THE INHERITANCE OF REACTION TO LEAF RUST IN BARLEY

by

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INTRODUCTION

The dwarf leaf rust of barley caused by *Puccinia hordei* Otth. (*P. simplex* Erikss. & Henn.; P. *anomala* Rost.; *P. rubigovera* (DC.) Wint. var. *hordei* L. & C.) is a comparative newcomer to the field of cereal rusts. It was for many years considered to be the "least conspicuous of the grain rusts in point of economic importance (9)." By the middle thirties, it had become relatively important on the winter barley crop of the southern United States, and during the past decade it has begun to threaten the southern spring barley areas (5). The barley crop of that area suffered rather severely from leaf rust attack during the 1950 growing season. Several southern states reported considerable losses (8) and North Carolina alone recorded a 10% average loss. Entire fields were completely destroyed in that state (20).

Some (23) have attributed this increased prevalence of barley leaf rust to the changing pattern of commercially grown varieties. The Manchurian barleys, which exhibited a moderate degree of resistance, have been largely replaced by varieties resistant to the "major" diseases, but often highly susceptible to leaf rust.

"Leaf rust of barley occurs to some extent in all nine provinces of Canada.... As this rust thrives under comparatively cool conditions it is more prevalent in the cooler areas of Canada. It sometimes causes heavy infection in quite localized areas.... (21)"

Brown and Newton (2) first noted the occurrence of this rust in Manitoba in 1922; it was not again recorded until 1927. Since that time it has been collected every year, but has never been considered a limiting factor in local barley production. However, Newton et al (21) have shown that a moderately heavy infection of this rust on barley in Manitoba could cause yield and, in some cases, grade reductions, as well as significant decreases in kernel weight and nitrogen content of barley and wort.

The accepted alternate host, the Star of Bethlehem, (*Ornithogalum umbellatum* L.) occurs throughout the settled eastern part of the North American continent (11). This plant is not indigenous to Manitoba. Its role in the spread of the disease is problematical, as it has seldom been reported infected in nature. Aecidia of *P. hordei* were discovered on *O. pyreniacum* and further studies indicated that "several hosts proved to be congenial to this heteroecious rust (7)." This may prove to be a further centre of infection and source of spread of the disease. The primary importance of the alternate host in the hybridization of new physiologic races should not be underestimated.

Sources of resistant parental varieties have been established by several workers in Europe, Australia and North America (13, 19, 29). Utilization of these sources would be aided by a knowledge of the mode of inheritance of resistance and susceptibility. This study was undertaken in an effort to provide some of this genetical information.

REVIEW OF LITERATURE

There is a dearth of available literature on the genetics of leaf rust reaction in barley. It is only during the past two decades that pathologists have devoted sufficient attention to the causal organism to facilitate intelligent planning of inheritance studies. A short review of the literature on the causal organism pertaining to nomenclature, physiologic specialization and environmental relations is presented here. This information is valuable, although not entirely essential, in studying the inheritance of disease reaction. Mention is also made of the surveys of leaf rust resistant germ plasm that have been made. It is from these studies that resistant varieties can be chosen for intensive genetic study. Earliest reports of inheritance studies indicated that the resistance of barley to leaf rust is conditioned by a single dominant factor. Later studies revealed that some varieties possessed different factors which conditioned their particular type of resistance. These studies were conducted largely in the greenhouse. No conclusive results have been reported in field studies to date, but preliminary evidence suggests that several factors, perhaps possessing pleitropic effects may be involved, in conditioning reaction of barley under field conditions.

Much confusion has arisen in the nomenclature of the causal organism of the dwarf leaf rust of barley.

Körnicke, in 1865, differentiated a variety of barley leaf rust which he named P. straminis simplex. In 1894, Eriksson and Henning raised the varietal name to specific rank. This name was accepted by German workers. Meanwhile, at least three investigators had described the organism as a distinct species. One of these P. anomala Rostr., published in 1878 was used by English and Scandinavian workers. Buchwald, in 1935, discovered that P. hordei had been described and published in 1871 by Otth., and thus maintains that this is the correct epithet for the causal organism of the dwarf leaf rust of barley, according to the International Rules of Botanical Nomenclature (3). Examination of the pertinent literature convinced Levine and Cherewick (17) that this rust deserves no more than varietal rank and they, therefore, suggest that "the dwarf leaf rust of barley be joined as a variety with the orange leaf rust of wheat and the brown leaf rust of rye under the trinomial epithet Puccinia rubigovera (DC.) Wint., var. hordei (Otth.) comb. nov." The binomial P. hordei Otth. will be used throughout this paper as the validity of the trinomial has not yet been established.

"Evidently sensing the latent threat of the dwarf leaf rust to the barley crop of the United States, Mains a quarter of a century ago, undertook the study of the possible physiologic specialization in this fungus (17)." He demonstrated the occurrence of two races of P. anomala (P. hordei) in the United States at that time (18).

Waterhouse (29) tested a number of varieties to an Australian collection of leaf rust. The results indicated that this collection constituted a race different from those isolated by Mains.

By 1931, Brown (1) had demonstrated the occurrence of four races in Canada. Several other physiologic races were reported from Germany (3, 28), Argentine (14), Portugal and England (6). Similarity among the races could not be determined for, as stated in 1933 by Stakman et. al. (27): "Owing to the use by different investigators, in different countries, of different varieties for the determination of physiologic races of the leaf rust of barley, comparison of the racial identity has become extremely difficult if not altogether impossible."

Consolidation of physiologic races was attempted by German workers (24) but they met with limited success. Recently Levine and Cherewick (17) constructed a key using sixteen differential hosts, by which they are able to distinguish all the authentic physiologic races reported in the literature. Consolidation of the singularly important races with those of lesser importance enabled them to establish a set of nine differential hosts for the identification of leaf rust races.

The race composition of leaf rust collections on different continents differs considerably. The most common race in North America is Race 4. This race has predominated in collections of barley leaf rust in Manitoba and the United States for several years. It was the only race isolated from leaf rust collections made in Manitoba in 1951 (16). Changes in racial composition sometimes occur. New races become evident which have developed through hybridization on the alternate host, or by mutation in the uredial stage of already established races.

The pathogen and host are very sensitive to environmental conditions, particularly light and temperature. Hey (13) states: "There is an increase in resistance with different rust races with some specific barley varieties. In some cases this manifestation occurs at high and in other cases at low temperatures. Some races could be distinguished at all temperature levels." He coined the terms "Absolute" resistance and "Relative" resistance to be applied to barley varieties normally grown in the temperate regions. The former maintain their resistance at all temperatures, while the latter are resistant within certain temperature ranges.

Straib (28) reported that generally the degree of infection varied with the temperature, variety and biotype. He stated that susceptibility increased generally as the temperature was raised from 12° - 20°C. Highly susceptible varieties showed no change with increased temperature. This may be a case of "Absolute" susceptibility, similar to the "Absolute" resistance reported by Hey.

Waterhouse (30) working with "moderately resistant" varieties, found that the typical 2/ pustule type normally occurring during the winter months of reduced light intensity and lower temperatures, changed to a susceptible 4 type pustule during the summer with increased light and temperature. These varieties apparently exhibited "Relative" resistance.

A survey of leaf rust resistant germ plasm was begun in the United States by Mains and Martini (19). From tests of over 600 barley varieties, comprising types from the major barley "groups" to the two races of the pathogen previously isolated by Mains, they found resistant varieties scattered throughout all the "groups." Eleven varieties were outstanding in their resistance to both races under greenhouse and field conditions. Other varieties differed in the type and stability of reaction.

Hey (13) tested the reaction of several barley varieties to leaf rust, and found that some were resistant to all races studied, while others "segrated" under field conditions.

Straib (28) tested 508 varieties to eight of the most common German races of P. simplex (P. hordei). He found resistant varieties scattered throughout the "three main species of barley." No variety resistant under greenhouse conditions was susceptible in the field. Some varieties that showed susceptibility in the seedling stage, exhibited resistance in the adult plant stage. This indicated the possibility that some varieties exhibit "mature plant resistance", a phenomenon previously reported for leaf rust of wheat as well as stem rust (10, 27).

D'Oliveira (6), using eighteen physiologic races collected in Portugal and England, studied the reaction of a large number of previously reported resistant varieties under greenhouse conditions. He found no varieties that showed resistance to all of the races studied.

Henderson (12) tested 246 barley varieties (which he obtained from the USDA) to seventeen collections of leaf rust in the greenhouse and field. Of the 211 varieties which showed resistance in the field, 180 were resistant in the seedling stage as well, indicating that they possessed a "physiologic" type of resistance. The rest appeared to possess the "mature plant" type of resistance, previously reported to occur in some varieties by Straib (28). Resistance to leaf rust was highly correlated with spot blotch

(Helminthosporium sativum) susceptibility, although five varieties exhibited a high degree of resistance to both diseases.

Smith (25) has briefly reviewed the literature available on inheritance studies on the reaction of barley to leaf rust up to 1946.

Waterhouse (29) was the first to report studies on the mode of inheritance of barley to leaf rust. From crosses involving resistant and susceptible varieties, he concluded that resistance was completely dominant and conditioned by a single factor. Later (30) he published the results of further inheritance studies in a large number of crosses. These results were based on the reaction of a relatively small population in each of several crosses studied. In resistant-susceptible crosses, the F_1 indicated complete dominance of resistance. The F_2, F_3 and backcross populations verified the simple factor hypothesis. Resistance appeared completely dominant in crosses with moderately resistant varieties, and conditioned by a single factor. Moderate resistance appeared to be conditioned by a simply inherited dominant, as evidenced by segregations in crosses with susceptible varieties. No association was found between leaf rust reaction and hooded vs. awned lemma and hulled vs. naked caryopsis. This worker indicated the necessity of studying crosses between resistant varieties to establish the identity of the resistance factors involved.

D'Oliveira (6), while not determining the type of segregation, suggested that several factors were involved in conditioning leaf rust resistance under field conditions.

Honecker (15) stated that he had not yet achieved conclusive results, but that his preliminary results suggested that resistance to leaf rust under field conditions is determined by one to several factors, some perhaps possessing pleitropic effects. He concluded that there is probably "a partial linkage between the factors for number of rows and factors for resistance to dwarf rust."

Henderson (12) chose nine resistant varieties and one susceptible selection for intensive genetic study. The results obtained in all resistant x susceptible crosses indicate that each resistant variety possesses a single factor for resistance, which is incompletely dominant. In crosses involving resistant parents, eight appeared to carry the same factor for resistance, as evidenced by lack of segregation in hybrid populations. The ninth variety appeared to carry a different factor for resistance, as crosses between it and the other eight resistant varieties gave a 15 resistant: 1 susceptible segregation. This worker concluded that two loci are involved in determining reaction to leaf rust, but that the majority of varieties studied carry a single incompletely dominant factor conditioning resistance. The two loci are independent. There were distinct differences in the degree of resistance exhibited by the varieties studied. This worker suggests that this is due "either to modifying factors present in some varieties, or to the existence of a multiple allelic series at the first resistant locus. The data do not serve to distinguish between these two alternatives." Independence of the factors conditioning leaf rust reaction and hooded vs. awned lemma, hulled vs. naked caryopsis, blue vs. yellow aleurone, rough vs. smooth awns and long vs. short haired rachilla is indicated.

Watson and Butler (31) studied a hybrid population obtained from a cross of two resistant varieties which differed in the type of resistance. Earlier tests with susceptible varieties indicated that each possessed a single major gene which differentiates its type of resistance. The results indicated that the single factor for resistance carried by each is non-allelic and independently inherited. The F_2 ratios obtained, namely 12:3:1 indicated epistasis of one type of resistance over the other. The F_1 results indicated epistasis also. No association between leaf rust reaction and type of lemma appendage, rough vs. smooth awns, short vs. long haired rachilla and reaction to race 3 of *Erysiphe graminis* was found. These workers concluded that there are relatively few loci involved in determining reaction of barley to leaf rust.

MATERIAL AND METHODS

Varieties:

Four barley varieties were used in this investigation. The three resistant varieties, Kwan, Ricardo and C. I. 4219 were selected from a large number that had been reported resistant under Minnesota conditions by Henderson (12). The susceptible variety was Montcalm.

Montcalm is a smooth awned, six-rowed variety of hybrid origin. It resulted from the cross (Michigan 31604 x Common six-rowed M. C.)x Mandscheuri 1807 M. C. made at MacDonald College and released in 1945.

Ricardo, a six-rowed, rough awned variety, was obtained by the USDA from Uruguay. Henderson (12) reported that the resistance exhibited by this variety is conditioned by a single factor. This factor is common to eight of the nine leaf rust resistant varieties which he studied.

Kwan originated in India. Several workers had recommended it as a particularly valuable source of leaf rust resistant germ plasm (19). This is a compact headed, six-rowed, rough awned variety, which exhibits a semi-winter habit of growth in some seasons.

"A partial linkage between the factor conditioning number of rows and certain components of field resistance" had been reported (15). For this reason, a two-rowed variety, C. I. 4219, was included in this study. It is a rough awned variety of Abyssinian origin, and was believed resistant on the basis of Henderson's work (12) as well as two field observations reported from the USDA (32).

Both Montcalm and Ricardo are used in the Barley Breeding Program of the Plant Science Division, University of Manitoba. Montcalm has been used extensively as a source of agronomic and quality characters while Ricardo is used as a source of leaf rust resistance.

As the resistant varieties have originated from widely separated geographic locations, it was thought that a diverse genetic complement would be encountered, and hence possibly permit more complete analysis of the number of loci involved in conditioning reaction to leaf rust.

<u>Hybrids</u>:

Reciprocal crosses between the varieties Ricardo, Kwan, C. I. 4219 and Montcalm were made in all combinations in the field during the summer of 1949. The seed set obtained was sufficient in all but the Ricardo by Kwan cross. In this case only 12 F_o seeds were obtained, probably due to the divergence in heading dates and a possible incompatibility between the two varieties.

As this experiment was originally designed to study the reaction to leaf rust of hybrid populations under field conditions, two generations of each of the crosses were grown in the greenhouse during the fall and winter of 1949-50. The seed obtained made it possible to grow parental varieties, together with hybrid populations of F_1, F_2 and F_3 in the field simultaneously. As the importance of environmental variations on the expression of reaction to leaf rust had been reported by several workers (13, 17, 30), the growing of all hybrid generations under comparable conditions was particularly desirable.

A successful leaf rust epiphytotic was produced in the crossing block during the summer of 1949, by dusting uredospores mixed in talc over the varietal plots on an evening when dew was expected. This method has been described by Cherewick (4). The inoculum used represented several races of *P. hordei*, and was supplied by the Dominion Laboratory of Plant Pathology at Winnipeg.

Rust reaction was determined on the basis of percentage leaf area covered by pustules, using the scale devised by Peterson *et al* (22).

Field Investigations:

The 1950 leaf rust nursery consisted of F_1 and F_2 plants, and F_3 lines in rows six feet long, each containing approximately twenty-five plants. Parental checks were placed every twenty rows. A border row of Montcalm (a susceptible variety) was seeded to facilitate spread of the disease.

Several attempts to induce a leaf rust epiphytotic were made during July and early August, but no leaf rust pustules developed. A spore germination test was conducted in an effort to determine the cause of the epiphytotic failure. No germ tubes appeared in any of the spores examined. Lack of refrigeration during the flood period earlier in the spring was probably the cause of this spore inviability.

The natural epiphytotic was negligible and as a result no rust readings could be made. Morphologic characters were recorded. At maturity, seed of each individual F_1 and F_2 was harvested. Seed from each F_3 line was also obtained in all crosses except C. I. 4219 by Kwan in which the individual F_3 plants were harvested.

In 1951, the same general field plan was adopted. However, the F_3 lines were seeded in 10' rows and contained an average of fifty plants. A small population of F_4 lines, each containing approximately one hundred plants was also grown in each of the crosses. The artificial epiphytotic was retarded because of drought during the early part of the growing season; thus only the late sown material carried a sufficiently heavy infection to permit reliable rust readings. Kwan had previously been reported to exhibit the semi-winter habit in some seasons. Morphologic character data were collected on the late material. The semi-winter trait was evident during the 1951 season on Kwan and Kwan hybrids sown after June 1. The F_3 plant progenies of the Kwan x C. I. 4219 cross could therefore be classified for growth habit in addition to the other characters. The rust reaction of the remainder of the material present in the field at this time could not be determined. However, individual F_1 and F_2 plants which headed were individually harvested and their morphologic characters recorded.

The field rust reactions were determined on the basis of pustule type. Five classes of pustules were recognized as outlined by Henderson (12): .0, .2, .4, .6, .8, and 1.0. The .0 class representing high resistance and the 1.0 class indicating complete susceptibility. The individual classes may be described as follows.

Only flecking on leaf or no evidence of infection whatever No open pustules	.0
Pustules not open or very small. Severe necrosis surrounding each pustule	.2
Small scattered pustules. Each pustule delimited by well-defined necrosis	.4
Complete range in pustule types on same leaf All other classes represented	.6
Pustules larger than in .0, .2 and .4 No necrosis but often definite chlorosis	.8
Large full pustules, sometimes coalescing	1.0

Henderson adds: "Based on injury to the plant .0, .2 and .4 are considered resistant type pustules; .6 is intermediate and .8 and 1.0 are susceptible."

Field reactions were determined about ten to fourteen days before maturity except in those cases in which heading was delayed, i.e. in those lines which exhibited the semi-winter habit. Readings were taken on these lines at the same time as the heading lines were studied.

Greenhouse Investigations:

In view of the failure of the leaf rust epiphytotic during the summer of 1950, it was deemed advisable to conduct greenhouse leaf rust tests during the ensuing fall and winter, in order to obtain some information on the rust reaction of the hybrid populations.

The leaf rust reaction genotype of each F_2 plant was determined on the basis of the reaction of the F_3 line arising from it. Each F_2 plant that had been harvested the previous fall was individually threshed and a sample of 10 to 15 seeds was tested in the greenhouse. A somewhat larger seed sample of the F_3 plants in the Kwan by C. I. 4219 cross was studied by testing the reaction of the F_4 line. Two pots of parental varieties were grown with each batch of hybrids to provide a standard for rust readings.

Inoculation Procedure:

As this study was originally designed to be conducted under field conditions, a bulked collection of races was used in the first greenhouse tests, to simulate field conditions as closely as possible. The reactions obtained were not sufficiently clear cut to enable accurate determinations. The reaction of the parental varieties to each of the races was not known at the time, and it was thought that the difficulty encountered in classification of resistant and susceptible seedlings arose from the differential reaction of the parental varieties to the races present in the inoculum. It was, therefore, decided to use an individual race in all further tests.

Workers on other cereal rusts recommended the use of individual physiologic races in greenhouse tests (10). Henderson (12) had suggested the value of individual races in inheritance studies of barley reaction to leaf rust conducted, under greenhouse conditions. However, his investigation was designed to aid in a breeding program, and there was at that time no reliable information on the predominating races present in the Upper Mississippi Valley. He therefore used a collection of races.

In Manitoba, Race 4 has predominated for several years. Mr. A. M. Brown therefore recommended its use for this study. He kindly furnished a pure culture of Race 4 inoculum. At various times during this investigation, the differential host varieties were inoculated with the rust culture in use to ensure that the same race was used throughout. This was deemed necessary as mutations had been reported to occur in the pathogen (17). Several inoculated pots of Montcalm were retained at all times to provide a continuous supply of inoculum.

The seed sample from each F_2 plant was placed in a 4" clay pot. Inoculations were made when the plants were in the first leaf stage generally. The waxy bloom was first removed by fingering. The rust inoculum was then applied about mid-way up the leaf by means of a small spatula or needle. The leaves were then sprayed with a light water spray. At first the spray was produced by means of a hand atomizer; a more effective and rapid method was later adopted, by which a fine-bore nozzle attached to a hose was used. Incubation followed inoculation. The incubation chamber used consisted of a water-sealed galvanized metal tub provided with a glass top, and accommodated fourteen 4" pots. The incubation period was approximately 24 hours. This period had been reported sufficient for spore germination (29). The infections obtained were very satisfactory.

The rust reaction of the seedlings in each pot were individually read 14-17 days after inoculation. Classification was made according to pustule type, and was similar to the infection types first described by Stakman and Levine (26) for similar studies on Puccinia graminis. These types, with modifications, have been used for studies of barley leaf rust by several workers (6, 17, 18, 30). The pustule types may be described as follows:

No pustules developed. Infection visible only as minute flecks or necrotic areas over the leaf	Type 0;
Pustules very small, delimited by sharp necrotic areas	Type 1
Pustules fairly small, each surrounded by a necrotic ring	Type 2
Pustules of moderate size, without necrotic rings but usually surrounded by chlorotic areas	Type 3
Pustules relatively large, with little or no chlorosis	Type 4
Pustules of all classes appearing on same leaf	Type X

These types may be described qualitatively as:

0; - extremely resistant
1 - highly resistant
2 - moderately resistant
X - heterogeneous reaction - moderately susceptible
3 - highly susceptible
4 - extremely susceptible

0;, 1 and 2 type pustules were classed as resistant while X and 3 type pustules were considered susceptible. The 4 type pustule was not generally recorded in this investigation, as the most highly susceptible variety usually exhibited a fair degree of chlorosis.

A great deal of difficulty was encountered in determining genetic ratios from the data obtained in the 1950-51 greenhouse studies. Accordingly, greenhouse tests were continued during the fall of 1951.

To provide data on the F_2 phenotypic reaction, fairly large F_2 populations were tested in the seedling stage on all but two of the crosses. Populations in excess of 1000 F_2 plants were grown of Montcalm by Ricardo and Montcalm by Kwan crosses. To enable better detection of segregating F_3 lines, larger seedling populations of each line were tested than in the previous season.

As no information was available on the correlation between seedling and adult plant reaction, several F_1 plant progenies of two of the crosses were planted in a large greenhouse bed; inoculations and readings were made in both the seedling and adult plant stages. The inoculation procedure was modified slightly for this test. After the waxy bloom had been removed from the seedlings in the usual manner, the inoculum was applied by fingering. A canvas tarpaulin placed over the bed, after inoculation, provided a satisfactory incubation chamber. The inoculated plants and the tarpaulin were sprayed with water at regular intervals to maintain a high humidity level. Owing to the difficulty of fingering individual adult plants, inoculation was accomplished by spraying the plants in the shot blade stage with a suspension of spores in a .25% gelatin in water solution. A Flit sprayer was used for this purpose. To ensure infection, three sprayings were applied on each of two successive days. The water-sprayed canvas tarpaulin was again used to maintain a high humidity level. Excellent infections were obtained. Rust reaction was determined by pustule type in both stages of development.

At the conclusion of the greenhouse tests, analysis of the mode of inheritance of reaction to leaf rust was made by means of the x^2 test of Goodness-of-Fit.

Association of Characters:

In addition to segregating for leaf rust reaction, several of the crosses were heterozygous for one or more of the following character pairs whose linkage relationships have been fairly well established (25).

Character Pairs		Linkage Group
Rough vs. Smooth Awns	(Rr)	V
	(R_4r_4)	III
Deficiens vs. Six-Row Ears	(Vt v)	I
Lax vs. Dense Spike	(Ll)	1, III, IV
	(L_3l_3)	V

Spring vs. Winter Growth Habit (Sh sh) Group V

Several factors have been reported which condition spike density and growth habit, not all of which have been mapped. The mode of inheritance of these two characters has not been established conclusively, as different results have been obtained by different investigators.

There have been four factors reported which condition rough and smooth awns, only two of which have been mapped.

X_2 tests of Independence were calculated for segregation of leaf rust reaction and one or more of the morphologic characters concerned.

EXPERIMENTAL RESULTS

The leaf rust reaction of the four parental varieties used in this study had not been determined, under local conditions, at the time that they were selected and intercrossed. A successful leaf rust epiphytotic in the crossing block, during the summer of 1949, permitted determination of the parental rust reaction to a collection of races.

The reaction of the parental varieties to the races of leaf rust present in the field during 1949, and to race 4, in the greenhouse are shown in Table I. The source of each, and morphologic characters that were used in association tests are also indicated.

Both field and greenhouse studies confirmed the reported resistance of Ricardo and Kwan. Montcalm was found to be susceptible as was previously believed. C. I. 4219 proved to be more susceptible than previous reports had indicated. It had been reported to carry less than 5% infection in the field and to exhibit a 1 type pustule. It was found to carry an average of 30% infection in the field and to exhibit an X type pustule to race 4 in the greenhouse. Both of these reactions indicate that the variety is moderately susceptible. The reaction of Ricardo, Kwan and Montcalm, when tested to several races by Brown[x] was similar to the reaction of these varieties to Race 4, but C. I. 4219 was found to react differently to the various races. It was resistant to some and moderately susceptible to others.

X unpublished data supplied by A. M. Brown, Dominion Laboratory of Plant Pathology, Winnipeg.

TABLE I PARENTAL VARIETAL CHARACTERISTICS STUDIED IN THIS INVESTIGATION

Variety	C. I. Number	Source	Leaf Rust Reaction %Infection Field 1949	Leaf Rust Reaction Pustule Type Race 4	Awn Type	Row Number	Density
Ricardo	C. I. 6306	Uruguay	Trace	1(+)	Rough	Six	mid-dense
Kwan	C. I. 1016	India	Trace-10%	0;	Rough	Six	dense
——	C. I. 4219	Abyssinia	20%-40%	x	Rough	Deficiens	lax
Montcalm	C. I. 7149	hybrid	60%-80%	3(+)(x-3(‡))	Smooth	Six	mid-dense

The parental seedling reaction to race 4 is shown in Plate I of Appendix A.

The rust reactions of the hybrid populations were determined in the greenhouse in all cases. Several F_4 lines of the cross C. I. 4219 x Kwan, which carried sufficient infection in the field in 1951, were classified for rust reaction in both field and greenhouse. The general epiphytotic in both 1950 and 1951 was insufficient to permit adequate classification for rust reaction. As a result, greater reliance had to be placed on greenhouse results than was originally intended. This failure to obtain the desired field data is not, however, believed to affect the accuracy of the conclusions drawn from this study. The use of race 4, the predominating race in this area, allows the results obtained in this study to be utilized in local barley breeding programs.

Intercross of resistant varieties:

As the reported resistance of C. I. 4219 was not confirmed in these studies, Kwan and Ricardo constituted the only resistant parental material in this investigation. Only twelve F_0 seeds were obtained in the cross of Ricardo x Kwan. Two generations were grown from ten of these, during the fall and winter of 1949-50, to produce seed for F_2 and F_3 generations for field study. The two remaining F_0 seeds were planted in the field in 1950. Therefore, no seed was available for the determination of F_1 reaction, in the greenhouse.

The occurrence of susceptible plants in the hybrid populations derived from a cross involving two resistant varieties, is genetic evidence that these two varieties possess different factors for resistance, while the absence of susceptible segregates in a fairly large population suggests that the loci conditioning resistance are common to both.

A small F_2 population of the Ricardo x Kwan cross was tested in the greenhouse in 1950 and no susceptible plants appeared. However, of the forty-eight F_3 lines tested, forty were resistant and eight segregated for reaction to leaf rust, and of the thirty F_4 lines tested, twenty-five were resistant, three segregated and two were susceptible. The results indicated that different factors are involved in conditioning resistance in the two varieties, but the population was too small to determine the number of factors involved. A reasonably large reserve of seed, from two F_1 plants was available for further study in 1951. Two hundred and twenty-five F_2 plants were inoculated with race 4 in the seedling stage. The reaction of this population is given in Table II. Goodness-of-fit to a 15:1 ratio was tested by the x^2.

TABLE II RICARDO X KWAN

Reaction of F_2 Plants to Race 4 of P. hordei

F_1 progeny number	Rust Class		Total	Assumption 15:1	
	Resistant	Susceptible		x^2	P value
1	125	11	136	.7843	.50-.30
2	82	7	89	.3963	.90-.80
Total	207	18	225	.1760	.30-.20

The P values obtained indicate satisfactory agreement to a 2 factor hypothesis.

The reaction of the parental varieties Kwan and Ricardo, and the range in pustule types observed in the segregating hybrid populations when tested to Race 4 are shown in Plate II of Appendix A.

Crosses Between Montcalm and Two Resistant Varieties:

F_1 plants of the crosses between Montcalm and each of the resistant varieties were classified for reaction to Race 4 of leaf rust in the greenhouse. Variations in reaction between F_1 plants arising from different Montcalm female plants were noted in each of the crosses. The pustule types recorded varied from 1(+) to 2 in the Ricardo cross, and from 1 to 2(-) in the Kwan cross. To the writer, these reactions appeared to be intermediate between the resistant and susceptible parents indicating lack of dominance in each case. The variations within the crosses suggested heterogeneity in the Montcalm parent.

F_1 plant progenies of each of the crosses were tested in the greenhouse in the seedling stage, as were random individual F_2 plant progenies.

As other workers had reported single factor segregation for leaf rust reaction in resistant by susceptible crosses, the results obtained in each of the crosses were tested to a 3:1 ratio, While the pooled F_2 population of the Ricardo x Montcalm cross indicated reasonable agreement to this hypothesis, the pooled F_2 population in the Kwan by Montcalm cross did not appear to fit this ratio. In addition, the high x^2 value obtained when the F_3 population of the Ricardo by Montcalm cross was tested to a 1:2:1 ratio, and the occurrence of a preponderance of susceptible plants in the small proportion of the segregating F_3 lines in both of the crosses, suggested a more complex explanation of the segregation obtained in the crosses of Montcalm with each of the resistant varieties.

In Table III are presented the reactions of eighteen individual F_1 plant progenies in the Ricardo x Montcalm cross. The pooled data and each of the individual progenies were tested to a three factor ratio of 51 resistant: 13 susceptible plants.

TABLE III RICARDO X MONTCALM

Reaction of 18 F_1 Plant Progenies to Race 4 of P. hordei

Line	Rust Class		Assumptions					
	Resistant	Susceptible	51:13		43:21		15:1	
			x^2	P value	x^2	P value	x^2	P value
1	76	12	2.4231	.20-.10				
2	83	17	.6779	.50-.30				
3	67	20	.4240	.70-.50				
4	63	23	2.1978	.20-.10				
5	66	25	2.8826	.10-.05				
6	81	12	3.1541	.10-.05				
7	63	23	2.1978	.20-.10				
8	80	25	.7933	.50-.30				
9	102	30	1.0656	.50-.30				
10	135	36	.0579	.90-.80				
11	81	19	.8696	.50-.30				
12	98	17	2.1726	.20-.10				
13	60	29	8.2803	>.01	.0021	.98-.95		
14	72	50	32.2059	>.01	3.0335	.10-.05		
15	82	10	5.0681	>.01			3.3507	.10-.05
16	88	5	12.8175	>.01			2.1212	.80-.70
17	110	12	8.2723	>.01			2.6775	.20-.10
18	130	4	24.8552	>.01			2.4375	.20-.10
Total of 18 x^2's			111.4841	>.01				
Pooled	1537	369	1.0685	.50-.30				
x^2 for homogeneity			110.4156	>.01				

TABLE III A   RICARDO X MONTCALM

Reaction of F_3 lines to Race 4 of P. hordei

Rust Class			Total	Assumption	
Resistant	Segregating	Susceptible		19:38:7 (51:13) x^2	P value
76	131	33	240	2.979	.20-.30

The x^2 for homogeniety (P .01) indicated that the 18 F_1 plant progenies do not represent samples drawn from the same population. The pooled results indicate satisfactory agreement to the ratio tested. The P values obtained from the first twelve progenies listed indicate that they are likely samples from a population segregating in the proportion of 51 resistant to 13 susceptible plants. The other six progenies deviate significantly from this ratio.

Goodness-of-Fit to other ratios was tested by the x^2 and applied to those 5 progenies which did not fit a 51:13 ratio. The x^2 values obtained indicate that 13 and 14 segregate in the ratio of 43 resistant to 21 susceptible, while the remaining four progenies gave satisfactory agreement to a two factor ratio of 15 resistant to 1 susceptible.

The F_3 data presented in Table III A confirms the general conclusions drawn from the F_2. On the basis of the 51:13 ratio obtained on the pooled data in F_2, a 19:38:7 ratio was expected in the segregating F_3 lines. The x^2 value obtained indicates agreement to this factor ratio.

The hypothesis upon which the ratios are based is discussed after the presentation of the results.

The parental reaction of Ricardo and Montcalm and the range observed in pustule types of segregating generations, tested to Race 4, is shown in Plate III of Appendix A.

In Table IV are presented the reactions of fourteen individual F_1 plant progenies in the Kwan and Montcalm cross. The pooled data and each of the individual progenies were tested to a three factor ratio of 43 resistant:21 susceptible plants.

Examination of the P values obtained indicated the first ten progenies segregate in the same manner as the pooled data, and suggest that they are probably samples from a population segregating in the ratio of 43 resistant:21 susceptible plants. The following two progenies appear to segregate in the ratio of 51:13 (resistant : susceptible.)

Explanation of the segregation obtained in progenies 13 and 14, which showed a preponderance of susceptible types, could not be made in terms of the hypothesis evolved for the other progenies in this cross. This abnormal segregation may have resulted from stray pollination in the field, or from some chromosomal aberration. The removal of these two progenies from the pooled results does not alter the significance of the x^2 value obtained in the homogeneity test. This heterogeneity can be explained on the assumption that

TABLE IV KWAN X MONTCALM

Reaction of 14 F_1 Plant Progenies to Race 4 of P. hordei

Line	Rust Class		Assumptions			
	Resistant	Susceptible	43:21		51:13	
			x^2	P value	x^2	P value
1	77	39	.0344	.90-.80		
2	90	47	.1387	.80-.70		
3	89	42	.0355	.90-.80		
4	88	50	.7319	.50-.30		
5	105	53	.0384	.90-.80		
6	70	44	1.6838	.20-.10		
7	81	53	2.7581	.10-.05		
8	28	18	.8328	.50-.30		
9	70	24	2.2601	.20-.10		
10	70	24	2.2601	.20-.10		
11	86	24	6.0312	.02-.01	.1541	.70-.50
12	86	22	7.5837	>.01	.0003	.99 +
13	51	65	28.3744	>.01		>.01
14	80	71	7.1172	>.01		>.01
Sum of 14 x^2's			59.8783	>.01		
Pooled	1071	576	3.4861	.10-.05		
x^2 for homogeneity			56.3922	>.01		

TABLE IV A KWAN X MONTCALM

Reaction of F_3 Lines to P. hordei

Rust Class			Total	Assumption 19:32:13 (43:21)	
Resistant	Segregating	Susceptible		x^2	P value
54	93	40	187	.6260	.50-.30

two populations are represented, one consisting of ten families which represent samples drawn from a population segregating in the ratio of 43 resistant:21 susceptible plants, and the other containing two samples from a population segregating in the ratio of 51 resistant:13 susceptible plants.

The F_3 data presented in Table IV A offers general confirmation of the conclusions drawn from the F_2 population studied. From the 43:21 ratio obtained on the pooled F_2 data, a 19:32:13 ratio was expected in the F_3 population. The x^2 value obtained indicated agreement to this three factor hypothesis. Plate IV shows the range in pustule types observed in segregating hybrid populations together with the parental reaction to Race 4 of leaf rust.

Crosses Involving C. I. 4219:

C. I. 4219 exhibited a mesothetic reaction to Race 4 of P. hordei. Although temperature and light variations resulted in slight differences in the reaction of C. I. 4219, it was considered mesothetic throughout. With the higher temperature and light intensities that occurred during certain times of the year, there was a greater proportion of susceptible (i.e. chlorotic ringed) pustules noted, while during December and January, when the period of daylight was less and the temperature did not rise greatly during the day, a greater proportion of resistant (i.e. necrotic ringed) pustules was noted, on the C. I. 4219 parent.

The general mesothetic reaction of this variety made classification of the hybrid material rather difficult. Therefore, only limited data was collected from the three crosses in which it was involved.

In the hybrid populations, resulting from the cross of C. I. 4219 with Montcalm, only susceptible plants appeared in the tests conducted. The variations in susceptibiltiy that were seen are shown in Plate V of Appendix A. However, classification into these types was not made for purposes of analysis.

A random F_3 population of the Ricardo x C. I. 4219 cross, when tested for reaction to race 4 of leaf rust segregated in a manner that suggested a two factor difference between these two varieties. The results obtained are shown in Table V.

TABLE V RICARDO X C. I. 4219

Reaction of random F_3 lines to Race 4 of P. hordei

Rust Class			Total	Assumption			
Resist.	Segr.	Suscept.		15:1		11:4:1	
				x^2	P value	x^2	P value
203	77	14	294	1.1111	.30-.20	1.2122	.70-.50

The P value (.30-.20) obtained when the population was tested to a ratio of 15 (resistant ≠ segregating) : 1 (susceptible) indicates satisfactory agreement to this two factor ratio. The theoretical segregation expected in the F_3 lines is 7 resistant:8 segregating:1 susceptible, if two independent factors are involved. This segregation was not obtained; instead the proportion of lines noted was 11 resistant:4 segregating:1 susceptible. Of the eight F_3 lines that should theoretically segregate, four would be expected to do so in the proportion of 15 resistant:1 susceptible plant (s). However, a population of over 70 plants in each F_3 line would be necessary to have a 99% chance of recovering the susceptible plant in these lines. As the F_3 lines tested consisted of an average of fifteen plants, it is highly likely that the segregation in 4/16 of the population would have been missed, and they would therefore have been recorded as resistant. Assuming this to be the case, the F_3 lines would be expected to segregate in the ratio of 11:4:1. The P value (.70-.50) obtained, when the population was tested to this ratio indicates satisfactory agreement to this modified two factor ratio.

The variations in pustule types observed in the hybrid populations derived from the cross of Ricardo x C. I. 4219 are shown graphically in Plate VI of Appendix A.

There was available for study a rather large population of individual F_3 progenies, as well as a smaller number of F_1 and F_2 progenies in the cross of Kwan x C. I. 4219. The reaction of the F_2, F_3 and F_4 random populations in this cross is indicated in Table VI. The determination of the reaction of the F_4 lines was made on the basis of both field and greenhouse observations.

TABLE VI KWAN X C. I. 4219

Reaction of Random Sample of F_2, F_3, F_4 to Race 4 of P. hordei

Generation	Assumption	Rust Class			Total	x^2	P.value
		R	Seg	S			
F_2	13:3	401	0	91	492	.0407	.90-.80
F_3	7:8:1	40	37	8	85	2.2841	.20-.10
F_4	37:18:9	388	172	96	656	1.2012	.70-.50

There is evidence of segregation of two independent factors in all three generations of the cross of Kwan x C. I. 4219. The F_2 data agree satisfactorily to a ratio of 13 resistant:3 susceptible plants, (P .90-.80). The F_3 lines are expected to segregate in the ratio of 7 resistant:8 segregating:1 susceptible, and the P value (.30-.20) obtained suggests agreement of the observed results to this ratio. The F_3 plant progenies are expected to segregate in the proportion of 37 resistant:18 segregating:9 susceptible. The x^2 value (1.2012) obtained when the F_4 lines were tested to this ratio further substantiates the two factor hypothesis. The range in pustule types recorded within this cross is shown in Plate VII of Appendix A.

Correlation of Seedling and Adult Plant Reaction:

A greenhouse test was conducted in an effort to determine the degree of correlation between seedling and adult plant reaction. Two hundred fifty F_2 plants of the Kwan x Montcalm cross and one hundred F_2 plants of the Kwan x C. I. 4219 were inoculated with race 4 of P. hordei in both the seedling and adult plant stages. No significant differences were noted in the reaction of plants at the two stages of growth.

Association of Characters:

When this study was first undertaken, examination of the pertainent literature indicated that reaction to leaf rust in barley was generally conditioned by a single factor. There were two reports of two factor segregation in crosses between varieties exhibiting different types of resistance (12, 31). Therefore, an investigation of possible association between the factor (s) determining certain morphologic characters, by which the parents differed, and the factor (s) conditioning reaction to leaf rust was originally planned.

However, the results obtained from this study indicate that reaction to leaf rust is conditioned by no less than four independent loci.

No evidence of association between the factors conditioning reaction to leaf rust and the factors determining number of rows, rough vs. smooth awns, growth habit or density was found in any of the crosses studied. This does not preclude the possibility of linkages between one or more of the components of leaf rust reaction, and any of the factors determining the morphologic characters named.

The x^2 for independence is designed to test association (or independence) of attributes, rather than linkages between individual genes. When the attributes are conditioned by relatively few factors, it is often possible to detect association between the individual loci involved.

When, however, one attribute is conditioned by several factors, as appears to be the case in leaf rust reaction in barley, the independence test is not sufficiently precise to detect linkages of individual loci conditioning leaf rust reaction, and loci determining the morphologic attributes. The results of the independence tests are, therefore, not included in this report.

DISCUSSION

The results presented on the reaction of hybrid populations derived from the crosses involving Montcalm, Kwan and Ricardo, indicate that reaction to leaf rust in barley is influenced by factors located at four independent loci. Each of the resistant varieties, Kwan and Ricardo, carry a single major, incompletely dominant, resistance factor. The two major factors are independent, as evidenced by the P value (.30-.20) obtained when the F_2 population of the cross between these two varieties was tested to a 15:1 ratio. In addition, each appears to carry a common minor factor for resistance. Evidence for the presence of the minor factor is found in the three factor segregation obtained in the hybrid populations resulting from crosses of each of these varieties with Montcalm.

The susceptibility exhibited by Montcalm appears to be primarily conditioned by a dominant factor, hypostatic to the major resistance factors carried by Kwan and Ricardo, but epistatic to the minor factor present in these varieties. Montcalm also carries the recessive alleles of the major resistance factors of Kwan and Ricardo. Montcalm is apparently heterogeneous for leaf rust reaction. Although this variety has been recorded susceptible to race 4 in all cases, the degree of sporulation varied from plant to plant. This slight variation in reaction of different Montcalm plants has also been observed by Brown.[X] The heterogeneity in reaction observed in the F_1 individuals derived from different Montcalm plants, and the high x^2 value obtained in the homogeneity test conducted on the F_2 populations studied, suggests that the variations observed in the reaction of different Montcalm individuals are due to genetic differences.

The presence of an allelic series at the minor locus is suggested to account for these differences. Those Montcalm plants whose F_2 populations represent samples drawn from a population segregating in the ratio of 43 resistant: 21 susceptible plants are thought to carry a susceptible factor which is the prime member of the series. The resistant allele present in Kwan and Ricardo and in those Montcalm plants whose resulting F_2 populations segregate in the ratio of 15 resistant:1 susceptible, is the second member of the series. The F_2 populations that appear to fit the ratio of 51 resistant:13 susceptible are believed to be derived from Montcalm plants carrying the recessive susceptible allele at the minor locus.

The hypothesis outlined above is further elucidated, in terms of genotypes, in Appendix B. The individual genes

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X Personal communication from A. M. Brown, Dominion Laboratory of Plant Pathology, Winnipeg.

are simply referred to as A, B and C, as their proper nomenclature has not been established. The major resistance factors of both Kwan and Ricardo are referred to as A, in view of their apparent similarity of behaviour in crosses with susceptible Montcalm. The three genetic groups found in Montcalm are referred to as Type I, Type II and Type III in order of the dominance in the allelic series at the minor locus.

In view of the significant heterogeneity between the F_2 progenies of different F_1 plants in the population derived from crosses of each of the resistant varieties with Montcalm, the fact that the pooled F_2 results from the two crosses do not fit the same ratio is not unexpected. As no selection was practised in the choice of individual plants from the parental varieties, the results obtained probably represent the reaction of a random sample of Montcalm plants.

The limited results obtained from the hybrid populations derived from the crosses of C. I. 4219 with Ricardo and Kwan indicate two factor differences between the resistant varieties and C. I. 4219. The 13:3 ratio observed in the F_2 population of Kwan x C. I. 4219 is expected on the basis of the genotype assumed for Kwan, provided that the susceptibility of C. I. 4219 is conditioned by the prime member of the allelic series postulated at the minor locus. The absence of resistant segregates in the cross of C. I.

4219 x Montcalm further suggests that the locus involved in conditioning the susceptibility of C. I. 4219 is the prime member of the allelic series at the minor locus. In addition, C. I. 4219 appears to carry the recessive alleles of the major resistance factors of Kwan and Ricardo.

The results obtained in this investigation indicate the operation of a larger number of loci in conditioning reaction to leaf rust in barley, than had been previously reported. Some workers (31) have suggested the operation of single "major factors" for resistance. It is believed that the use in this study of parental material from such diverse sources was valuable in permitting a more complete analysis of the number of loci involved in conditioning reaction to leaf rust of barley.

SUMMARY AND CONCLUSIONS

1. The inheritance of reaction to race 4 of leaf rust of barley (<u>Puccinia hordei</u> Otth.) was studied in hybrid populations derived from crosses made in all combinations, between the varieties Montcalm, Ricardo, Kwan and C. I. 4219.

2. The use of race 4, the predominating race in this area, together with the high degree of correlation obtained on the reaction of seedling and adult plants in greenhouse tests, indicates that the seedling results offer a reasonable estimate of the field reaction of the populations studied.

3. Kwan and Ricardo were both highly resistant to race 4 of leaf rust. Montcalm was susceptible, but there were variations in the degree of susceptibility from plant to plant. C. I. 4219 exhibited a mesotheitc reaction to race 4.

4. The results obtained from the crosses studied, indicate that reaction to leaf rust is conditioned by factors located at four independent loci.

5. The resistance of each of Kwan and Ricardo is conditioned by two factors. The major resistance factors in each of these varieties are incompletely dominant and are independently inherited. The minor factor is

believed common to both.

6. The susceptibility of Montcalm is conditioned primarily by a dominant factor, hypostatic to the major resistance factors of Kwan and Ricardo, but epistatic to the minor factor. The presence of an allelic series at the minor locus is further suggested to account for the variations in susceptibility observed on different Montcalm plants.

7. Classification of the hybrid populations derived from C. I. 4219, was difficult because of the mesothetic reaction of this variety. Limited data indicated the operation of two factors in crosses of this variety with resistant types. No resistant types appeared in the cross between C. I. 4219 and Montcalm.

8. Reports of independence tests are not included in view of the large number of loci found to condition reaction to leaf rust in barley.

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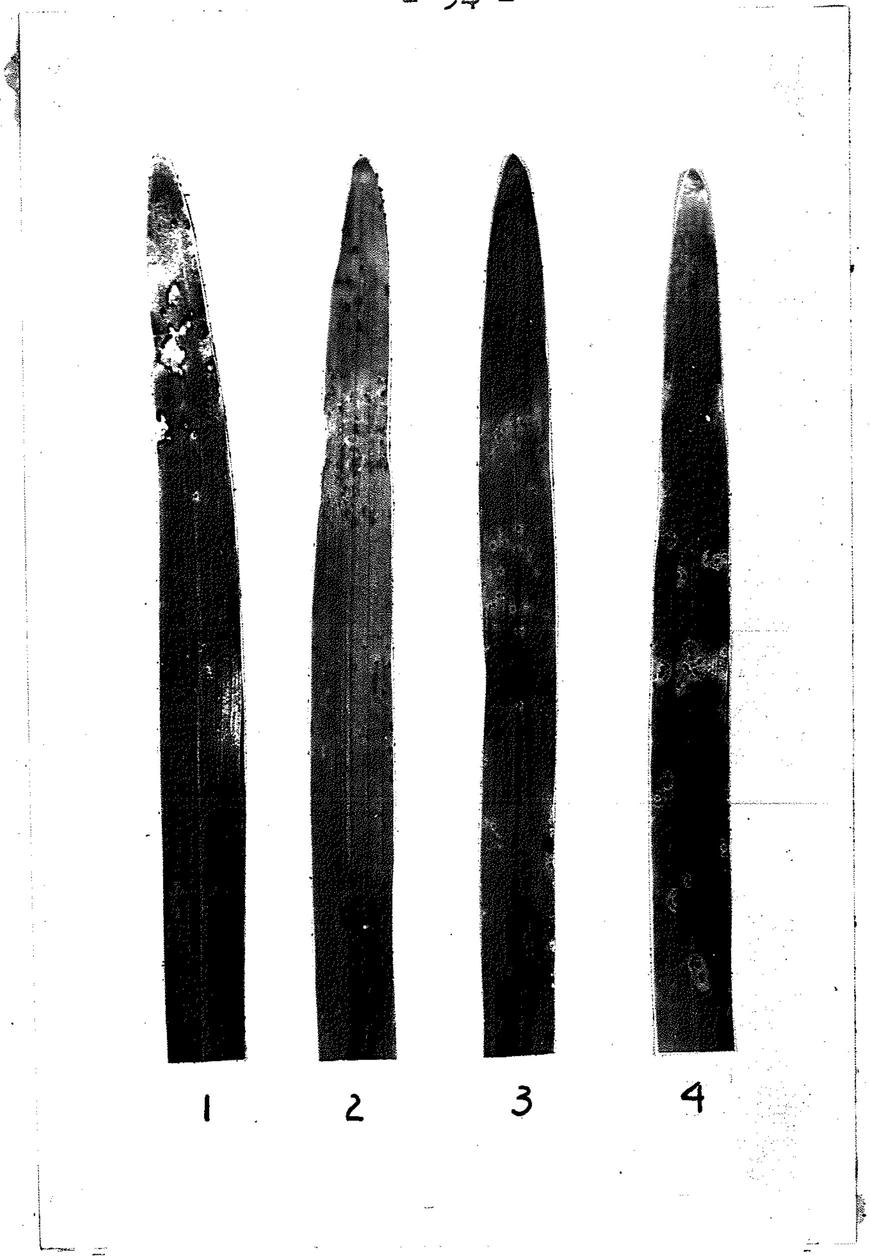
APPENDIX A

SEEDLING REACTIONS OF PARENTAL VARIETIES
AND
HYBRID POPULATIONS USED IN THIS STUDY

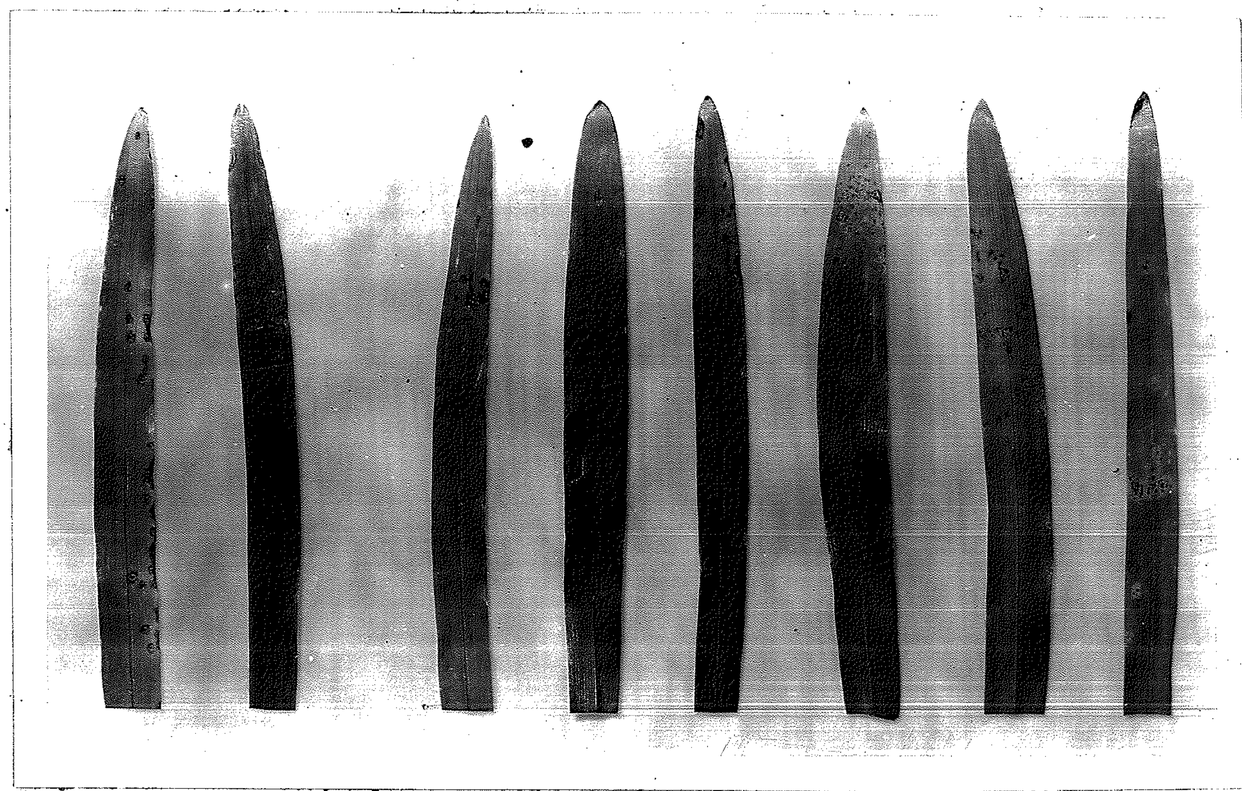


REACTION OF PARENTAL VARIETIES

TO RACE 4 OF PUCCINIA HORDEI

1) Kwan - 0;
2) Ricardo - 1+
3) C. I. 4219 - x
4) Montcalm - 3+

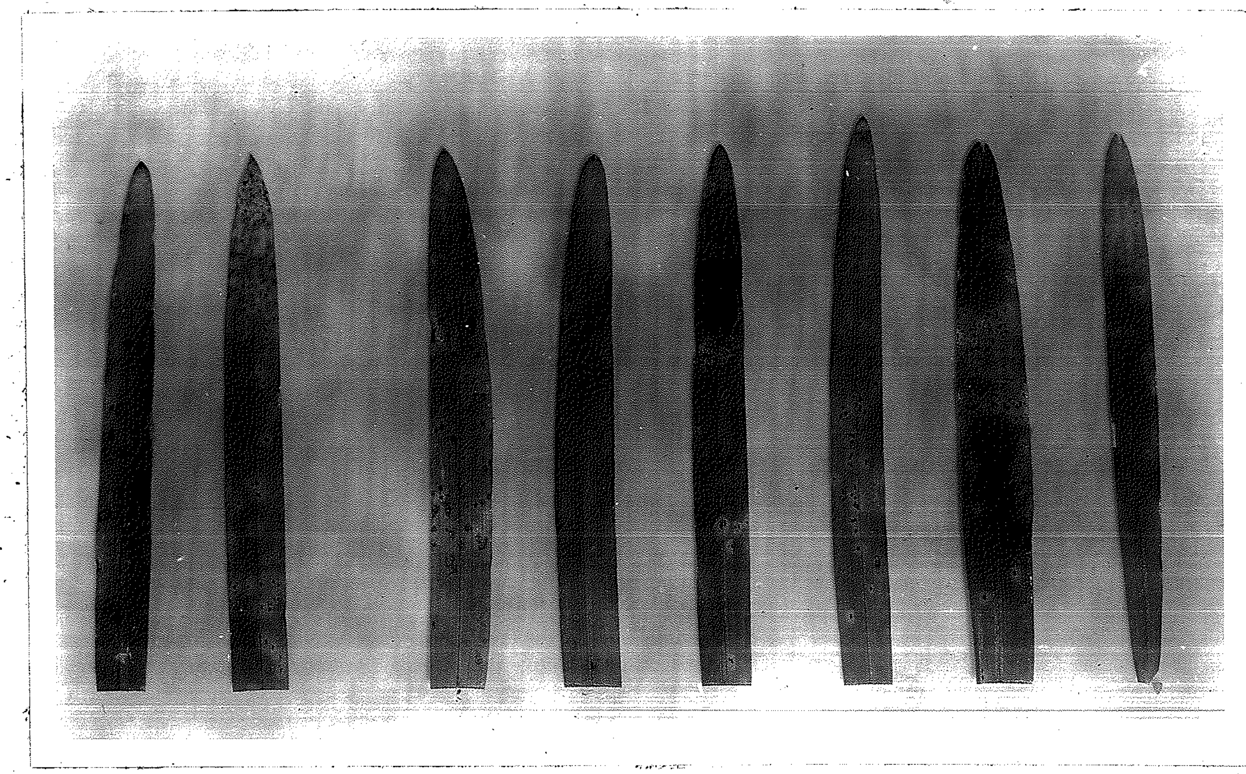
PLATE I



PUSTULE TYPES PRODUCED BY PARENTAL VARIETIES,
KWAN AND RICARDO, AND BY SEGREGATING HYBRID POPULATIONS,
TO RACE 4 OF PUCCINIA HORDEI

l-r: Kwan (R), Ricardo (R) and range in hybrid populations from resistant through to susceptible

PLATE II



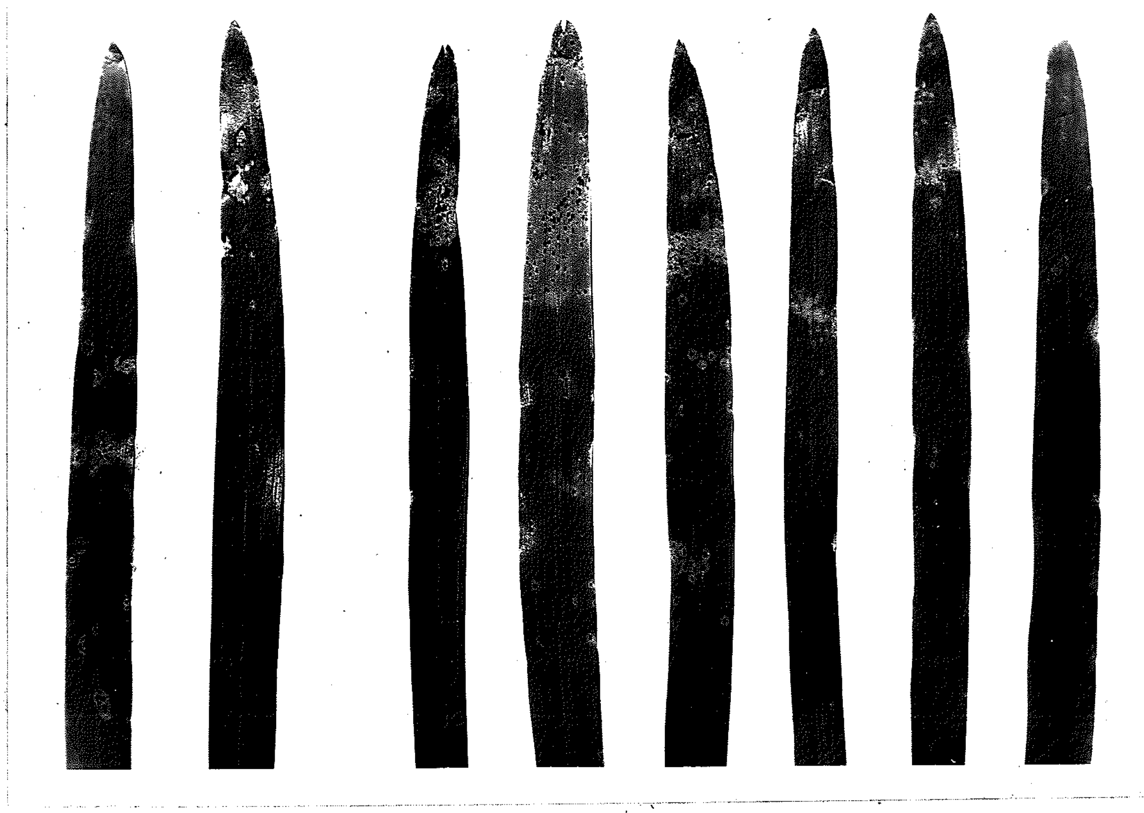
PUSTULE TYPES PRODUCED BY PARENTAL VARIETIES,

RICARDO AND MONTCALM,

AND BY SEGREGATING GENERATIONS

l-r: Ricardo (R), Montcalm (S) and range in hybrid populations from resistant through to susceptible

PLATE III



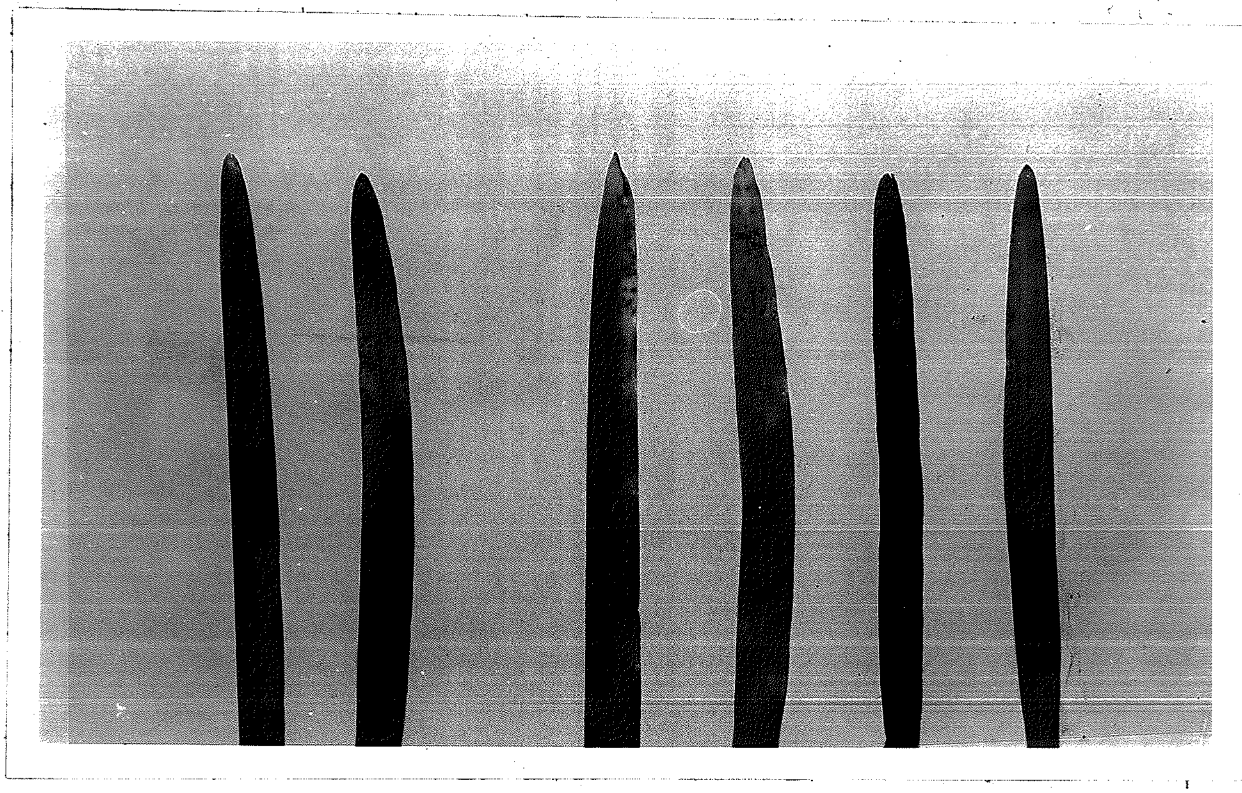
PUSTULE TYPES PRODUCED BY PARENTAL VARIETIES,

MONTCALM AND KWAN,

AND BY SEGREGATING GENERATIONS

l-r: Montcalm (S), Kwan (R) and range in hybrid populations from susceptible through to resistant

PLATE IV



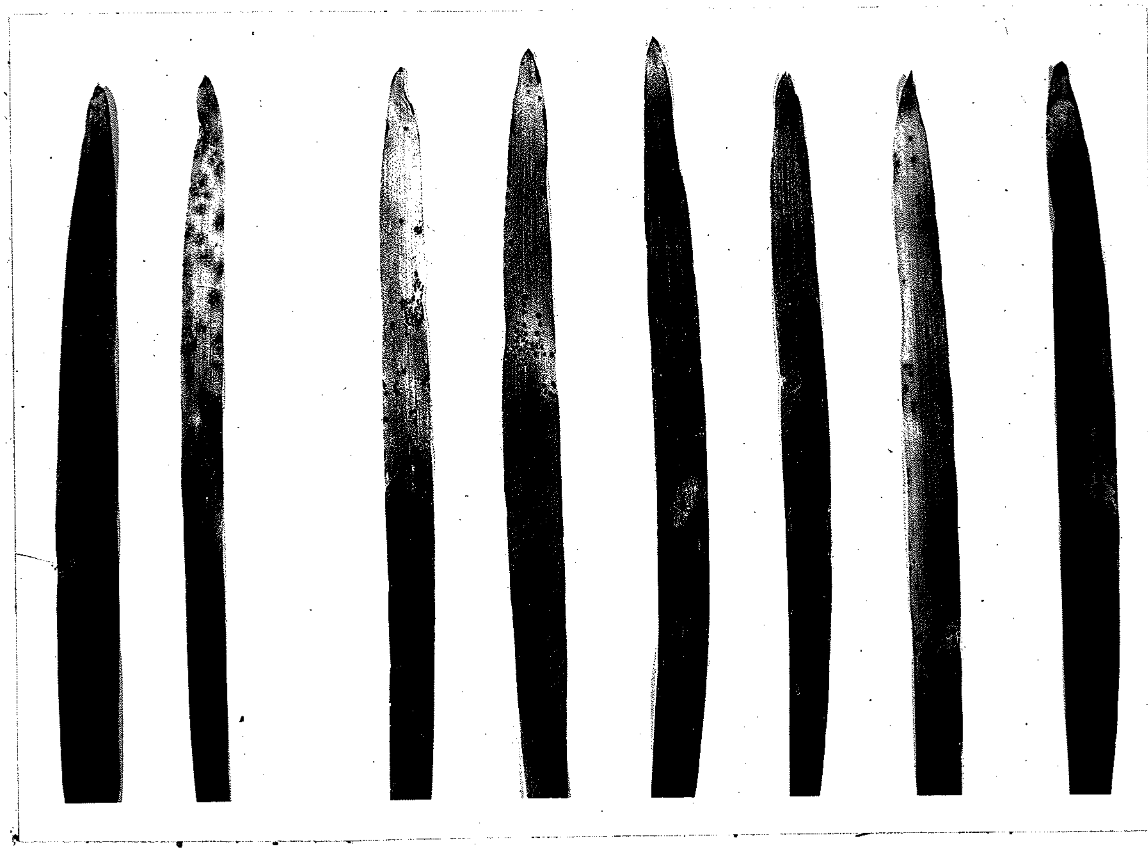
PUSTULES TYPES PRODUCED BY PARENTAL VARIETIES,

C. I. 4219 AND MONTCALM,

AND BY SEGREGATING GENERATIONS

l-r: C. I. 4219 (MS), Montcalm (S) and range in susceptible seedlings observed in segregating generations

PLATE V



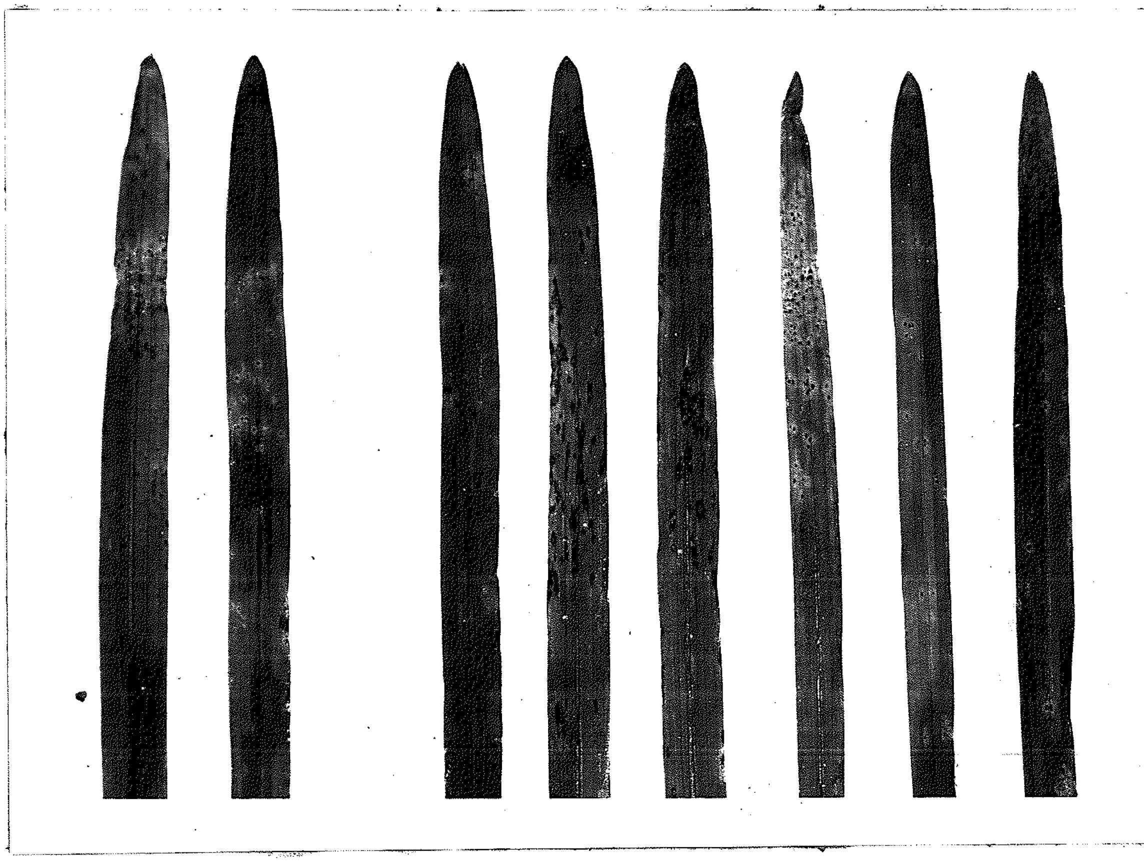
PUSTULE TYPES PRODUCED BY PARENTAL VARIETIES,

KWAN AND C. I. 4219,

AND BY SEGREGATING GENERATIONS

l-r: Kwan (R), C. I. 4219 (MS) and range in hybrid populations from resistant through to susceptible

PLATE VI



PUSTULE TYPES PRODUCED BY PARENTAL VARIETIES,

RICARDO AND C. I. 4219,

AND BY SEGREGATING GENERATIONS

l-r: Ricardo (R), C. I. 4219 (MS) and range in hybrid populations from resistant through to susceptible

PLATE VII

APPENDIX B

TABLE OF GENOTYPES FOR THREE SEGREGATING FACTOR PAIRS

<u>Hypothesis suggested to explain segregation in crosses involving Montcalm</u>

AA - major resistance factor of Kwan or Ricardo

BB - susceptibility factor of Montcalm

CC - minor locus (possessing allelic series)

C^1C^1 - prime member of series - conditioning susceptibility (present in Montcalm plants Type 3).

CC - second member of series - conditioning resistance (present in resistant parents and in Montcalm plants Type 2).

cc - lowest member of series - conditioning susceptibility (present in Montcalm plants Type 1).

AA epistatic to BB epistatic to CC

I Resistant Parent x Montcalm Type 1

Frequency	Genotype	Phenotypic Ratio F_2	Phenotypic Ratio F_3
1	AA BB CC		
2	AA BB Cc		
1	AA BB cc		
2	AA Bb CC		
4	AA Bb Cc	16R	16R
2	AA Bb cc		
1	AA bb CC		
2	AA bb Cc		
1	AA bb cc		
2	Aa BB CC		
4	Aa BB Cc		
2	Aa BB cc		
4	Aa Bb CC		
8	Aa Bb Cc	32R	32 Seg.
4	Aa Bb cc		
2	Aa bb CC		
4	Aa bb Cc		
2	Aa bb cc		
1	aa BB CC		
2	aa BB Cc		4S
1	aa BB cc	12S	
2	aa Bb CC		2R
4	aa Bb Cc		4 Seg.
2	aa Bb cc		2S
1	aa bb CC		1R
2	aa bb Cc	3R	2 Seg.
1	aa bb cc	1S	1S
64		51R:13S	19R:38 Seg:7S

II Resistant Parent x Montcalm Type 2

CC common to both parents

Frequency	Genotype	Phenotypic Ratio F_2	F_3
1	AA BB CC		
2	AA Bb CC		4R
1	AA bb CC		
2	Aa BB CC	12R	
4	Aa Bb CC		6 Seg.
2	Aa bb CC		2R
1	aa BB CC	1S	1S
2	aa Bb CC	3R	2 Seg.
1	aa bb CC		1R
16		15R:1S	7R:8 Seg:1S

III Resistant Parent x Montcalm Type 3

Frequency	Genotype	Phenotypic Ratio F_2	Phenotypic Ratio F_3
1	AA BB C^1C^1		
2	AA BB C^1C		
1	AA BB CC		
2	AA Bb C^1C^1		
4	AA Bb C^1C	16R	16R
2	AA Bb CC		
1	AA bb C^1C^1		
2	AA bb C^1C		
1	AA bb CC		
2	Aa BB C^1C^1		
4	Aa BB C^1C	6S	6S
2	Aa BB CC		
4	Aa Bb C^1C^1		
8	Aa Bb C^1C		
4	Aa Bb CC		
2	Aa bb C^1C^1	26R	24 Seg.
4	Aa bb C^1C		
2	Aa bb CC		2R
1	aa BB C^1C^1		
2	aa BB C^1C		4S
1	aa BB CC		
2	aa Bb C^1C^1		2S
4	aa Bb C^1C	15S	
2	aa Bb CC		6 Seg.
1	aa bb C^1C^1		1S
2	aa bb C^1C		2 Seg.
1	aa bb CC	1R	1R
		41R:23S	19R:30Seg:15S