance was explained on the basis of two complementary factors and, as Timstein was susceptible in the field, it was assumed that Thatcher contributed these resistant factors. In greenhouse tests where F_3 lines were tested to physiologic races, the reaction to any single race was shown to be conditioned by one factor pair, with resistance dominant. Thatcher itself was found to carry high resistance to a group of races, 17, 19, 29, 69, 80 and 139. This high resistance was epistatic and non-allelic to the resistance of Timstein. In addition, Thatcher had a somewhat lower resistance to a second group of races, 16, 24, 24A, 52, 59, 59A, 90 and 116, but was susceptible to a third group of races, 11, 34, 36, 38, 56 and 133, as well as 15B.

The papers reviewed, particularly those of Waddell (27), 1940, and Hayes et al. (14), 1925, indicate that Iumillo carries at least two factors for resistance.

Several studies have been made on other durum varieties. Notable among these are the studies conducted on Mindum.

In 1921, Puttick (23) crossed Mindum × Marquis. The progeny were tested to races 1 and 19 in the greenhouse. Mindum was susceptible to race 19 and resistant to race 1, whereas Marquis showed the opposite reaction. The F_2 progeny segregated to give all gradations between immunity and complete susceptibility. An interesting method was employed, which consisted of testing to one of the races, removing the infected leaves, and re-inoculating the same plants with the second race.

Harrington (12), 1925, tested a cross of Mindum × Pentad to race 1. The resulting data indicated the presence of two factors.

A Mindum factor appeared dominant for immunity, and a Pentad factor dominant for slight resistance. With race 34, to which Mindum is susceptible and Pentad resistant, more than one factor for resistance was indicated. Reaction to race 21 was similar to the reaction to race 34, and was believed to be controlled by the same factor. A negative correlation was obtained between greenhouse reaction to race 1 and the reaction to a mixture of races in the field, but no correlation could be demonstrated between the reaction of races 34 and 21 in the greenhouse and field resistance.

Waddell (27), 1940, in the cross Iumillo × Mindum, found that field reaction was correlated with greenhouse reaction to race 21. As a result, the inheritance of reaction was considered to be relatively simple. However, a single factor for resistance was not indicated by the data.

Macindoe (16), 1948, in crosses between the resistant (Gaza × $Bobin_2$) with the two susceptible varieties Eureka and Pusa 111, found that a single major factor R_3 governed resistance in the field, as well as seedling resistance to race 34 in the greenhouse. In (Gaza × $Bobin_2$), a second factor for moderate resistance to race 19 was named R_4. As Bobin is a susceptible common wheat variety, the resistance observed in this cross must have been contributed by the Gaza parent.

The author was unable to find literature in which Carleton was used in an inheritance study. In general, however, it has been noted in field testing that Carleton carries a higher resistance than Mindum. It was assumed that this increased resistance was directly attributable to its Vernal emmer parent.

In summation, the resistance of Iumillo would appear to be conditioned by at least two factors, one being of major importance, and a second of minor importance. Mindum does not carry high resistance to stem rust, but is known to be resistant to a number of races. Gaza is believed to carry one major and one minor factor for resistance to Australian races. Insofar as could be determined, the factors for resistance which are present in Carleton have not been studied, but Carleton has been found to be more resistant than Mindum in the field. This greater resistance is assumed to have been contributed by Vernal emmer.

MATERIALS AND METHODS

Varieties

The varieties Carleton, Mindum, Gaza and Iumillo were chosen for this investigation. These particular varieties were selected because in field tests, the two commercial varieties, Carleton and Mindum, were only moderately resistant to stem rust, while the two commercially unsuitable varieties, Gaza and Iumillo, were nearly immune and consequently represented an available source of resistance. These 4 varieties are listed below:

Mindum	R.L. 1344*	C.A.N. 1418**
Carleton	R.L. 1663	C.A.N. 3588
Iumillo	R.L. 7	C.A.N. 1356
Gaza	R.L. 1664	C.A.N. 3529

According to Clark (8), Mindum was selected at Minnesota by C. P. Bull, H. K. Hayes and J. H. Parker from an admixture of durum wheat in a spring wheat sample, and was distributed in 1917. It is an amber durum of high macaroni quality, but is moderately susceptible to stem rust.

Carleton was developed by Smith (24) at the North Dakota Agricultural Experiment Station from a Vernal emmer × Mindum cross made in 1930. Rust resistant lines were selected and backcrossed to Mindum. After further selection, a second backcross was made from which Carleton was derived. In the durum wheat area of the North Central Great Plains,

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*Laboratory of Cereal Breeding Accession Number.

**Canadian Accession Number.

Carleton has consistently proven itself to be more resistant to stem rust than is Mindum. It is an amber durum with high macaroni quality.

Iumillo, according to Peterson and Love (22), was introduced into North America from Italy in 1901. It has been reported, as previously outlined, to be highly resistant to stem rust, but it was early recognised that the variety comprised a number of strains with varying degrees of resistance. However, Newton et al. (20) tested one strain of Iumillo to 22 physiologic races of Puccinia graminis tritici and found it immune to all of them in the seedling stage. This was the strain which was used in this study. Several workers have found, inexplicably, that the immunity of Iumillo is unstable. The progeny always contain a few susceptible plants. Iumillo is a red durum variety which is not suitable for the macaroni trade.

Correspondence with Dr. S. L. Macindoe revealed that Gaza was introduced into Australia in 1917 from southern Palestine by Mr. Williams, late Experimentalist of the Bathurst Experiment Farm. In 1924, Pridham sent a sample of Gaza to Professor Waterhouse, who subsequently used it in the breeding of Gabo. Gaza is a white durum which is unsuitable for the production of macaroni.

Rust Study

Diallel crosses of these 4 varieties were made in 1947, at the Laboratory of Cereal Breeding, by D. H. Fraser*. The F_1 population was grown in the following summer, but the 3 Iumillo crosses were accidentally

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destroyed. The author took over this thesis project in 1949, and made new crosses using the same parental material. At the same time, the F_2 population of the 3 crosses, Gaza × Mindum, Gaza × Carleton and Carleton × Mindum, were grown in the field. During the following winter, the F_1 of the three Iumillo crosses was grown.

In 1950, F_2 families of all crosses, as well as F_3 lines of those which did not involve Iumillo, were space-seeded in a rust nursery. Seven sets of the 4 parents were placed throughout the block for comparison. The nursery was subjected to an artificial epidemic of stem rust. All F_2 families and F_3 lines were pulled and later classified for stem rust percentages in the laboratory.

In 1951, F_3 lines of the 3 Iumillo crosses were selected at random from the F_2 population of the preceding year. These lines were space-seeded with 5 sets of parents in a nursery similar to that used in 1950. Stem rust readings were again taken in the laboratory.

Inoculation

Inoculation rows of a mixture of Little Club, Garnet and Red Bobs were sown in both years between each of the series in the nursery. These varieties are susceptible to most races of stem rust.

Rust spores were mixed with talc in a ratio of approximately 1 part spores to 50 parts talc. The races used in the epidemic included 15B and races 56, 17, 38, 69 and 19, which were common to this area. All races were applied in approximately equal proportions with the exception of 15B, which made up $\frac{1}{4}$ of the inoculum. The spore-talc mixture was applied to the inoculation rows with a garden duster in the late evening, when dew was beginning to appear.

Plant Examination

An arbitrary scale for stem rust classification on a per cent basis was devised, as shown in Appendix A, in such a manner as to approximate, as nearly as possible, the scale outlined in the chart by Peterson et al. (21). The percentage of rust on individual plants of each F_3 line was recorded. From these percentages the average reaction of each line was determined, and a frequency distribution of these values was established.

Stem rust examination in the F_2 was found to be unsatisfactory, because of the difficulty in establishing definite classes. Thus, the F_2 plants were classified on the basis of their breeding behaviour in the F_3.

A Study of Colour

As was mentioned earlier, the F_2 and F_3 of crosses involving Iumillo showed a number of plants which appeared to be deficient in chlorophyll. A study was undertaken to determine whether this was caused by a chromosome abnormality in Iumillo. Meiotic samples were taken from F_1 plants in the greenhouse in 1950. These were studied cytologically by means of the acetocarmine smear technic, as outlined by Luther Smith (25). No abnormalities were observed. Additional samples taken from F_3 plants which were chlorophyll deficient in the field, failed to exhibit abnormal behaviour at meiosis. Consequently, counts were made of the F_3 lines which were normal, segregating and chlorophyll deficient. Simultaneously, counts were made for the segregation of Gaza colour and Iumillo colour. Gaza is bright green, whereas Iumillo is bluish green. These characters segregated into distinct classes.

Gene Nomenclature

Rust resistant genes were named according to the system proposed by Ausemus et al. (3). This system suggests the use of "Sr" for stem rust resistance, followed by a subscript. It is preferable that this subscript should be the first letter of the name of the variety in which the gene is located.

RESULTS AND DISCUSSION

Rust Study

Figures 1 to 6 show the distribution for the average stem rust reaction of F_3 lines in the field. In addition, the average reactions of the parental plots are included in the lower part of each figure. Data were available for parental reactions in both 1950 and 1951. Table I presents the ranges of parental reactions during these two years.

Table I

PARENTAL RUST REACTIONS IN PER CENT FOR 1950 AND 1951

Varieties	Range of Reaction in per cent stem rust	
	1950	1951
Gaza	0 - 1	0 - 1
Iumillo	0 - 1	0 - 2
Carleton	5 - 17	21 - 28
Mindum	16 - 41	40 - 58

An examination of this table reveals a notably higher infection during the second year, particularly in the 2 most susceptible parents. Also, it may be noted that the range of reaction of Mindum and Carleton is relatively wide as compared to the reaction of Gaza and Iumillo, which remained at a level of near immunity. Iumillo, however, under the higher infection of 1951, showed 1 plot (figure 4) which was slightly more susceptible than the other 4 plots. Carleton, in both years, was more resistant than Mindum. The higher resistance of Carleton must have been derived from Vernal emmer, as Mindum was its other parent.

In spite of the fact that a large proportion of 15B inoculum was used, only traces of it were observed in the field. This race seems to compete poorly with other races. As a result, it might be advisable, in producing an epidemic, to use, in the inoculation rows, some variety such as Lee, which is resistant to common races and susceptible to 15B.

It has been noted in the Literature Review that there were indications of two factors in Iumillo, and a major and minor factor in Gaza. The inheritance of stem rust resistance in Carleton was unknown, but evidently it carried a higher resistance than Mindum.

Figures 1 to 3 graphically illustrate the rust reactions of the crosses grown in 1950. The lines shown in the cross Gaza × Carleton (figure 1) exhibit a greater tendency toward high resistance than those in the cross Gaza × Mindum (figure 2); also, there are groups of 4 and 3 lines, respectively, in the two cases which are in a susceptible class by themselves. However, in figure 1 these 4 lines comprise approximately 1/64 of the total number , while in figure 2, the 3 lines comprise about 1/15 of the total. This would suggest the presence of a three-factor difference between Gaza and Carleton, and a two-factor difference between Gaza and Mindum. The most susceptible lines, in figure 1, are more susceptible than the Carleton parent, while in figure 2, there was no transgressive segregation. In the Carleton × Mindum cross (figure 3), there are 2 lines which exhibit a greater degree of susceptibility than the Mindum parent. As these 2 lines comprise about 1/15 of the total number, there is some indication of a two-factor difference between Carleton and Mindum. Further, the fact that these 2 lines are more susceptible than Mindum, suggests that Mindum carries one of these factors for resistance. This factor exhibits a lesser degree of resistance than the Carleton factor.

Figures 4 to 6 illustrate the rust reactions of the crosses grown in 1951. In the Carleton × Iumillo cross (figure 4), 2 lines are shown which are distinctly more susceptible than any of the remaining lines. These 2 lines comprise exactly 1/64 of the total number, indicating a difference of three factors between Carleton and Iumillo. The most susceptible lines have a lower resistance than the Carleton parent, which suggests that they are of a genotype which governs a lower degree of resistance than does the Carleton genotype. In the Mindum × Iumillo cross (figure 5), there appear to be 3 breaks in the frequency distribution at the 12, 18 and 26% levels of infection. These breaks divide the lines into 4 groups in a ratio of about 9 : 3 : 3 : 1, indicating a two-factor difference between Mindum and Iumillo. There is no transgressive segregation, which suggests that the least resistant segregates from this cross are of the Mindum genotype. Finally, in the Gaza × Iumillo cross (figure 6), the distribution indicates a two-factor difference. The transgressive segregation observed, suggests the presence of segregating genotypes, which are responsible for greater susceptibility than either parent.

From a consideration of these observations, the following hypothesis was formulated with respect to parental genotypes:

Gaza - Sr_G Sr_G sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M

Iumillo - sr_G sr_G Sr_I Sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M

Carleton - sr_G sr_G sr_I sr_I Sr_C Sr_C sr_M sr_M

Mindum - sr_G sr_G sr_I sr_I sr_C sr_C Sr_M Sr_M

It is proposed that the major factor of Gaza, Sr_G, is responsible for slightly greater resistance than the major factor Sr_I found in Iumillo. Sr_M, a Mindum factor, also thought to be present in Gaza and Iumillo, is believed to impart a minor degree of resistance. Sr_C is considered to be a factor responsible for the moderate resistance of Carleton. A factor Sr_C', allelic to Sr_C, appears to be present in Gaza and Iumillo, and apparently imparts almost the same degree of resistance as Sr_M.

The following paragraphs present a discussion of the segregations obtained in the different crosses, and their fit to the foregoing hypothesis. Only those factors which are segregating in a specific cross will be discussed. The segregating genotypes for each cross are listed in Appendix B.

In the first cross, Gaza × Carleton (Sr_G Sr_G Sr_C' Sr_C' Sr_M Sr_M × sr_G sr_G Sr_C Sr_C sr_M sr_M), $\frac{1}{4}$ of the lines had the same resistance as the Gaza parent. This seemed to indicate that the major factor of Gaza, Sr_G, in the homozygous condition, was completely epistatic to factor Sr_C. There are 3 natural breaks which occur at the 13, 18 and 26% levels of infection. The most susceptible group, consisting of 4 lines, was believed to have the genotype sr_G sr_G Sr_C' Sr_C' sr_M sr_M. The more susceptible of the 2 intermediate groups of 6 lines was believed to have the additional resistance contributed by Sr_M. The more resistant of the 2 groups of 6 lines was thought to carry the resistance of Sr_C without the resistance of Sr_M, and all other genotypes were grouped in the remaining lines. The observed ratio of 36 : 90 : 6 : 6 : 4, closely approaches that which was calculated, 35.5 : 90.9 : 6.7 : 6.7 : 2.2, on the basis of a 16 : 41 : 3 : 3 : 1 segregation. A Chi-square test for

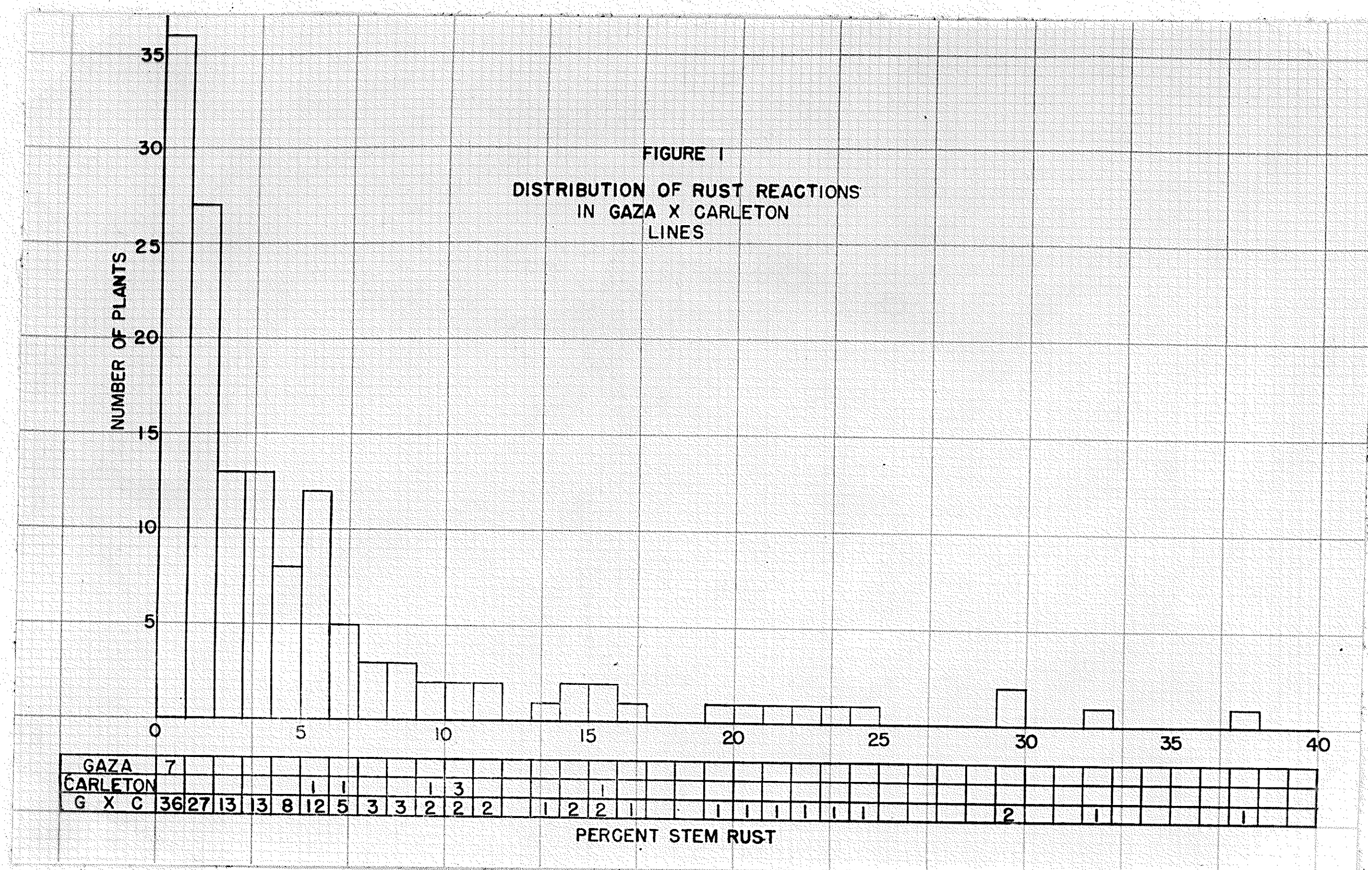

FIGURE I

DISTRIBUTION OF RUST REACTIONS
IN GAZA X CARLETON
LINES

goodness of fit gave a P value of .80. This indicates that the deviation from expected was no greater than would be expected on the basis of chance alone.

In figure 2, Gaza × Mindum (Sr_G Sr_G Sr_C' Sr_C' × sr_G sr_G sr_C sr_C), there are 2 natural breaks at the 16 and 24% levels of infection. The most susceptible group (3 lines) was considered to be of the genotype sr_G sr_G sr_C sr_C having only the resistance of Sr_M, and the intermediate group (9 lines) was considered to have the additional resistance contributed by Sr_C'. All other genotypes were grouped in the remaining lines. The observed ratio of 51 : 9 : 3 closely approaches that which was calculated, 47.2 : 11.8 : 3.9, on the basis of a 12 : 3 : 1 segregation. A Chi-square test gave a P value of .56, which indicates a close fit. As the group of susceptible lines in figures 1 and 2 were nearly equal in susceptibility, it was considered that the factors Sr_M and Sr_C' imparted approximately equal degrees of resistance.

The Carleton × Mindum (Sr_C Sr_C sr_M sr_M × sr_C sr_C Sr_M Sr_M) F_3 lines are shown in figure 3. Unfortunately, there were only 46 lines available, so that all classes could not be accurately distinguished. However, there is an indication of 4 separate groups, but only the 2 most susceptible lines appear to be distinctly divergent from the remaining lines. These 2 lines were considered to be of the genotype sr_C sr_C sr_M sr_M. A second division might be made at the 23% level. All lines to the left of this level would then be considered to carry both Sr_C and Sr_M. All other genotypes were believed to be represented in the intermediate group between the 23 and 41% levels. The observed ratio of 23 : 21 : 2 closely approaches that which was calculated, 25.9 : 17.2 : 2.9, on the basis of a 9 : 6 : 1 segregation. A Chi-square test gave a P value

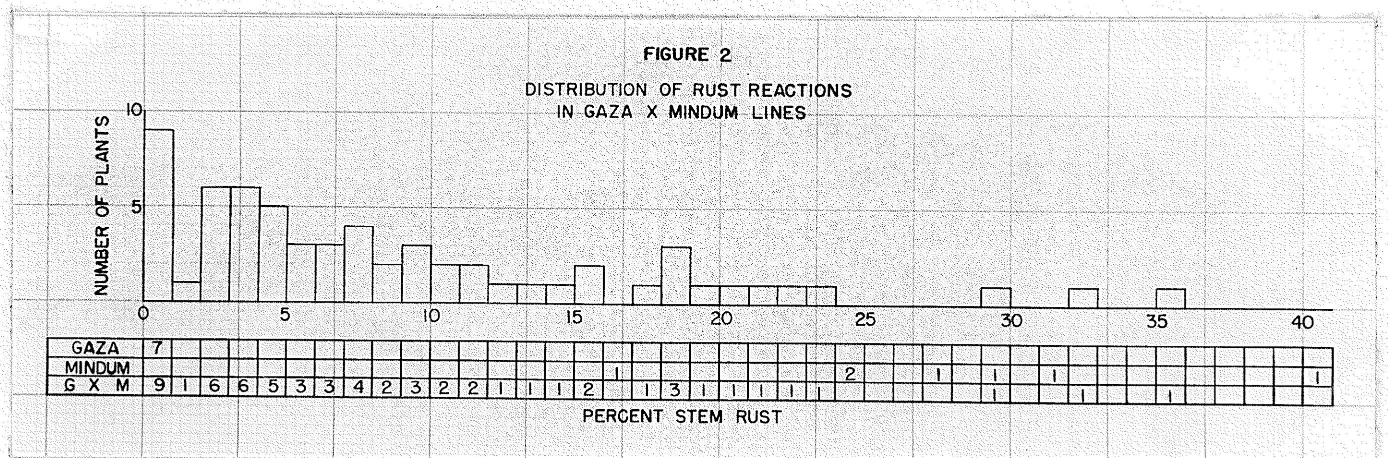
FIGURE 2
DISTRIBUTION OF RUST REACTIONS
IN GAZA X MINDUM LINES
NUMBER OF PLANTS
GAZA
MINDUM
G X M
PERCENT STEM RUST

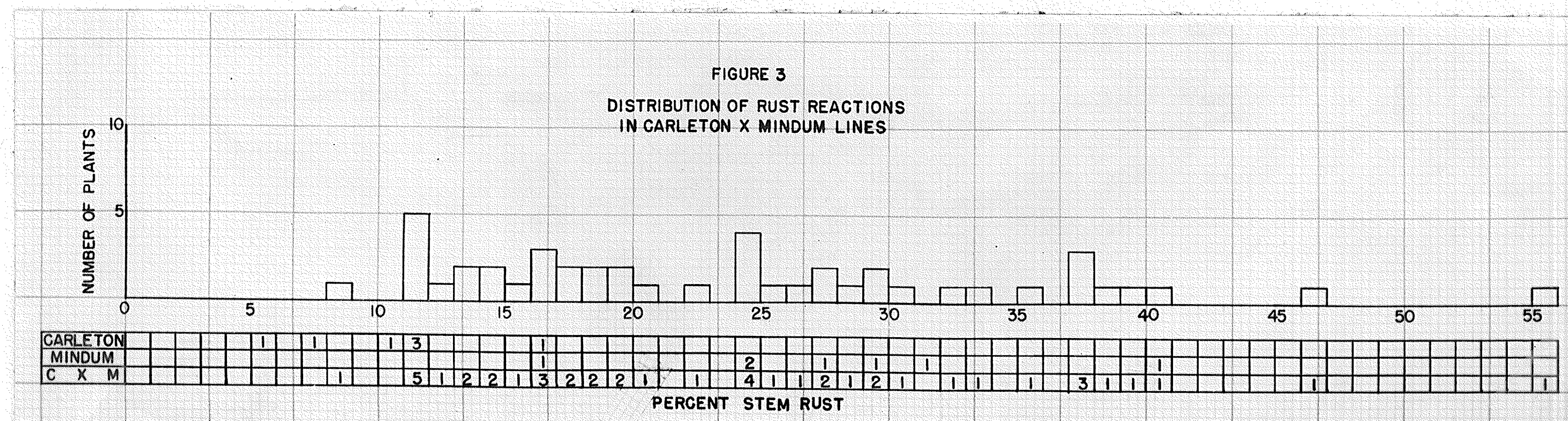
FIGURE 3
DISTRIBUTION OF RUST REACTIONS
IN CARLETON X MINDUM LINES
NUMBER OF PLANTS
CARLETON
MINDUM
C X M
PERCENT STEM RUST

of .49. In this cross Carleton is the more resistant parent. In figure I, the position of the lines considered to be of the Carleton genotype, are comparable to Carleton in reaction, whereas in figure 3, the lines of this genotype have been shifted toward a slightly more susceptible reaction. This shift could have been caused by a greater "build-up" of inoculum in this, the most susceptible cross. Unfortunately, a direct comparison could not be made, as no Mindum check occurred in that section of the nursery.

The Carleton × Iumillo (sr_I sr_I Sr_C Sr_C sr_M sr_M × Sr_I Sr_I Sr_C' Sr_C' Sr_M Sr_M) F_3 lines of figure 4, in contrast to the Gaza × Iumillo cross of figure I, are distributed more evenly over the range between the parental reactions. Thus, Sr_I does not appear to have the same epistatic effect as Sr_G does over Sr_C. An examination of the distribution in figure 4 reveals 3 natural breaks which separate groups of 6, 2 and 2 lines, respectively, from the major group. The lines of the most susceptible group were considered to have the genotype sr_I sr_I Sr_C' Sr_C' sr_M sr_M. The more susceptible of the 2 intermediate groups (2 lines) was considered to carry the additional resistance contributed by Sr_M. The more resistant of the 2 intermediate groups (6 lines) was believed to have the factor Sr_C, in the absence of Sr_M. All other genotypes were considered to be represented in the remaining lines. The observed ratio of 118 : 6 : 2 : 2, closely approaches the calculated, 114 : 6 : 6 : 2, on the basis of a 57 : 3 : 3 : 1 segregation. A Chi-square test gave a P value of .41. It was observed in the field that a higher degree of infection was attained in the section of the nursery where this cross was grown, than in the portion occupied by the Mindum × Iumillo cross. This resulted in a relatively higher reading than would be suggested by the parental checks.

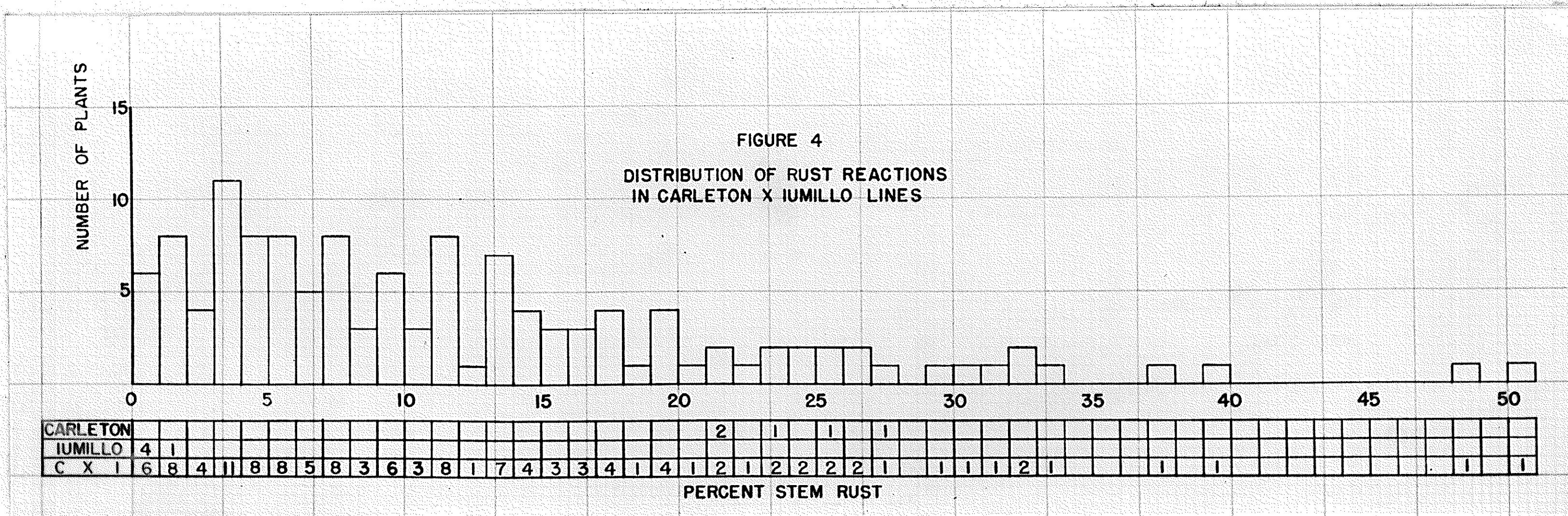

FIGURE 4

DISTRIBUTION OF RUST REACTIONS IN CARLETON X IUMILLO LINES

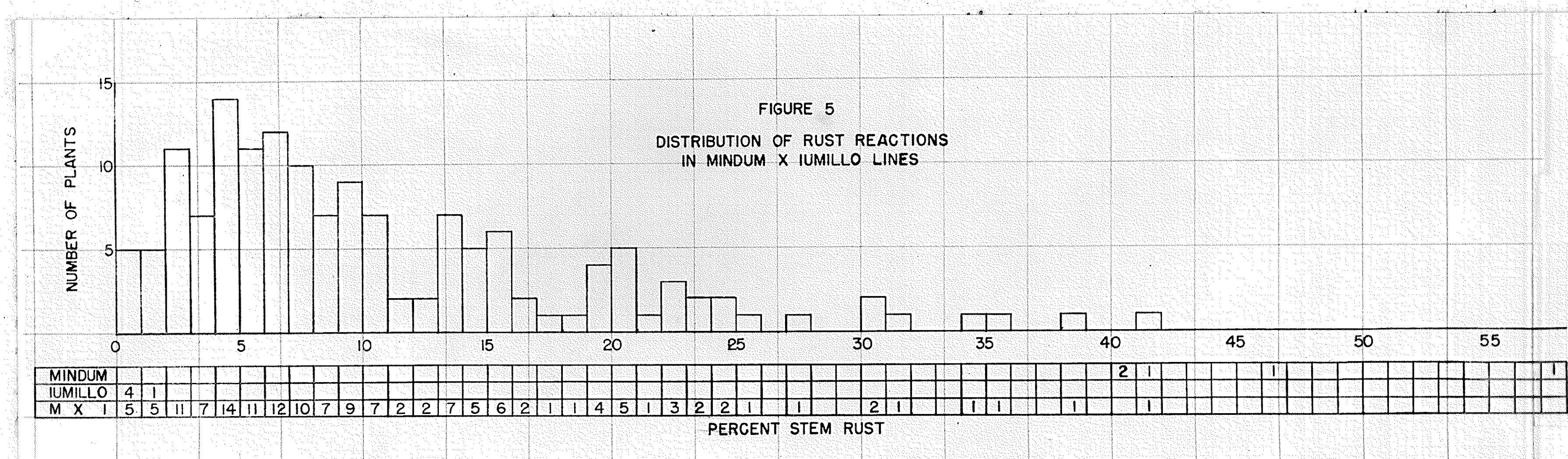

FIGURE 5

DISTRIBUTION OF RUST REACTIONS IN MINDUM X IUMILLO LINES

In the Mindum × Iumillo (sr_I sr_I sr_C sr_C × Sr_I Sr_I Sr_C' Sr_C') F_3 lines of figure 5, there appear to be 4 modal classes. Lines to the right of the 26% level of infection were considered to have the genotype sr_I sr_I sr_C sr_C. Arbitrary divisions might be made at levels of 12 and 18% infection, which are the low frequency points in the group of lines to the left of the 26% level of infection. The observed ratio of 100 : 23 : 19 : 8 approaches that which was calculated, 84.4 : 28.1 : 28.1 : 9.4, on the basis of a 9 : 3 : 3 : 1 segregation. A Chi-square test gave a P value of .08. This low P value, although not indicating a significant difference, is in accord with the observation that the degree of infection was not as great in this portion of the nursery. This resulted in too many lines appearing in the most resistant group. On the basis of a 15 : 1 segregation, the observed ratio of 142 : 8 approaches the calculated 140.6 : 9.4, with a P value of .66, indicating a better fit to this ratio.

The distribution of the line reactions in the cross between the most resistant parents, Gaza × Iumillo (Sr_G Sr_G sr_I sr_I × sr_G sr_G Sr_I Sr_I), is shown in figure 6. In the parental plots, Iumillo exhibited a slightly higher degree of susceptibility than Gaza. This suggests a lesser degree of resistance, resulting from Sr_I than from Sr_G. In relation to parental reactions, one might place the first 2 classes together as having a reaction similar to that of the parents. It was considered that this combined class would consist of genotypes which carried Sr_G with or without Sr_I, and Sr_I in the homozygous condition without Sr_G. In the remaining lines, there appears to be a break at the 5 or 6% level of infection. The 6% level was chosen, and all the lines showing greater infection were considered to be recessive for Sr_G and Sr_I. Those lines between the 6%

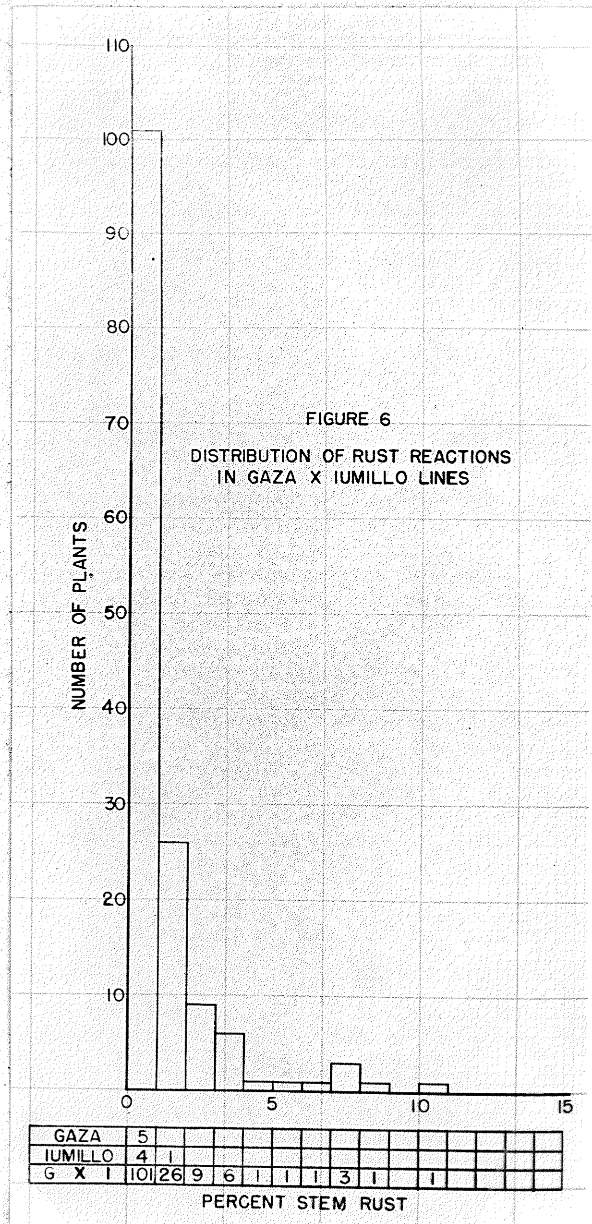

FIGURE 6

DISTRIBUTION OF RUST REACTIONS IN GAZA X IUMILLO LINES

GAZA	5														
IUMILLO	4	1													
G X I	101	26	9	6	1	1	1	3	1		1				

PERCENT STEM RUST

level and the parental types were considered to carry Sr_I in the heterozygous condition without Sr_G. The observed ratio of 127 : 17 : 6 closely approaches the calculated, 121.9 : 18.8 : 9.3, on the basis of a 13 : 2 : 1 segregation. A Chi-square test gave a P value of .46. Considering the genotype of the most susceptible lines, it would be expected that they would show a higher degree of infection. However, as this is the most resistant cross, there would be a tendency to"build-up" less inoculum in these lines than in those of the other 5 crosses.

The proposed hypothesis for the parental genotypes appears to be internally consistent under the conditions prevailing in 1950 and 1951.

Colour Study

In the cross Gaza × Iumillo, the F_3 lines segregated into 34 light green of Gaza : 77 segregating : 39 blue green of Iumillo. This closely approaches the 1 : 2 : 1 segregation of 37.5 : 75.0 : 37.5. A Chi-square test of significance showed that the deviation from the theoretical was not significant (P = .93). Thus, there is strong evidence that the difference in colour between these 2 varieties is conditioned by one factor.

Results obtained from the chlorophyll deficiency in the crosses involving Iumillo, are presented in Table II.

Although ratios could be fitted to this data, such a treatment was not considered to be valid. The very deficient plants in the F_2 were found to produce no seed. This would tend to reduce the size of the chlorophyll deficient class, and the amount of this reduction could not be estimated with any degree of confidence. However, as the Iumillo parent is not chlorophyll deficient, a single factor segregation is not indicated.

Table II

SEGREGATION FOR CHLOROPHYLL DEFICIENCY

IN CROSSES INVOLVING IUMILLO

Cross	G x I	C x I	M x I
Normal	54	47	59
Segregating	87	79	89
Chlorophyll deficient	9	2	2

Thus, at least two factors, and, in the case of the crosses with Mindum and Carleton, possibly three were believed to be involved in the inheritance of chlorophyll deficiency in these 3 crosses.

SUMMARY AND CONCLUSIONS

1. Diallel crosses were made among the varieties Gaza, Iumillo, Carleton and Mindum.

2. F_3 lines of each cross were subjected to an artificial field epidemic of 15B and a number of common races of stem rust.

3. Results indicated that Mindum carried a minor factor for resistance, which has been designated Sr_M. Carleton appeared to carry a factor for moderate resistance, which has been termed Sr_C. Gaza was believed to carry a major factor Sr_G, in addition to Sr_M, and a minor factor Sr_C', which was allelic to Sr_C. Iumillo also carried Sr_M and Sr_C', but owed the greater part of its resistance to a major factor Sr_I.

4. The factor Sr_G appeared to impart a higher degree of resistance than did the factor Sr_I and, in the homozygous dominant condition, appeared to be completely epistatic to Sr_C. Although apparently not allelomorphic, the minor factors Sr_M and Sr_C' appeared to control a degree of resistance which was quite similar in effect. The factor Sr_C, responsible for the moderate resistance of Carleton, appeared to be allelomorphic and dominant to the minor factor Sr_C'. Sr_I was believed to impart a slightly lower degree of resistance than Sr_G, and was not epistatic to Sr_C.

5. The difference between the light green of Gaza and the blue green of Iumillo, appeared to be conditioned by one factor.

6. There were indications of two, or possibly three factors,

responsible for chlorophyll deficiencies in the crosses which involved Iumillo.

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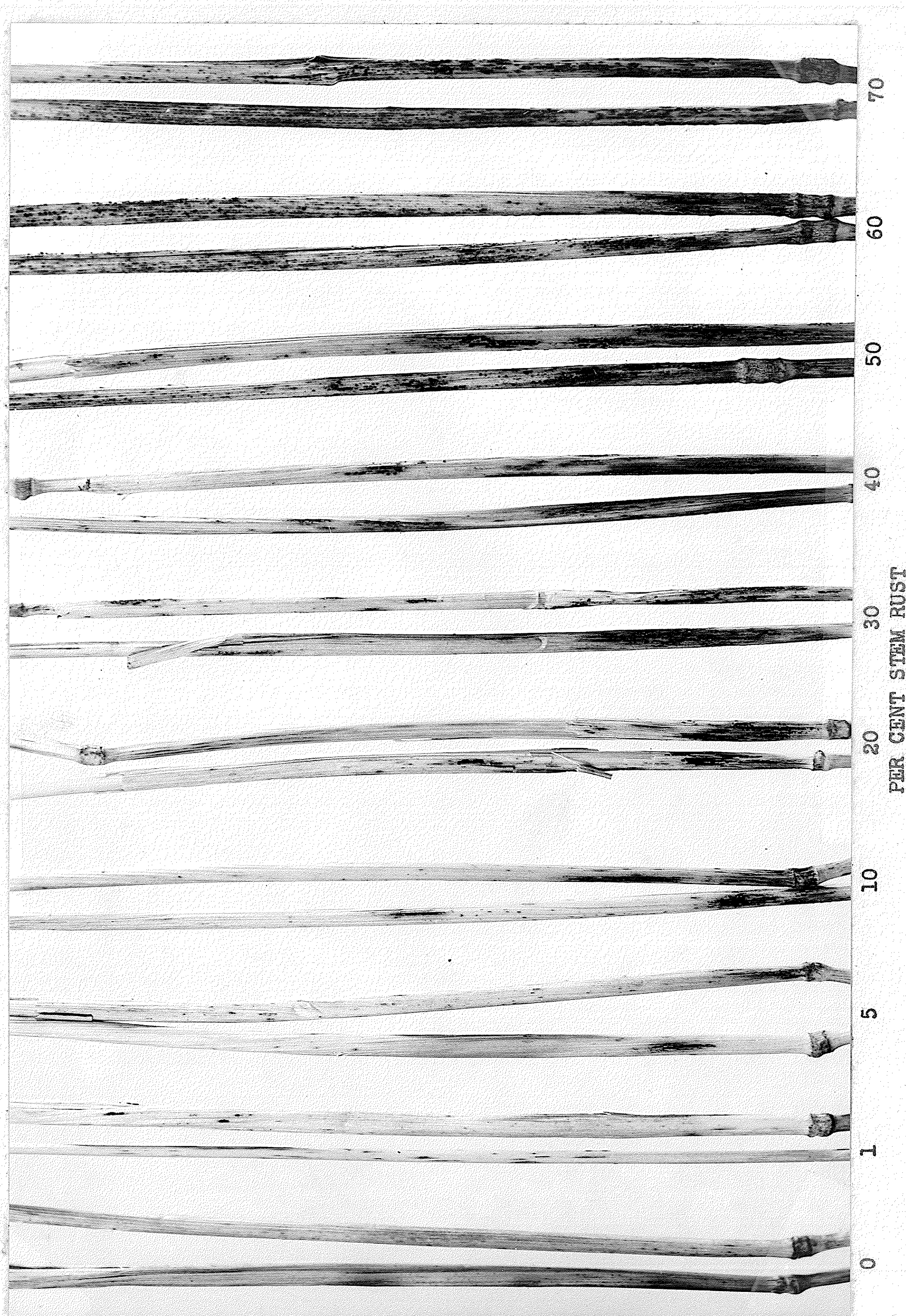
APPENDIX A

DURUM WHEAT CULMS SHOWING STEM RUST INFECTION

FROM 0 TO 70 PER CENT


0
1
5
10
20
30
40
50
60
70
PER CENT STEM RUST

APPENDIX B

A LIST OF THE SEGREGATING GENOTYPES
SHOWING THE FREQUENCY WITH WHICH THEY OCCUR
AND THE RATIOS SUGGESTED IN THE TEXT

Gaza × Carleton

Frequency	Genotypes	Ratio
1	Sr_G Sr_G Sr_C Sr_C Sr_M Sr_M	
2	Sr_G Sr_G Sr_C Sr_C Sr_M sr_M	
1	Sr_G Sr_G Sr_C Sr_C sr_M sr_M	
2	Sr_G Sr_G Sr_C $Sr_{C'}$ Sr_M Sr_M	
4	Sr_G Sr_G Sr_C $Sr_{C'}$ Sr_M sr_M	16
2	Sr_G Sr_G Sr_C $Sr_{C'}$ sr_M sr_M	
1	Sr_G Sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	
2	Sr_G Sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
1	Sr_G Sr_G $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	
2	Sr_G sr_G Sr_C Sr_C Sr_M Sr_M	
4	Sr_G sr_G Sr_C Sr_C Sr_M sr_M	
2	Sr_G sr_G Sr_C Sr_C sr_M sr_M	
4	Sr_G sr_G Sr_C $Sr_{C'}$ Sr_M Sr_M	
8	Sr_G sr_G Sr_C $Sr_{C'}$ Sr_M sr_M	
4	Sr_G sr_G Sr_C $Sr_{C'}$ sr_M sr_M	
2	Sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	41
4	Sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
2	Sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	
1	sr_G sr_G Sr_C Sr_C Sr_M Sr_M	
2	sr_G sr_G Sr_C Sr_C Sr_M sr_M	
2	sr_G sr_G Sr_C $Sr_{C'}$ Sr_M Sr_M	
4	sr_G sr_G Sr_C $Sr_{C'}$ Sr_M sr_M	
1	sr_G sr_G Sr_C Sr_C sr_M sr_M	3
2	sr_G sr_G Sr_C $Sr_{C'}$ sr_M sr_M	
1	sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	3
2	sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
1	sr_G sr_G $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	1

Gaza × Mindum	Frequency	Genotypes	Ratio
	1	$Sr_G\ Sr_G\ Sr_{C'}\ Sr_{C'}$	
	2	$Sr_G\ Sr_G\ Sr_{C'}\ sr_C$	
	1	$Sr_G\ Sr_G\ sr_C\ sr_C$	12
	2	$Sr_G\ sr_G\ Sr_{C'}\ Sr_{C'}$	
	4	$Sr_G\ sr_G\ Sr_{C'}\ sr_C$	
	2	$Sr_G\ sr_G\ sr_C\ sr_C$	
	1	$sr_G\ sr_G\ Sr_{C'}\ Sr_{C'}$	3
	2	$sr_G\ sr_G\ Sr_{C'}\ sr_C$	
	1	$sr_G\ sr_G\ sr_C\ sr_C$	1

Carleton × Mindum	Frequency	Genotypes	Ratio
	1	$Sr_C\ Sr_C\ Sr_M\ Sr_M$	
	2	$Sr_C\ Sr_C\ Sr_M\ sr_M$	9
	2	$Sr_C\ sr_C\ Sr_M\ Sr_M$	
	4	$Sr_C\ sr_C\ Sr_M\ sr_M$	
	1	$Sr_C\ Sr_C\ sr_M\ sr_M$	
	2	$Sr_C\ sr_C\ sr_M\ sr_M$	6
	1	$sr_C\ sr_C\ Sr_M\ Sr_M$	
	2	$sr_C\ sr_C\ Sr_M\ sr_M$	
	1	$sr_C\ sr_C\ sr_M\ sr_M$	1

Carleton × Iumillo	Frequency	Genotypes	Ratio
	1	Sr_I Sr_I Sr_C Sr_C Sr_M Sr_M	
	2	Sr_I Sr_I Sr_C Sr_C Sr_M sr_M	
	1	Sr_I Sr_I Sr_C Sr_C sr_M sr_M	
	2	Sr_I Sr_I Sr_C $Sr_{C'}$ Sr_M Sr_M	
	4	Sr_I Sr_I Sr_C $Sr_{C'}$ Sr_M sr_M	
	2	Sr_I Sr_I Sr_C $Sr_{C'}$ sr_M sr_M	
	1	Sr_I Sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	
	2	Sr_I Sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
	1	Sr_I Sr_I $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	
	2	Sr_I sr_I Sr_C Sr_C Sr_M Sr_M	
	4	Sr_I sr_I Sr_C Sr_C Sr_M sr_M	57
	2	Sr_I sr_I Sr_C Sr_C sr_M sr_M	
	4	Sr_I sr_I Sr_C $Sr_{C'}$ Sr_M Sr_M	
	8	Sr_I sr_I Sr_C $Sr_{C'}$ Sr_M sr_M	
	4	Sr_I sr_I Sr_C $Sr_{C'}$ sr_M sr_M	
	2	Sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	
	4	Sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
	2	Sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	
	1	sr_I sr_I Sr_C Sr_C Sr_M Sr_M	
	2	sr_I sr_I Sr_C Sr_C Sr_M sr_M	
	2	sr_I sr_I Sr_C $Sr_{C'}$ Sr_M Sr_M	
	4	sr_I sr_I Sr_C $Sr_{C'}$ Sr_M sr_M	
	1	sr_I sr_I Sr_C Sr_C sr_M sr_M	3
	2	sr_I sr_I Sr_C $Sr_{C'}$ sr_M sr_M	
	1	sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M Sr_M	3
	2	sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ Sr_M sr_M	
	1	sr_I sr_I $Sr_{C'}$ $Sr_{C'}$ sr_M sr_M	1

Mindum × Iumillo	Frequency	Genotypes	Ratio
	1	$Sr_I\ Sr_I\ Sr_{C'}\ Sr_{C'}$	9
	2	$Sr_I\ Sr_I\ Sr_{C'}\ sr_C$	
	2	$Sr_I\ sr_I\ Sr_{C'}\ Sr_{C'}$	
	4	$Sr_I\ sr_I\ Sr_{C'}\ sr_C$	
	1	$Sr_I\ Sr_I\ sr_C\ sr_C$	3
	2	$Sr_I\ sr_I\ sr_C\ sr_C$	
	1	$sr_I\ sr_I\ Sr_{C'}\ Sr_{C'}$	3
	2	$sr_I\ sr_I\ Sr_{C'}\ sr_C$	
	1	$sr_I\ sr_I\ sr_C\ sr_C$	1

Gaza × Iumillo	Frequency	Genotypes	Ratio
	1	$Sr_G\ Sr_G\ Sr_I\ Sr_I$	13
	2	$Sr_G\ Sr_G\ Sr_I\ sr_I$	
	1	$Sr_G\ Sr_G\ sr_I\ sr_I$	
	2	$Sr_G\ sr_G\ Sr_I\ Sr_I$	
	4	$Sr_G\ sr_G\ Sr_I\ sr_I$	
	2	$Sr_G\ sr_G\ sr_I\ sr_I$	
	1	$sr_G\ sr_G\ Sr_I\ Sr_I$	
	2	$sr_G\ sr_G\ Sr_I\ sr_I$	2
	1	$sr_G\ sr_G\ sr_I\ sr_I$	1