

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 x 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 \times Iumillo.

Ausemus (1), 1934, reported the results from crosses of Hope \times Marquillo and Marquillo \times Supreme. In the first cross, Hope \times 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 \times 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 \times Bobin₂) with the two susceptible varieties Eureka and Pusa III, found that a single major factor R₃ governed resistance in the field, as well as seedling resistance to race 34 in the greenhouse. In (Gaza \times Bobin₂), a second factor for moderate resistance to race 19 was named R₄. 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.