

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.



A Thesis

Submitted to the Committee on Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree of
MASTER OF SCIENCE

THE UNIVERSITY OF MANITOBA

April 1955

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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 $MS + MR + R = 21$.

Figure 2 shows the distribution of the F₂ plant responses as evaluated by averaging their F₃ progeny grown in 1954. Infection was poor as compared to that within the Valkie x Montcalm cross. As Montcalm and Valkie averaged 6% and 5% rust respectively it was difficult to distinguish between the lines concentrated about the parental types. However the distribution was of the same general form as that of its reciprocal. Since only 33 lines were available for study, statistical analysis of the results would be unreliable.

III (Valkie x Montcalm) x Montcalm

In this backcross the Bc₂₋₁ plants were grown in the field in 1953. The theoretical genotypes of these are 1 TTT₁t₁ : 1 TtT₁t₁ : 1 ttT₁T₁ : 1 ttT₁t₁; 1/4 should be highly resistant, 1/4 segregating for both genes and intermediate in reaction to Montcalm and Valkie, 1/4 equal to Montcalm in response, and 1/4 more susceptible than Montcalm. The Montcalm checks in 1953 averaged slightly more than moderately susceptible while Valkie was slightly less than moderately resistant. The distribution of Bc₂₋₁ plants was read as follows: 14 = S, 16 = MS, 4 = MR. The Montcalm-like genotypes and those more susceptible should be contained in the S group and should overlap into the MS. The MS and MR groups should be composed of the segregating genotypes and plants more resistant than Valkie. Approximately equal numbers of

14% rust and Valkie 7%; therefore it was difficult to distinguish between resistant genotypes.

Bc₂₋₁ Plant A

In 1953 12 Bc₂₋₂ plants were placed in the susceptible class and one in the moderately susceptible class. This distribution, though limited, suggested segregation from a ttT_1T_1 or a ttT_1t_1 genotype.

The 1954 Bc₂₋₂ evaluations from Bc₂₋₃ progeny averages in Figure 4 did not include many lines. However none surpassed Valkie in resistance as would be expected of segregants from a #I or #II genotype (Table II). As there were no lines averaging greater susceptibility than 43%, a Montcalm ttT_1T_1 genotype is suggested as the source of these lines.

Individual Bc₂₋₃ readings were found to have a distribution mean of 16% rust, close to the Montcalm average of 14%.

The evidence of these three sets of data points to a ttT_1T_1 genotype for Bc₂₋₁ Plant A.

Bc₂₋₁ Plant B

The 1953 Bc₂₋₂ plants were classified as follows: s = 13, MS = 4, MR = 2. These readings suggested segregation from a #III or #IV genotype (Table II). 1954 line averages of Bc₂₋₃ plants concentrated about the Montcalm average, or they were more resistant than Montcalm, suggesting a TtT_1T_1 constitution (Figure 5). The mean of Bc₂₋₃ plant distribution was 11% which was more resistant

TABLE II

Montcalm x (Valkie x Montcalm) Genotypes

| Bc ₂₋₁ Genotype | Type of Segregation or Proportion of Segregates in Bc ₂₋₂ Generation |
|--------------------------------------|--|
| #I TtT ₁ T ₁ | 1 TTT ₁ T ₁ : 2 TtT ₁ T ₁ : 1 ttT ₁ T ₁ |
| #II TtT ₁ T ₁ | 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 |
| #III ttT ₁ T ₁ | all ttT ₁ T ₁ |
| #IV ttT ₁ t ₁ | 1 ttT ₁ T ₁ : 2 ttT ₁ t ₁ : 1 ttt ₁ t ₁ |

than Montcalm. Except for 1953 readings then, the data support a Bc₂₋₁ genotype of TtT₁T₁ for Plant B.

Bc₂₋₁ Plant C

There were 29 plants classified as susceptible and 6 as moderately susceptible in 1953, suggesting segregation from a ttT₁t₁ plant. The Bc₂₋₃ evaluations of these 1953 plants (Figure 6) centred about the Montcalm average. None of the lines equalled Valkie in resistance, and none was more susceptible than 35%, indicating a Montcalm-like background. The distribution mean of the individual Bc₂₋₃ plants was 18% which may indicate either a #III or #IV parentage. More data would be required to determine therefore the precise genotype of Plant C.

Bc₂₋₁ Plant D

This plant segregated in the Bc₂₋₂ generation of 1953 with 8 plants susceptible, 2 moderately susceptible and 2 moderately resistant. Since the Montcalm average was MS - S this distribution, though small, seemed to have come from a TtT₁t₁ genotype. The few lines averaged in Figure 7 are scattered between 10% and 43% and could represent a ttT₁T₁ parent. The distribution mean of individual 1954 Bc₂₋₃ plants was 23% -- somewhat greater than we would expect from a ttT₁T₁ constitution. As there was a large number of plants as resistant as Valkie in 1954, the distribution could hardly represent a ttT₁t₁ genotype. Therefore a Bc₂₋₁ genotype of TtT₁t₁ is suggested for Plant D.

Bc₂₋₁ Plant E

In 1953, 13 Bc₂₋₂ plants fell in the S class, 13 in the MS, 11 in the MR and 5 in the R class. This distribution suggested a segregating population from TtT₁t₁ parentage. The Bc₂₋₂ evaluations shown in Figure 8 were also rather generally distributed. The Bc₂₋₃ plants showed a distribution mean of 18% which could indicate a Montcalm background, but there was a high proportion of resistant plants in this distribution also. Therefore it is assumed that this population was derived from a TtT₁t₁ genotype.

Bc2-1 Plant F

The 1953 Bc2-2 segregates appeared to have arisen from a Montcalm-like genotype. They were read thus: S = 6, MS = 13, R = 1. In the 1954 evaluations of Figure 9, only one line surpassed Montcalm in resistance, and one line had 53% rust, suggesting a Montcalm or ttT_1t_1 constitution. However, the distribution mean of the 1954 individual plants was 27%. Therefore we can assume the genotype of Plant F to be ttT_1t_1 .

Bc2-1 Plant G

Only 13 plants were available for study in 1953 -- 8 susceptible and 5 moderately susceptible. These might have indicated a Montcalm-like parent but both the 1954 evaluations and the 1954 Bc2-3 individual plant readings were evenly distributed among the classes, suggesting a segregating parental genotype of TtT_1t_1 .

V Montcalm x U.M. 45-1477

In 1953 the F₂ generation of this cross was grown in the field. If we assume the constitution of Montcalm to be ttT_1T_1 and that of U.M. 45-1477 to be TTT_1T_1 , the F₂ population should segregate only for the Peatland gene Tt. i.e. 3 highly resistant: 1 equal to Montcalm in susceptibility. Throughout the cross Montcalm averaged S - MS and U.M. 45-1477 averaged R - MR. Let us suppose that the MR and R classes are composed of the TTT_1T_1 and TtT_1T_1 genotypes and that the S and MS classes contain the remaining 1/4 equal to Montcalm in susceptibility.

Though the observed ratio of 128 resistant: 60 susceptible plants does not equal a 3:1 ratio, allowance must be made for the fact that the classes undoubtedly overlap.

The F₃ plants averaged in 1954 to clarify 1953 genotypes appear in Figure 11. Here Montcalm averaged 30% rust and U.M. 45-1477, 5%. A good 3/4 of the distribution developed less than 17% rust. It is quite possible that the remaining more susceptible lines scattered about the Montcalm point composed the 25% expected to be ttT₁T₁ or Montcalm-like in rust response.

VI (Valkie x U.M. 45-1477) x U.M. 45-1477

In 1953 the Bc₂₋₁ generation of this backcross was grown in the field. 17 of these were resistant, 15 moderately resistant, 4 moderately susceptible and one susceptible. Valkie averaged MS; U.M. 45-1477 averaged R. On the basis of the classification mentioned above it was expected that these two genotypes would appear in equal proportions in the Bc₂₋₁ generation : TTT₁T₁ and TTT₁t₁. These would be highly resistant. This evidence was supported by the fact that a large number of resistant and moderately resistant plants was observed in 1953.

The following generation of Bc₂₋₂ plants were examined in 1954. The Bc₂₋₁ genotypes would be expected to segregate in 1954 thus: 5 TTT₁T₁ : 2 TTT₁t₁ : 1 TTT₁t₁. Therefore 1/8 of the population should be as susceptible as Valkie. U.M. 45-1477 averaged 5% rust in this cross;

Valkie 19%. In Figure 12 it is observed that 759 of the plants were classified as either 5 or 10%, and 138 were more susceptible. Possibly some of the 20% lines should have been classified as 10%. At any rate the expected 7:1 ratio was suggested by 759:138.

It will be seen from this discussion of the results of adult plants grown in the field that the two-factor hypothesis for rust response in barley is indicated. This theory was also suggested by Lejeune (8) and Patterson (11).

Clearcut results would probably have been more evident had the infection been heavier in 1954 and more uniform in both years. It is recommended that for future studies of this type wheat inoculation rows should be seeded as well since wheat is far more susceptible to stem rust and would therefore provide more inoculum.

Temperature, moisture and light averages for the months of June, July and August of both years, were furnished by the Weather Bureau at Winnipeg and compared to the normal for those months. They were recorded in Table III.

GREENHOUSE RESULTS

Tests with Race 15B and Race 11 indicated that susceptibility to stem rust in the seedling stage was dominant. Similar findings are reported by Tchermak (17), Reid (14) and Waterhouse (17). The author believes that the post-inoculation temperatures were insufficiently high. The temperature varied between 60 and 70° F. as a rule with occasional rises to 80° at midday. Waterhouse reported (20) 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. His work was corroborated by Patterson. Miller recommends that post-inoculation temperatures for rust development range between 80 and 85° F.

It will be noted that the parental reactions are not listed within individual crosses. This is because no cross or backcross was tested all at once. Due to space shortage the investigation had to be divided into a number of trials. Each group was composed of lines from each cross and backcross in an attempt to counteract environmental variation, especially that due to day length. Therefore only the average reactions of checks throughout the winter are in any way comparable to the various distributions.

Race 15B Investigations

On the basis of pustule size, Montcalm was found to average 3.9 infection, Valkie 3.2, and U.M. 45-1477, 0.

From these and the following results it is suggested that the parental genotypes for seedling response are the same as in the mature plant except that the previously dominant genes behave as recessives.

The generation and type of the material studied are listed in Table IV.

I Valkie x Montcalm and the Reciprocal Cross

Figures 13 and 14 describe the distributions of the F₂ plants as evaluated by line readings for these two crosses. If the genotype of Montcalm is ttT_1T_1 and that of Valkie Tt_1t_1 , it is expected that in the F₂ populations some segregates would excel Valkie in resistance. According to the distributions this indeed appeared to be the situation as the Valkie genotype averaged 3.2.

II (Valkie x Montcalm) x Montcalm

The Bc₂₋₂ generation of this backcross was studied in the seedling stage. The expected Bc₂₋₁ genotypes were 1 ttT_1t_1 : 1 ttT_1T_1 : 1 Tt_1t_1 : 1 Tt_1T_1 . As only 16 Bc₂₋₁ plant progenies were examined, it is possible that not all genotypes were equally represented. Therefore the 16 plant progenies were evaluated individually. They are listed in Table V. In Column III Table V, a designation such as "4(4)" indicates that 4 F₂ plants exhibited Number 4 pustules. The ttT_1t_1 genotype should be more susceptible than Montcalm, the ttT_1T_1 constitution should equal Montcalm, the Tt_1t_1 genotype

should be slightly more resistant than Montcalm, and TtT_1T_1 genotype should approach the Valkie (TTt_1t_1) reaction. Therefore plant numbers 5, 6, 8 and 15 would be classified as ttT_1t_1 , number 16 would be of the Montcalm type, numbers 1, 2, 10, 11 and 12 would be segregating for both genes and plant numbers 3, 4, 7, 9, 13 and 14 would be of the TtT_1T_1 genotype.

III Montcalm x (Valkie x Montcalm)

The Bc_{2-3} generation of this backcross was grown in the greenhouse. Line averages were calculated to evaluate Bc_{2-2} plants which were listed in Table VI. The expected Bc_{2-1} genotypes were 1 TtT_1T : 1 TtT_1t_1 : 1 ttT_1T_1 : 1 ttT_1t_1 .

Bc_{2-1} Plant A was likely of the constitution ttT_1t_1 . Such a constitution should segregate 1 ttT_1T_1 : 2 ttT_1t_1 : 1 ttt_1t_1 and all progeny should be quite susceptible. None of the lines studied was more resistant than 3.2.

Plant B readings suggest a TtT_1t_1 background as they ranged from 2.8 to 3.2.

Plant C appeared to segregate more definitely for both genes as Bc_{2-2} plants were distributed through all classes.

Plant E was evaluated by only 9 plants which ranged in reaction between 2.6 and 4.0. Either a ttT_1t_1 or a TtT_1t_1 genotype was suggested.

TABLE IV

Material Selected for Seedling Studies

| Cross or Backcross | Generation Studied in Greenhouse | Generation Evaluated by Averaging Greenhouse Lines |
|--|----------------------------------|--|
| Montcalm x Valkie | F ₃ | F ₂ |
| Valkie x Montcalm | F ₃ | F ₂ |
| (Valkie x Montcalm) x Montcalm | Bc ₂ -2 | Bc ₂ -1 |
| (Montcalm x Valkie) x Montcalm | Bc ₂ -3 | Bc ₂ -2 |
| Montcalm x U.M. 45-1477 | F ₃ | F ₂ |
| (Valkie x U.M. 45-1477) x U.M. 45-1477 | Bc ₂ -2 | Bc ₂ -1 |

TABLE V

Evaluation of Bc₂-1 Genotypes of
(Valkie x Montcalm) x Montcalm

| Bc ₂ -1 Plant No. | F ₂ Line Average | Individual F ₂ Plant Readings | | | |
|------------------------------|-----------------------------|--|------|------|------|
| 1 | 3.4 | 4(4) | 3(3) | 1(2) | |
| 2 | 3.8 | 11(4) | 3(3) | | |
| 3 | 3.0 | 3(3) | | | |
| 4 | 3.1 | 4(4) | 5(5) | 1(2) | |
| 5 | 4.0 | 8(4) | | | |
| 6 | 4.0 | 10(4) | | | |
| 7 | 3.0 | 6(3) | | | |
| 8 | 4.0 | 7(4) | | | |
| 9 | 3.2 | 7(4) | 6(3) | 2(X) | 2(2) |
| 10 | 3.7 | 11(4) | 4(3) | | |
| 11 | 3.8 | 9(4) | 4(3) | | |
| 12 | 3.6 | 11(4) | 8(3) | | |
| 13 | 2.9 | 5(3) | 1(X) | | |
| 14 | 2.9 | 3(4) | 9(3) | 3(2) | 1(1) |
| 15 | 4.0 | 1(4) | | | |
| 16 | 3.9 | 9(4) | 1(3) | | |

Plant F Bc₂₋₂ lines ranged from 2.5 - 4.0, also indicating either a ttT₁t₁ or TtT₁t₁ background.

IV Montcalm x U.M. 45-1477

The F₃ generation was examined in the seedling stage. The F₂ genotypic ratio to be expected was 1 TTT₁T₁ : 2 TtT₁T₁ : 1 ttT₁T₁. Part of the F₂ generation should therefore equal Montcalm in susceptibility and another part surpass Valkie in resistance. The distribution of the F₂ plants shown in Figure 15 and evaluated by F₃ lines suggested that this was the situation.

V (Valkie x U.M. 45-1477) x U.M. 45-1477

This backcross was studied in the Bc₂₋₂ generation in the greenhouse. Each of the 26 Bc₂₋₁ plants was evaluated by averaging Bc₂₋₂ lines. The two possible genotypes for the Bc₂₋₁ plants were 1 TTT₁T₁ : 1 TTT₁t₁. The segregating genotype should average more susceptible than the non-segregating. Table VII lists the Bc₂₋₁ plants and their Bc₂₋₂ evaluations. The distribution was generally resistant as would be expected of the Bc₂₋₁ genotypes. Approximately half the population -- 11 out of 25 -- fell in the 3.0 group and probably represented the TTT₁t₁ genotype while the remaining more resistant 14 plants constituted the TTT₁T₁ portion.

TABLE VI

Montcalm (Valkie x Montcalm) Seedling Material

| <u>Bc2-1 Plant</u> | <u>Bc2-2 Plant</u> | <u>Pustule type of Bc2-2 Plant</u> |
|--------------------|--------------------|--|
| A | 1 | 3.5 |
| | 2 | 4.0 |
| | 3 | 3.4 |
| | 4 | 3.2 |
| | 5 | 3.4 |
| | 6 | 3.8 |
| B | 1 | 3.3 |
| | 2 | 3.0 |
| | 3 | 3.5 |
| | 4 | 3.0 |
| | 5 | 3.5 |
| | 6 | 3.0 |
| | 7 | 3.2 |
| | 8 | 3.0 |
| | 9 | 3.3 |
| | 10 | 3.4 |
| | 11 | 3.3 |
| | 12 | 2.8 |
| | 13 | 3.7 |
| | 14 | 3.0 |
| | 15 | 3.0 |
| | 16 | 3.0 |
| C | 1 | 3.6 |
| | 2 | 3.8 |
| | 3 | 3.8 |
| | 4 | 3.6 |
| | 5 | 1.6 |
| | 6 | 3.1 |
| | 7 | 3.4 |
| | 8 | 2.2 |
| | 9 | 3.0 |
| | 10 | 4.0 |
| | 11 | 1.8 |
| | 12 | 3.3 |
| | 13 | 3.0 |
| | 14 | 3.6 |
| | 15 | 3.5 |
| | 16 | 3.7 |
| | 17 | 3.7 |
| | 18 | 3.9 |
| | 19 | 3.7 |
| | 20 | 3.9 |

TABLE VI (Cont'd)

| Bc2-1 Plant | Bc2-2 Plant | Pustule Type of Bc2-2 Plant |
|-------------|-------------|--------------------------------|
| C | 21 | 2.8 |
| | 22 | 3.9 |
| | 23 | 4.0 |
| | 24 | 3.8 |
| | 25 | 3.6 |
| | 26 | 3.7 |
| | 27 | 3.2 |
| | 28 | 3.5 |
| E | 1 | 3.0 |
| | 2 | 4.0 |
| | 3 | 3.1 |
| | 4 | 3.7 |
| | 5 | 2.6 |
| | 6 | 3.3 |
| | 7 | 3.0 |
| | 8 | 3.0 |
| | 9 | 4.0 |
| F | 1 | 3.0 |
| | 2 | 3.5 |
| | 3 | 3.9 |
| | 4 | 2.7 |
| | 5 | 3.5 |
| | 6 | 4.0 |
| | 7 | 3.1 |
| | 8 | 3.9 |
| | 9 | 3.8 |
| | 10 | 2.9 |
| | 11 | 2.5 |

TABLE VII

(Valkie x U.M. 45-1477) x U.M. 45-1477

Bc2-1 Seedling Evaluations

| <u>Bc2-1 Plant No.</u> | <u>Reading as Evaluated by Bc2-2 Progeny</u> |
|------------------------|--|
| 1 | 3.6 |
| 2 | 3.0 |
| 3 | 2.3 |
| 4 | 3.8 |
| 5 | 3.4 |
| 6 | 3.5 |
| 7 | 2.8 |
| 8 | 2.8 |
| 9 | 3.0 |
| 10 | 3.1 |
| 11 | 3.0 |
| 12 | 2.1 |
| 13 | 1.0 |
| 14 | 3.0 |
| 15 | 2.1 |
| 16 | 1.0 |
| 17 | 2.5 |
| 18 | 1.0 |
| 19 | 0.6 |
| 20 | 2.7 |
| 21 | 3.0 |
| 22 | 3.0 |
| 23 | 1.0 |
| 24 | 2.0 |
| 25 | 2.7 |

Race 11 Investigations

Due to infection failures and a shortage of time insufficient data were available to evaluate significantly the response to Race 11 of the crosses and backcrosses. However Figures 16, 17 and 18 show the F_2 distributions of the Montcalm x Valkie and reciprocal cross and the Montcalm x U.M. 45-1477. As with Race 15B it appeared that susceptibility was dominant.

CORRELATION STUDIES

Observations from the 4 different sets of data were compared within separate plants and their progenies. Separate sets were compiled for each cross and backcross. The comparisons included:

- 1953 adult plants vs seedling response to Race 15B
- 1953 adult plants vs seedling response to Race 11
- 1953 adult plants vs 1954 adult plants
- 1954 adult plants vs seedling response to Race 15B
- 1954 adult plants vs seedling response to Race 11
- Seedling response to Race 15B vs seedling response to Race 11.

The scatter diagrams in Appendix B suggest that there is no correlation either negative or positive, between any of the pairs. There are several explanations for this.

As mentioned before the field epidemics in both years were neither uniform nor heavy. Only 4 classifications were used to determine 1953 mature plant reactions and considerable overlapping must have occurred.

Although the inoculum provided artificially in both years was mostly Race 15B, natural infection may have provided a few races eliciting different genetic responses within the nursery. Several writers (4) report that mature plant reaction is common to most races but Johnson (7) at Winnipeg observed that in 1952, varieties usually resistant to most races became susceptible to a strain of Race 11.

Though none of this Race was isolated in 1953 or 1954 in the field, it is quite possible that such a race appeared in small but significant quantities.

Theoretically, seedling responses in the greenhouse should have been negatively correlated with adult reactions, and seedling reactions to Races 11 and 15B should have been positively correlated. However low temperature studies are often erratic (10) (11) (20) and further investigations at high temperatures undoubtedly would have clarified the picture.

6. There was no correlation within lines between seedling responses to Races 15B and 11, probably because greenhouse temperatures were unsuitable.
7. Line responses of adult plants were not correlated between 1953 and 1954 probably because of unequal infections between years.

ACKNOWLEDGMENTS

Grateful acknowledgments are made to Dr. S. B. Helgason, of the University of Manitoba, for his guidance and encouragement during the course of the experiment; to Dr. L. H. Shebeski, also of the University of Manitoba, for his aid and advice; to Dr. T. Johnson of the Dominion Laboratory of Plant Pathology, Winnipeg, for his assistance with rust problems; and to Mr. A. Chernick for the photographic work contained herein.

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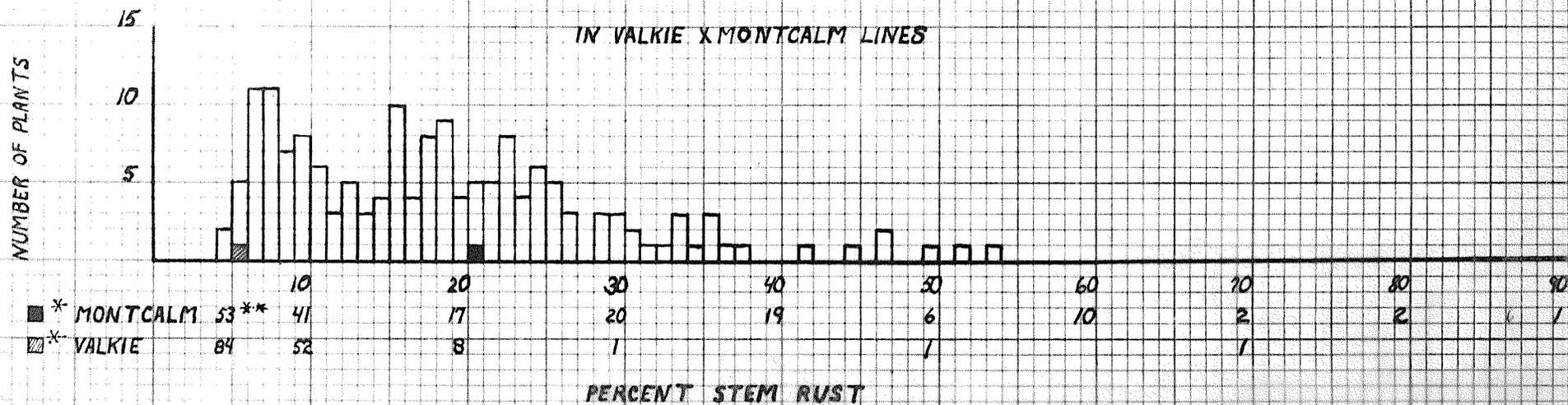
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APPENDIX A

FIGURE 1
 DISTRIBUTIONS OF RUST REACTIONS
 IN VALKIE X MONTCALM LINES



* PARENTAL RUST PERCENT AVERAGES

** INDIVIDUAL PLANTS OF PARENTAL CHECKS IN EACH RUST PERCENT CLASS

-177-

FIGURE 2

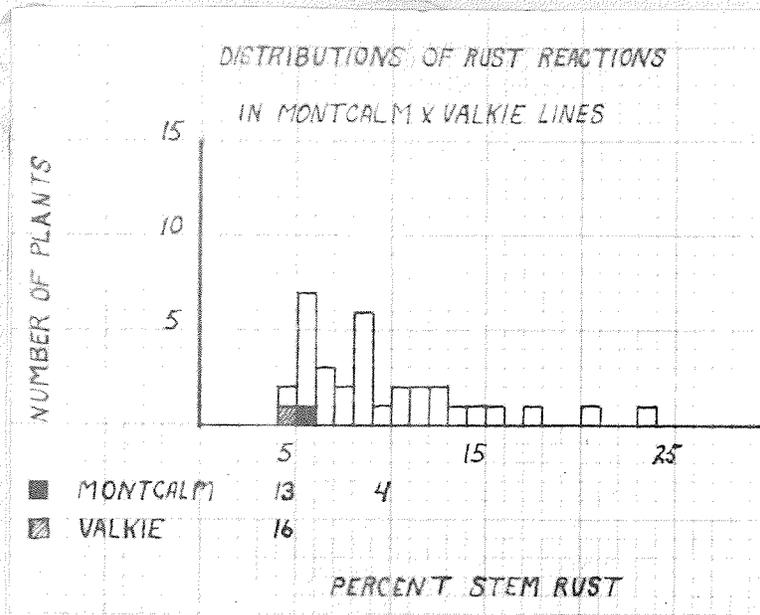
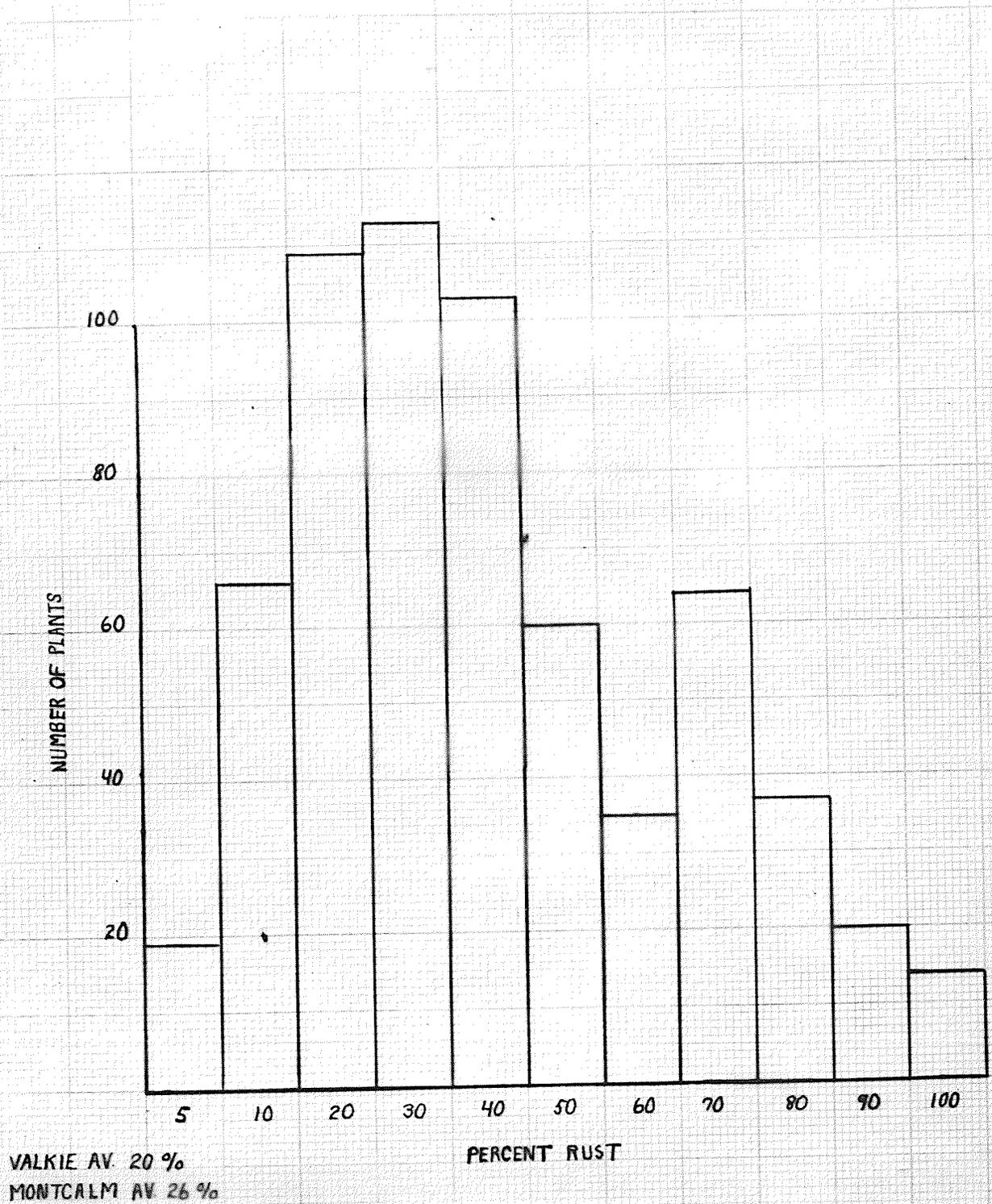
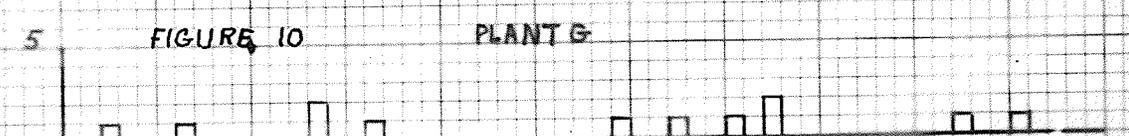
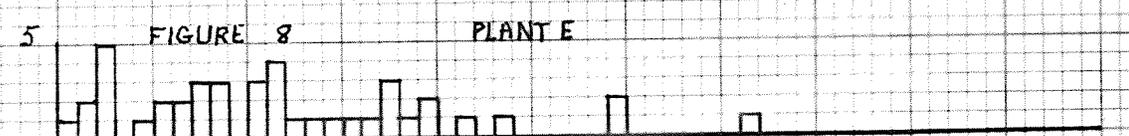
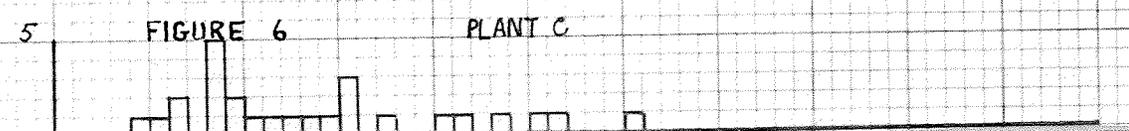
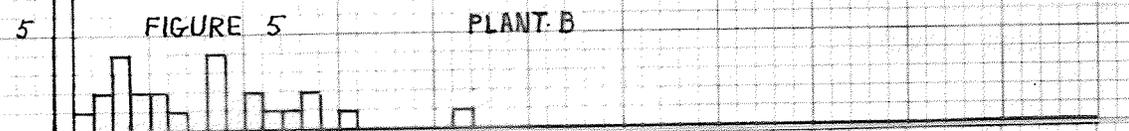
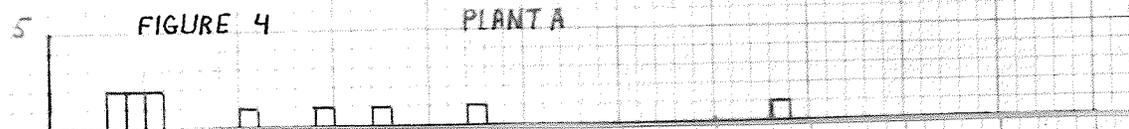


FIGURE 3
DISTRIBUTION OF RUST REACTION
IN VALKIE X MONTCALM₂-(2) PLANTS

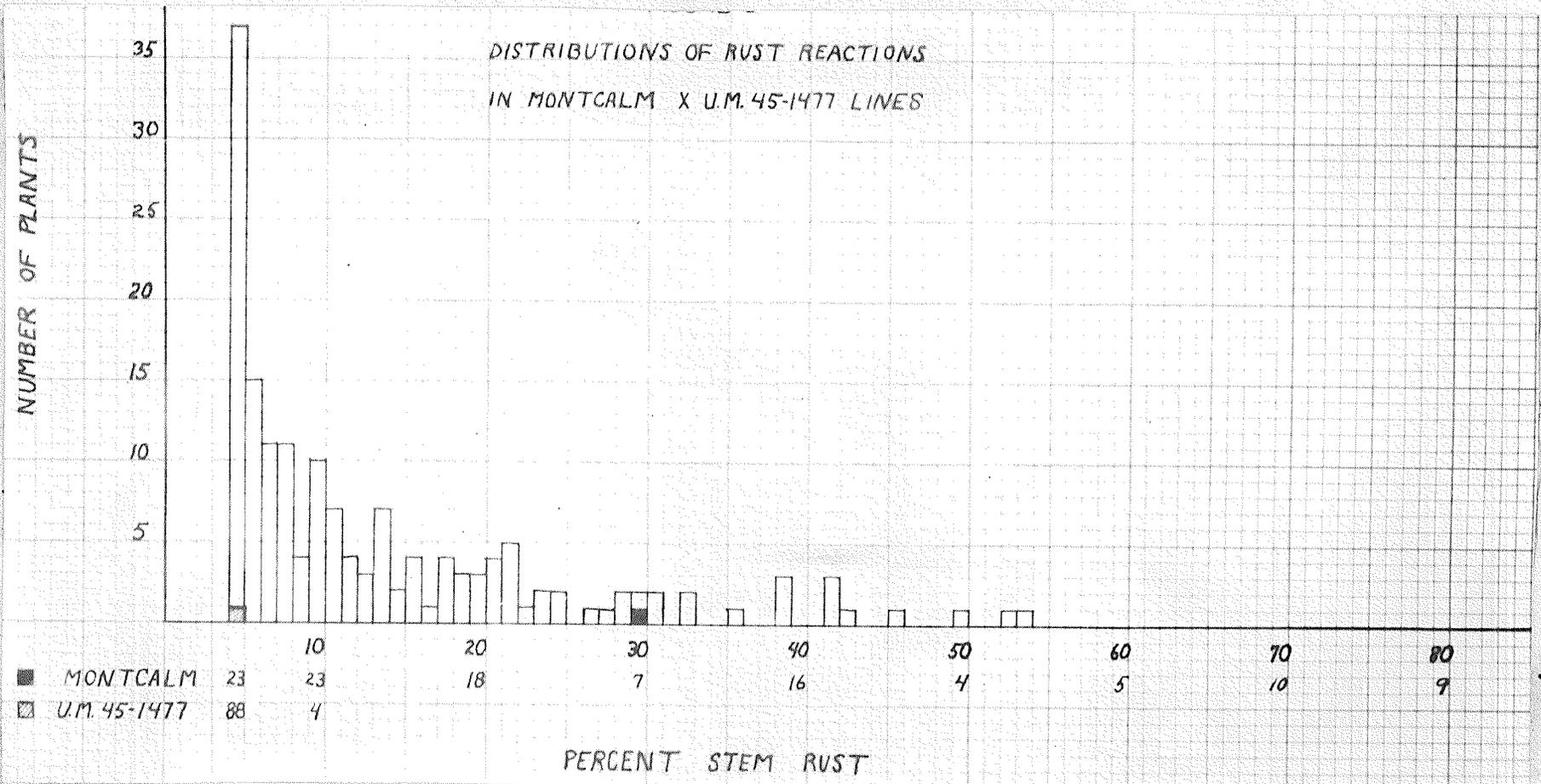




MONTCALM AV 14%
VALKIE AV ? %

PERCENT RUST

FIGURE 11



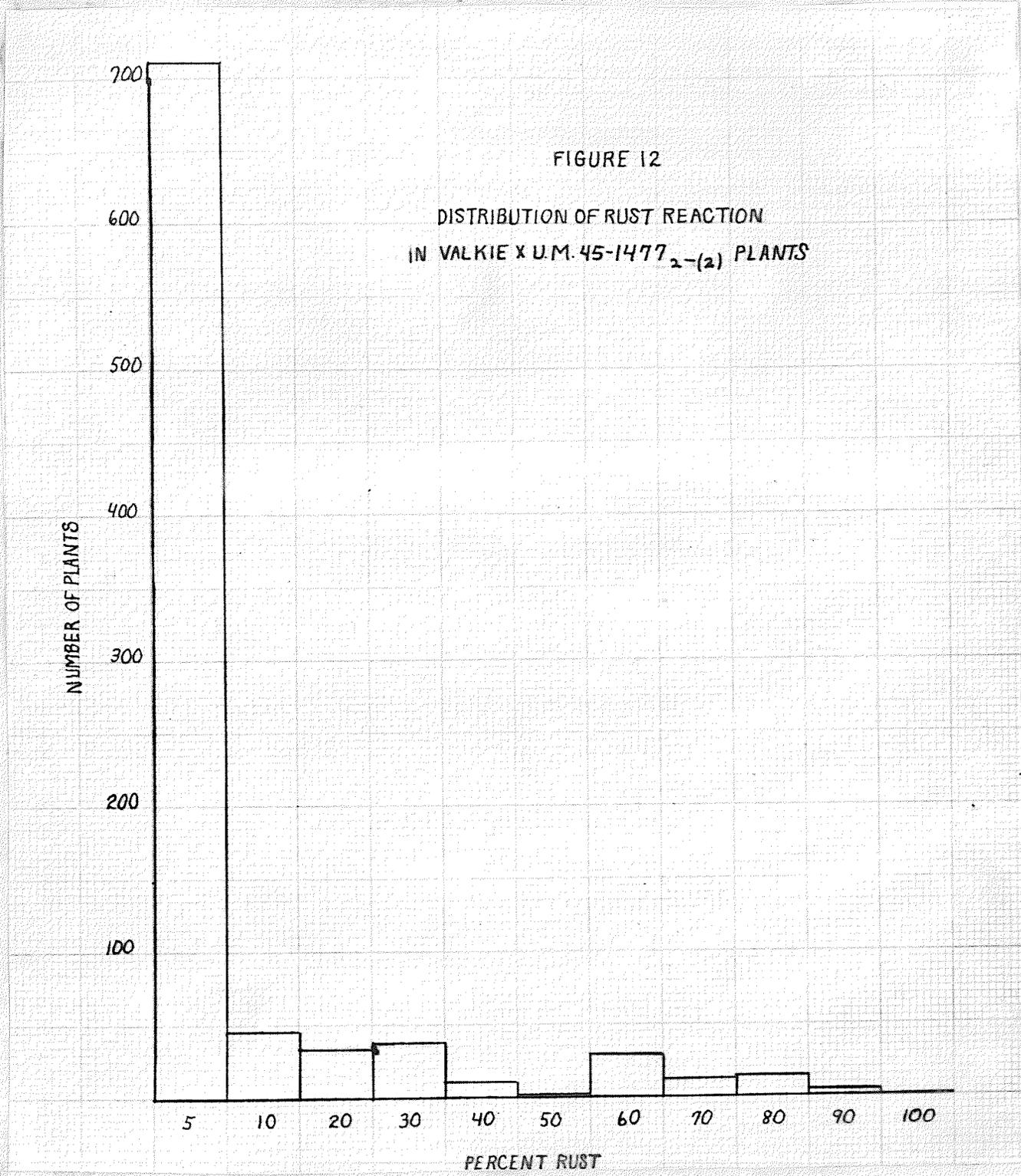


FIGURE 12
DISTRIBUTION OF RUST REACTION
IN VALKIE X U.M. 45-1477 2-(2) PLANTS

FIGURE 13

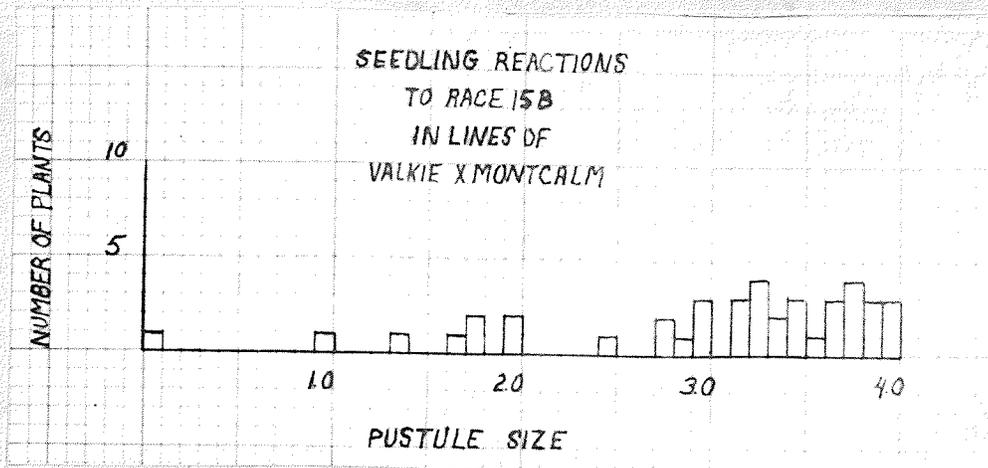


FIGURE 14

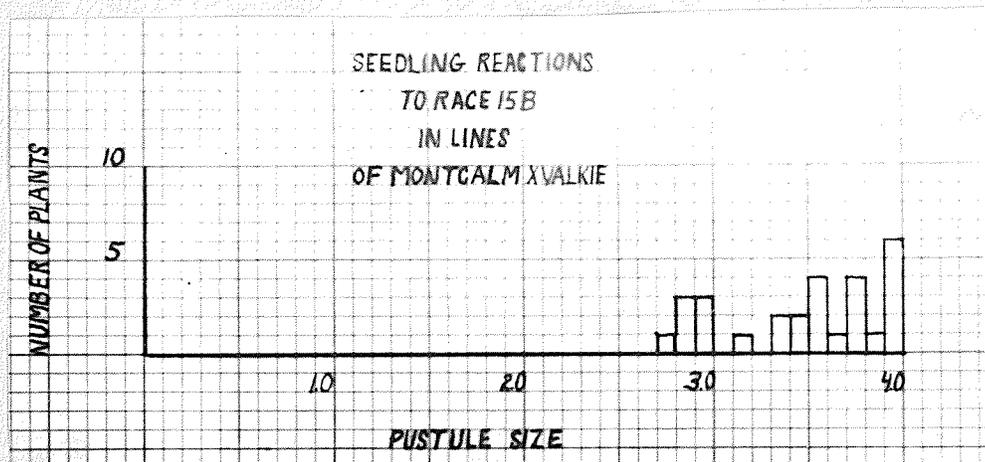


FIGURE 15

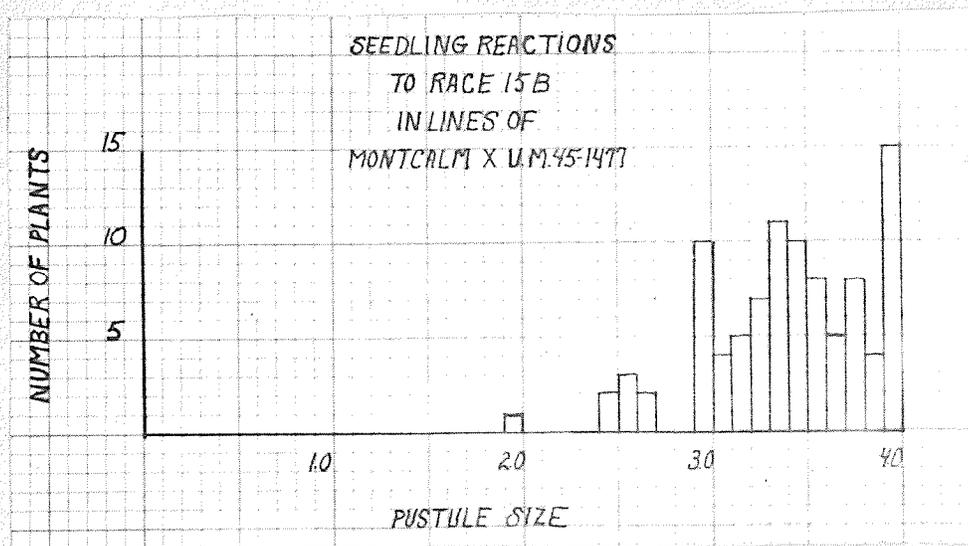


FIGURE 16

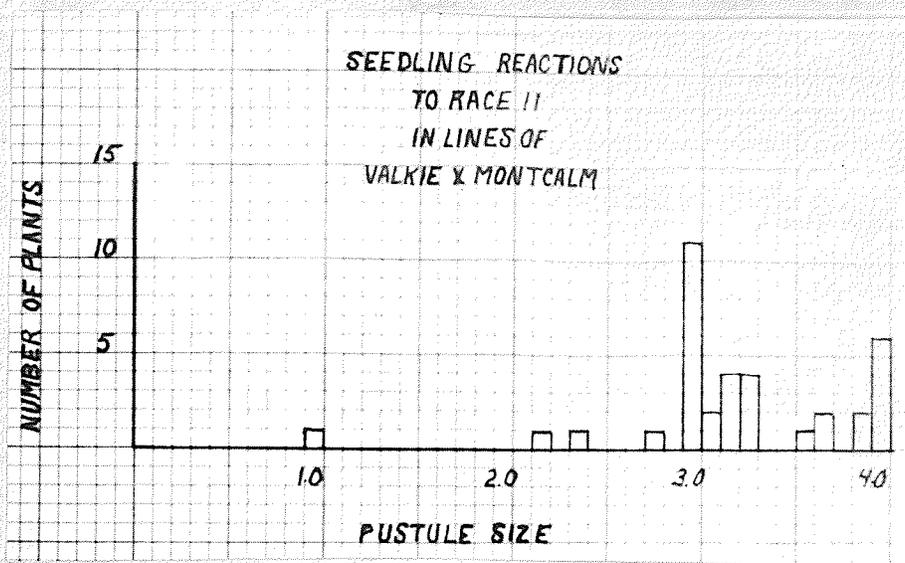


FIGURE 17

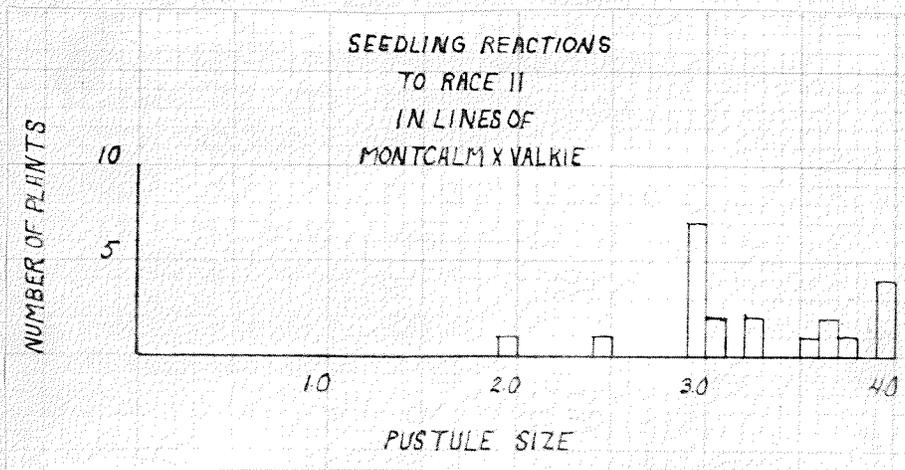
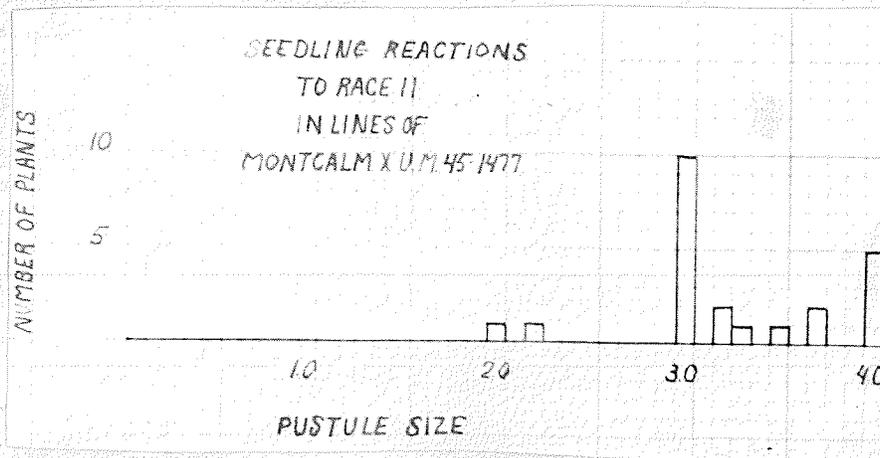


FIGURE 18



APPENDIX B

