

THE INHERITANCE OF REACTION IN THREE BARLEY
VARIETIES TO TWO RACES OF PUCCINIA GRAMINIS TRITICI
ERIKSS. AND HENN.

by

Barbara Anne Chernick, B.S.A.



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INTRODUCTION

During the past 40 years numerous investigators have studied the problem of black stem rust, Puccinia graminis Pers. tritici Erikss. and Henn. Considerable research has been directed towards the improvement of its most vulnerable host -- the wheat crop. Barley is also attacked but to a lesser degree, rust often becoming a major hazard where late seeding has been practised.

Stem rust is easily recognized by its brick-red lesions on the leaves and especially on the stems of susceptible plants. These uredosori produce red spores which are carried by the wind to neighboring plants where they initiate further pustules. This cycle is repeated several times throughout the growing season. The telial stage represents the overwintering form of the fungus. Teliospores appear at the onset of cool weather in former uredosori, germinating in the spring to infect the common barberry with haploid sporidia (9). After the completion of the sexual stage within the barberry plant, cluster cups containing chains of binucleate aeciospores appear on the undersides of the leaves. These are carried by the wind to infect young grain crops with the uredial cycle.

As a measure of control an extensive eradication program was initiated in 1918 in the 13 North Central States

and Manitoba (1) to eliminate the barberry. Although this venture significantly reduced the barberries, another source of inoculum is constantly available. Uredospores survive the winter in the Southern States and New Mexico on volunteer grains and wild grasses. These infect winter grains and then move northward with the progressive development of spring crops.

Physiological races of the stem rust organism have been isolated on the basis of host reaction. A standard set of differential hosts has been established (19). It consists of wheat varieties having specific responses to individual races. Should the differential set be expanded, undoubtedly many more races would become apparent. So far only the large and economically important subdivisions have been investigated. Even so, the races number approximately 240. However in any given year only a few of these are present in significant amounts. There is the ever-present threat of the appearance, through mutation or hybridization, of new, more virulent forms to which our currently resistant crops may prove susceptible. Races now present in insignificant quantities may become epidemic if crops susceptible to them are introduced. An example is Race 56 which in 1935 became most prevalent because only crops susceptible to it were being grown. Similarly Race 15B has become most significant since 1950. This biotype of Race 15 is distinguished by its virulence on the differential variety Rival which resists Race 15A (3).

Sources of resistance are being sought among barley varieties as among wheat. Perhaps the most important of these to date is the gene for resistance carried by Peatland and Chevron. From observations in field plots it is suspected that the variety Valkie C. I. 5748, an introduction from Southern Russia, may have valuable factors to contribute. The purpose of this study is to evaluate these factors and clarify their mode of inheritance.

REVIEW OF LITERATURE

It is the opinion of many writers that stem rust resistance of barley is controlled by a single dominant gene. This gene is found in the variety Chevron which is described by Shands (15). Chevron and Peatland are both selections from a seed sample introduced into the United States in 1914 from Switzerland. Shands (16) believed that the adult plant reaction of these varieties is controlled by the same single dominant gene. Powers and Hines (13) investigated crosses of Peatland with the rust susceptible varieties, Glabron and Minnesota 462, and found resistance in the mature plant stage to be due to a single dominant gene. Further evidence was presented by Brookins (2) who, in addition, located the gene on Linkage Group VII. In a cross of Wisconsin 38 x Peatland, Reid (14) found mature plant reaction to rust to be simply inherited with resistance dominant. Miller (10) reports that a single dominant gene pair appears to govern adult response to Race 15B in crosses of rust resistant Minnesota 615 x resistant Kindred and Minnesota 615 x susceptible Montcalm.

Two investigators report that more than one gene may influence adult plant response in barley. Lejeune (8) studied a cross of Chevron x rust susceptible O.A.C. 21 and found that none of the segregates equalled Chevron in resistance. He suggests that one or more modifying genes may have influenced the progeny toward susceptibility. Patterson (11) indicates that Peatland, Chevron and Valentine,

tested as adults to Races 17, 19 and 56, are commonly influenced by the single dominant gene of Linkage Group VII and at least one minor factor pair.

According to Luther Smith (17) two workers, Waterhouse and Tschermak, have found adult plant resistance in barley to be recessive. Waterhouse reports such a situation in studies with Races 34 and 45, and Tschermak indicates that "susceptibility tended to dominate over immunity to stem rust".

Some observers note that seedling response to rust is dependent on a single dominant gene which is probably the same one influencing adult plant reaction. Brookins (2) found this to be true in crosses with Peatland which were tested to Races 17, 19 and 56. Therefore he concluded that selection of rust resistant varieties or lines could be made on the basis of seedling reaction in the greenhouse rather than of mature plant response during a field epidemic. Miller (10) suggests from his observations of the Minnesota 615 x Kindred and Minnesota 615 x Montcalm crosses that it is the same dominant gene governing seedling resistance as is responsible for adult plant resistance.

Immer et al. (4) studied the crosses Minnesota 462 x Peatland and Barbless x Peatland. These hybrids were tested in the field and in the greenhouse to many physiologic races. As there was a high correlation between greenhouse and field responses, they concluded that seedling reaction could be used to eliminate lines of barley in the

seedling stage.

Two writers disagree with these findings. Patterson (11) was convinced that Peatland, Chevron and Valentine are influenced both as seedlings and adults not only by a major gene but also by at least one minor factor pair. Reid (14) reports that in a cross of Wisconsin 38 x Peatland, seedling reaction to Race 56 appeared to be simply inherited with susceptibility dominant, although seedling reaction to other races showed that resistance was dominant.

The disagreement among investigators as to seedling response might be explained by temperature effects. Miller (10) found that seedlings of varieties known to be susceptible in the adult stage tended to exhibit resistance when studied at low temperatures. It was also difficult to differentiate segregating lines in a cool greenhouse. Therefore, for successful adult plant predictions Miller suggests that seedlings be maintained at post-inoculation temperatures ranging between 80 and 85° F. Waterhouse (20) reports that his barley seedling reactions were neither consistently high nor low when temperatures fluctuated around 70° F. Readings seemed more reliable when temperatures varied between 75 and 82° F. Their findings are corroborated by Patterson (11). Miller (10), who studied over 1200 barley varieties in the field and in the greenhouse, noted a high correlation

between high temperature seedling reaction and adult field response to Race 59A.

Information regarding reactions of the parental varieties to be studied was obtained from Johnson and Buchannon (6). In their study of rye stem rust, comparisons were made with Race 15B. It was found that in the greenhouse Chevron and Peatland were most resistant to Race 15B with 10 and 20% rust respectively, Montcalm was most susceptible, averaging 50%, and Valkie was intermediate, developing 35% rust. These readings were taken from the stem examinations. It was observed that little rust appeared on the leaves. The same relationship among these 4 varieties was noted in field tests with Race 15B.

At Winnipeg, Lejeune (8) tested a number of barley varieties to 51 races of stem rust including Race 15B. He found that Montcalm was not as susceptible to any of the races as were Velvet, Rex or Canada Thorpe.

Johnson (7) reports that in 1952 some of the supposedly resistant hybrids studied at the University of Manitoba showed unexpected susceptibility. Race 11 was most frequently isolated from the plots but it seemed to be pathogenically different from other specimens of that race studied at Winnipeg. Adult plant reactions to this form of Race 11 were recorded in the greenhouse and were at the same time compared to responses to Race 15B, 56 and rye stem rust. Montcalm was highly susceptible to all

MATERIALS AND METHODS

Varieties Studied

The three varieties selected for this experiment were Montcalm, Valkie and U.M. 45-1477. Montcalm C.I. 7149, the most extensively grown barley variety in Manitoba, was produced at Macdonald College by E. A. Lods from a cross of Michigan 31604 x Common Six Row x Mandscheuri 1807 M.C. It is considered susceptible to most races of Puccinia graminis tritici although heavier damage on other varieties is reported by Lejeune (8).

U.M. 45-1477 is a selection from the cross (Newal x Peatland) x Olli. It is therefore thought to possess the Peatland gene for resistance. At the University of Manitoba it has proved highly resistant.

Valkie C.I. 5748 is an introduction from Southern Russia. It is a two-row variety in general unsuitable agronomically. Because a moderate degree of rust resistance has been observed in the adult stage at Winnipeg, it is of interest as a possible new source of rust resistance.

Crosses and Backcrosses of these Varieties

Crosses between Montcalm x Valkie, and Montcalm x U.M. 45-1477 were studied in the F₂ and F₃ generations. Data from the backcrosses Montcalm x (Valkie x Montcalm) and (Valkie x U.M. 45-1477) x U.M. 45-1477 was obtained from the first, second and third selfed generations. All cross and backcross seed was provided by Dr. S. B. Helgason

of the University of Manitoba. A list of the number of plants and the generations studied is shown in Table I.

Nomenclature

The backcross generations are designated according to the Alberta System (5). For instance, the "Bc₂₋₁ generation" of Montcalm x (Valkie x Montcalm) refers to the first selfed generation after the completion of the backcross.

The letters S, MS, MR and R are used to designate susceptible, moderately susceptible, moderately resistant and resistant respectively with reference to 1953 plant readings.

Planting Plan 1953, 1954

In 1953 the material listed in Table I columns II and III was space-planted in rows 12½ feet long. Eight sets of checks including Montcalm, Valkie and U.M. 45-1477 were distributed throughout the nursery.

In 1954 the succeeding generations (listed in Table I, Columns IV and V) was again space-seeded in 12½ foot rows, each row consisting of the progeny of a 1953 plant. Twenty-four sets of checks including Montcalm, Valkie, and U.M. 45-1477 were distributed throughout the nursery.

Methods of Inoculation in the Field

Inoculation rows of Montcalm and susceptible hybrids were sown around the nurseries both years. These were dusted with a 50:1 talc-spore mixture. The spore

TABLE I

Material Studied in the Adult Stage

| Constitution of Seed Received from Dr. S. B. Helgason | Generation Studied in Field 1953 | No. Plants Studied in Field 1953 | Generation Studied in Field 1954 | No. Plants Studied in Field 1954 | No. of Lines Evaluated by 1954 Progeny Averages |
|--|--|--|--|---|--|
| Valkie x Montcalm F ₁ Seed | F ₂ | 181 | F ₃ | 3794 | 162 |
| Montcalm x Valkie F ₁ Seed | F ₂ | 40 | F ₃ | 814 | 33 |
| (Valkie x Montcalm) x Montcalm Seeds Bc ₂₋₀ | Bc ₂₋₁ | 34 | Bc ₂₋₂ | 641 | 30 |
| Montcalm x (Valkie x Montcalm) Seed of Bc ₂₋₁ Plant | Bc ₂₋₂ | A 13 B 19 C 35 D 12 E 42 F 20 G 18 | Bc ₂₋₃ | A 282 B 728 C 729 D 230 E 850 F 420 G 145 | A 11 B 32 C 26 D 8 E 42 F 18 G 12 |
| Montcalm x U.M. 45-1477 F ₁ Seed | F ₂ | 188 | F ₃ | 3403 | 162 |
| (Valkie x U.M. 45-1477) x U.M. 45-1477 Bc ₂₋₀ Seed | Bc ₂₋₁ | 31 | Bc ₂₋₂ | 897 | 32 |

collections of Race 15B were obtained from the Dominion Rust Laboratory at Fort Garry. The inoculation took place several different evenings when dew was expected. In 1954, dusting was supplemented by hypodermic injections into plants every 1 - 2 feet along the inoculation row. The hypodermic contained a distilled water-spore suspension, and was directed into the centre of the stem. Pressure was applied to the barrel until liquid appeared at sheath edges. Pustules developed more quickly and most heavily on plants inoculated this way.

Method of Classification

In 1953 plants were classified in the field as to their stem rust reaction when the heads were turning color and the stems were still green. Readings were based largely on pustule size. The 1954 progeny were pulled and infection recorded indoors, as a very large number of plants was involved. The scale suggested by Peterson et al. (12) was followed closely in 1954, except that plants with 0 - 5% infection were all designated as 5%. It was decided to evaluate the 1953 generation by averaging individual progeny reactions obtained in 1954.

Seedling Studies Winter 1953-4

During the winter, seedling tests of the crosses and backcrosses were attempted. The generations studied are listed in Table I, Column IV. Because of a number of infection failures, not all of the available lines shown in Table I Column V could be classified. Two 4-inch pots

of approximately ten plants each represented the progeny of a 1953 plant. The readings of the two pots were averaged to evaluate the 1953 field plant. Reactions to Race 15B and Race 11 were recorded. Checks of Montcalm, Valkie and U.M. 45-1477 were included in each trial.

The method of seedling inoculation was that commonly used for wheat, except that the seedlings were left in moisture chambers only overnight instead of the usual 48 hours. When the young plants were 2 - 4 inches high, the waxy bloom was rubbed off the first leaf of each with moistened fingers. Then a spore-water suspension was gently applied in the same manner. A fine film of water was maintained on the inoculated leaves by means of a throat atomizer. The pots were then placed in a moisture chamber with 2 - 3 inches of water in the bottom, and covered. Inoculations made in the middle of the day when the greenhouse was warmest produced best results. The subsequent temperature drop tended to maintain the water droplets on the leaf surfaces, so necessary for spore germination.

During the tests with Race 15B, greenhouse temperature was recorded on a thermograph. Natural light was supplemented by fluorescent tubes which remained on between 5 and 10 P.M. daily.

Readings were made according to the method described by Stakman and Levine (19). Pustule size was

taken as the significant factor. As the regular "2" type, possessing a green island, was never observed, pustules intermediate in size between "1" and "3" were designated as "2".

OBSERVATIONS AND DISCUSSION

Field Results

The parental rust reactions in the field were averaged for 1953 and 1954. In both years it was found that Montcalm was most susceptible, U.M. 45-1477 most resistant and Valkie intermediate between the two. These results were corroborated by examination of data provided by the crosses and backcrosses. Let us assume therefore the following genetic constitution for rust response in the three parents, allowing Montcalm a degree of resistance in view of Lejeune's findings (8), and assuming incomplete dominance: Montcalm = ttT_1T_1 , Valkie = TTt_1t_1 , U.M. 45-1477 = TTT_1T_1 , where T is the Peatland gene for resistance and T_1 a secondary gene having less effect than T. (11).

The data to be presented were not, in a number of instances, suitable for interpretation by application of the usual mathematical tests. This is because in 1953 there was considerable overlapping among the four classes, and in 1954 infection was neither heavy nor uniform. Also, some of the crosses and backcrosses provided insufficient populations to warrant statistical analysis.

I Valkie x Montcalm

Assuming the foregoing parental constitutions, in the cross of Valkie x Montcalm the expected F_2 progeny would be of these genotypes:

| | | |
|-----------------------------------|-----------------------------------|-----------------------------------|
| 1 TTT ₁ T ₁ | | 1 ttT ₁ T ₁ |
| 2 TTT ₁ t ₁ | 4 TtT ₁ t ₁ | 2 Ttt ₁ t ₁ |
| 2 TtT ₁ T ₁ | | 2 ttT ₁ t ₁ |
| 1 Ttt ₁ t ₁ | | 1 ttt ₁ t ₁ |

Approximately 6/16 of the population should equal or surpass Valkie in resistance, 6/16 should equal Montcalm or be more susceptible, and the remaining 4/16 having the TtT₁t₁ genotype should be intermediate in response between Montcalm and Valkie. In the field it was found in 1953 that the reaction of Montcalm ranged from moderate susceptibility (MS) to susceptibility (S); that Valkie was slightly more resistant than MS. The F₂ population was classified thus: S = 95 plants, MS = 62, MR (moderately resistant) = 21 and R (resistant) = 3 plants. If it is assumed that the S class contained the hybrids equal to Montcalm and those more susceptible, and that the other three classes contained the Valkie-like and more resistant plants, it is found that the S group = 95 lines and the totalled MS, MR and R groups = 86 lines. This 95:86 ratio approaches the expected 1:1. The intermediate TtT₁t₁ plants could have been read as either S or MS and should not therefore obscure the ratio of the two main types.

Figure 1 shows the F₂ distribution of the Valkie x Montcalm cross as evaluated by averaging the F₃ lines grown in 1954. Each F₂ plant reaction was classified by averaging the reactions of its progeny, which grouped

themselves largely about each parental type. The distribution of the intermediate TtT_1t_1 genotypes may have accounted for the inequality of the two groups. Referring back to the expected F_2 genotypes it was observed that $1/16$ of the population should have no gene for resistance whatever. It was assumed that this class contained the 7 lines to the right of the break at the 38% point in the distribution of Figure 1. The resulting 155:7 ratio was fitted to a 15:1 ratio by the Chi square method and a good fit was obtained, the P value being .36 at the 5% point.

II Montcalm x Valkie

In the cross of Montcalm x Valkie the progeny in F_2 should be of the same genotypes as listed above for the reciprocal cross. Within the test of this cross in 1953, Valkie appeared to be moderately susceptible while Montcalm was susceptible. Of the F_2 plants, 19 were rated as susceptible, 15 as moderately susceptible, 5 as moderately resistant and 1 as resistant. If the "S" class represented the Montcalm genotype for rust reaction and those more susceptible ($6/16$ of the population), the two groups should have been composed of equal numbers of lines if the intermediate group was evenly distributed between the two. This appeared to be the case since $S = 19$ and $MS + MR + R = 21$.