THE INHERITANCE OF RESISTANCE TO RACE 15B OF STEM RUST OF NINE DURUM VARIETIES

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INTRODUCTION

Stem rust of wheat, Puccinia graminis tritici Eriks. and Henn., has always been a limiting factor in the production of wheat in Western Canada. According to Hanna (12), rust damage was first reported in 1891 and the first attack of epidemic intensity accurred in 1904. Other severe epidemics of stem rust accurred in 1916, 1923, 1927, 1935, 1938 and 1953. Attacks little short of epidemic intensity accured in 1919, 1921, 1925, 1930 and 1954. Greaney (11), estimated that during the 11 year period of 1925-1935, the average annual loss due to reduction in yield was approximately $30,000,000. In addition $2,000,000 was lost annually due to lowering of grade of the wheat.

After 1939, resistant varieties were widely grown in Western Canada. Craigie (8) estimated that in the 5 year period of 1939-1943, the average annual increase in farm income resulting from the growing of rust resistant varieties in Manitoba and Eastern Saskatchewan was approximately $27,000,000.

Unfortunately, the varieties grown in Western Canada after 1939, were not resistant to all races of stem rust. Races which were considered unimportant, but could attack the common varieties, were relieved of competition with the prevalent races and when environmental conditions were favorable, reached epidemic proportions. In addition, new, virulent races, hybridized on the common barberry, also had an opportunity to develop on the new varieties and become prevalent. Race 15B is a striking example of such a change.

According to Stakman (30), race 15B has been known to exist on the barberry since 1939, but was never abundant until 1950 when it

became prevalent on previously resistant varieties of bread wheat and durum. Durums, in particular, have been severely rusted. Rodenhiser and Moore (28) mention that 10,000,000 bushels of durum wheat, which was about one-fifth of the crop, was lost in the United States in 1951. In Western Canada, race 15B was first reported in 1946 and became widely distributed by 1950. Hanna (12), reported that three distinct strains of race 15B have been differentiated - 15B-1, 15B-2 and 15B-3. Strain 15B-2 which has recently been renamed 15B-4, is a specially virulent strain in durums and is rapidly increasing in prevalence.

The wheat stem rust situation in Western Canada was relatively stable from 1938 to 1949. During this time the durum varieties commercially grown were resistant to the prevalent races of stem rust. The varieties, Carleton and Stewart, which derived their resistance from Vernal emmer, were extensively grown.

After 1950 and the increase of race 15B, all commercially grown durum varieties were severely attacked. The epidemics of 1953 and 1954 almost completely destroyed the durum crops grown in Western Canada. As a result, the acreage of durum production was greatly reduced in following years and the area of production shifted westward, out of the main rust area of Manitoba and Eastern Saskatchewan.

The need for durum varieties resistant to race 15B is apparent. In order to develop these varieties, sources of resistance to this race must be available. One way of obtaining these sources is to make a collection of local and foreign varieties and to test their reaction under epidemic conditions of race 15B. Valuable work in testing of varieties for reaction to stem rust is done in the International Rust Nursery. Varieties from all parts of the world are introduced and tested in the nursery for their mature plant resistance to many races of stem rust.

A report is issued every year describing the performances of the durum introductions in the nursery. Many of the varieties have been found to be almost immune to race 15B, but usually possess many undesirable agronomic characteristics.

The purpose of this study was to determine the inheritance of resistance to race 15B of a number of durum varieties obtained from the International Rust Nursery.

REVIEW OF LITERATURE

The earliest report of hybridization work involving rust resistance was by Biffen (4), in 1905. He mentions that Thomas Knight, in 1815, appeared to be the first to realize the necessity of selection of resistant varieties. In the same paper, Biffen reports that Farrer, in 1899, working with a number of varieties showed that susceptibility to rust is hereditary in wheat. In 1907, Biffen (5), working with varieties susceptible and immune to yellow rust (Puccinia glumarum), found that susceptibility is dominant over immunity. He demonstrated that resistance is independent of any morphological character and therefore, it was possible to combine rust resistance and other desirable characters in a variety.

This early work served to convince the plant breeder of the value of hybridization and selection. Some of the work that followed was concerned with the determination of the nature of resistance of certain wheat varieties.

Stakman (29), 1915, showed that resistance in the seedling stage to physiologic forms of stem rust is due to a physiologic incompatibility between the resistant plant and the invading fungus. This is known as "protoplasmic" or "physiologic" resistance and functions throughout the life of the plant. The nature of the incompatibility or antagonism between the cereal host and the fungus is not known.

Hursch (20), 1924, suggested that in addition to the fundamental protoplasmic resistance, wheat varieties may possess morphological means of resistance against Puccinia graminis. The germ tubes of stem rust spores are able to enter the plant, but once inside, certain morphological characters may limit the extent of activity of the mycelium. According

to Hursch, the mycelium of stem rust within the host is limited entirely to chlorenchymatous collenchyma tissue of wheat. In morphologically resistant varieties of wheat, the collenchyma bundles are small isolated strands, separated by broad bands of schlerenchyma fibers. This forms a mechanical limitation to the spread of the mycelium. Morphological resistant varieties, therefore, have a large amount of schlerenchyma and a small amount of collenchyma. The relative amount of schlerenchyma increases as the plant grows older.

In 1930, Hart (15), agreed with Hursh's conclusions and added that in addition to the two types of resistance to stem rust, physiologic and morphological, there is a third type termed "functional resistance". She suggested that stomatal behavior of wheat varieties during the early morning hours might be related to stem rust resistance. There was a correlation between stomatal behavior and resistances of certain varieties of wheat to stem rust in the field. She found that in resistant varieties such as Hope, Webster and Acme, the stomata remained closed in the morning later than those of susceptible varieties such as Marquis and Mindum. Varieties which are moderately resistant in the field, for example Kota and Kubanka, have an intermediate type of stomatal behavior. Stomata of younger and more succulent plants parts open sooner and remain open longer than stomata in older or less succulent parts. This may explain the increase of resistance of plants in the mature stage over the seedling stage.

Peterson (24), 1931, made similar studies on a number of standard varieties and of hybrids from crosses between common wheat varieties. His results did not verify Hart's observations regarding the correlation between stomatal behavior and resistance to stem rust. Similar conclusions were reached by Ausemus (2), when he studied the

relationship between stomatal behavior and reaction to stem rust in the hybrids of crosses involving the three varieties, Marquillo, Supreme and Hope.

According to Ausemus (3), Eriksson first proved that there was several distinct varieties of rust, as differentiated by the hosts they attack. Stakman and Piemiesel (31), 1917, reported the existence of physiologic specialization within the rust fungus. It has been shown that new races originate by hybridization and mutation. Stakman et al. (32), suggested the possibility of stem rust races hybridizing on barberry and Craigie (7) demonstrated the function of pycnia and aecia in the hybridization of the fungi. Johnson (21) and others have studied a number of crosses and proved that new races of Puccinia graminis originated by crossing not only between races, but also between varieties. These discoveries complicated the breeding of varieties resistant to stem rust. The plant breeder could no longer consider stem rust as a single organism, but as a number of morphologically similar organisms, or races, fundamentally different in pathogenic capabilities. This made it necessary for the plant breeder to determine the inheritance of the reaction to individual races.

Early plant breeders recognized that some of the durum varieties carried considerable resistance to stem rust. Much of the work involved attempts to transfer the durum resistance to common wheat. Ausemus (3) made an extensive review of the studies with the durum sources of resistance to stem rust.

Puttick (27), 1921, studied the reaction of the F_2 generation of a cross between Mindum and Marquis to two physiologic forms of stem rust to which the parents reacted reciprocally. The F_2 progeny segregated to give all gradations between immunity and complete susceptibility.

Hayes et al.(16), 1920, crossed a number of susceptible vulgare varieties with resistant durum varieties including Iumillo. They found that in the crosses attempted, susceptibility was dominant and a strong linkage was present between rust resistance and durum characters. A few plants were selected in the F_3, which showed resistance comparable to that of the parent Iumillo and were vulgare type. These results indicated that it was not impossible to obtain plants with vulgare characteristics possessing the resistance of the durum parent.

In 1940, Peterson and Love (25), also studied crosses between Iumillo and susceptible common varieties. The study revealed that it was difficult to eliminate all durum morphological characters from 42 chromosome plants while retaining a high degree of the durum resistance to stem rust. However, a number of lines were obtained which were immune, or near immune in the mature plant stage to many physiological races in spite of the fact that most lines contained plants with abnormal chromosome numbers and behavior. Chromosome numbers found in the plants of these lines ranged from 38-43.

Hayes et al.(17), 1925, selected from a cross of Marquis x Iumillo a variety called Marquillo which was resistant to a collection of races in the field. Another selection, a sister of Marquillo, was also found to be resistant to many physiologic forms of stem rust under field conditions, but it is susceptible in the seedling stage in the greenhouse. This selection was used in a Double Cross (Marquis-Iumillo x Marquis-Kanred), to produce Thatcher, a variety possessing considerable resistance to stem rust along with high quality. At least two factors were found to control the resistance of Thatcher. The resistance in the field was inherited independently of the factor for immunity to certain races in the seedling stage. The field reaction was controlled by two main factors with

possible modifiers.

Neatby and Goulden (23) studied the inheritance of resistance of Marquillo to stem rust in a number of crosses. In the cross, Marquillo x H-44-24, they concluded that two or more factors for resistance were contributed by Marquillo. In crosses between Marquillo and susceptible varieties, only a small number of resistant plants were obtained in the F_2 generation indicating that Marquillo carries many factors for resistance to stem rust. In the three-way cross, Marquillo x (Marquis x Kanred), the presence of three or more factors was indicated.

In 1934, Ausemus (2) reported results from crosses, Hope x Marquillo, and Marquillo x Supreme. The Hope x Marquillo cross showed that inheritance of the seedling reaction to stem rust appeared to depend on three or more factors. Inheritance of the mature plant resistance of Marquillo appeared to depend on factors that were not allelomorphic to those controlling the inheritance of the mature plant resistance of Hope. In the cross, Marquillo x Supreme, at least three genetic factors controlled the inheritance of adult resistance to stem rust.

Waddell (34), in the cross, Iumillo x Mindum, found that Iumillo possessed a factor or factors for mature plant resistance as well as a factor, or factors for resistance at both stages of maturity. In the Pentad x Iumillo cross, the inheritance was complicated by the additional factors for resistance in the Pentad parent.

In 1929, Goulden (9) reported the transfer of the resistance of the durum, Pentad, to selections with common wheat characteristics. The cross used was Pentad x Marquis. Several F_3 lines were obtained which were homozygous and had high resistance to stem rust.

Harrington (13), 1925, tested a cross of Mindum x Pentad with race 1. The results obtained indicated the presence of two factors. A

Mindum factor was dominant for immunity and a Pentad factor was dominant for slight resistance. With race 34, to which Pentad is resistant and Mindum is susceptible, more than one factor for resistance was indicated. Reaction to race 21 was similar to the reaction to race 34 and was believed to be controlled by the same factor.

Correlative studies have been made between seedling reaction in the greenhouse and mature plant reactions in the field of a number of varieties to stem rust.

Hursch (20), 1924, called attention to the differences between the rust reaction of Acme seedlings and the mature plant reaction of the variety in the field. Aamodt (1) found that seedling reaction to particular rust forms in the greenhouse may not necessarily be an indication of the reaction of maturing plants in the field. His studies showed that high resistance in the seedling stage in the greenhouse usually indicated resistance in the field, but moderate resistance in the greenhouse does not always mean field resistance.

Harrington and Smith (14) studied the seedling and mature plant reaction of each of four varieties, Marquis, Marquillo, Iumillo and Vernal to three physiologic forms, 17, 21 and 26. In addition, they used a susceptible strain of Marquillo and a susceptible strain of Iumillo. Good agreement was obtained between the reactions in both stages with the exception that the susceptible strain of Iumillo seemed to be more resistant in the after heading stage. They concluded that the feasibility of using seedling tests to predict reaction in the mature plant stage depended on the variety under study.

Harrington (13), 1925, studied the realation between seedling and mature plant reaction in crosses between durum varieties. The two

crosses studied were Mindum x Pentad and Kubanka No.8 x Pentad. The physiologic races, 1, 21 and 34 were used in the seedling tests. In the Mindum x Pentad cross, Harrington reports a negative correlation between the seedling reaction to race 1 and the mature plant reaction to several races in the field. No correlation was found between reaction to rust under nursery conditions and reaction to races 21 and 34 in the greenhouse in the same cross. In the Kubanka No.8 x Pentad cross, there was no correlation between the mature plant reaction in the field and seedling reaction to race 34.

Goulden et al.(10), 1930, tested a number of varieties including Iumillo, Pentad, Acme and Marquillo to 16 physiologic races in the seedling and adult stage. They found that the resistance of Pentad was mainly controlled by genetic factors independent of those concerned in the reaction of seedlings in the greenhouse. Acme showed very little seedling resistance to any of the forms, but was resistant in the mature plant stage to all of them. In regard to Iumillo, there was almost perfect agreement between the seedling and the mature plant reactions and no additive resistance was obtained in the adult stage.

Neatby (22) made a comparable study of greenhouse reactions and field reactions in the crosses, Marquillo x Reward, Garnet x Marquillo and Garnet x Double Cross (Marquis- Iumillo x Marquis -Kanred). The results obtained in the crosses indicated that the inheritance of the field reaction of Marquillo and Double Cross to stem rust is mainly, if not entirely, controlled by the factors which govern the inheritance of the seedling reaction to form 21 of stem rust in the greenhouse.

Waddell (34) suggested that simple inexpensive greenhouse tests, using one physiologic race of stem rust, may be employed to eliminate lines that will be susceptible in the field in the durum crosses involving Iumillo.

With the appearance and increase of Race 15B in 1950, the need for new durum varieties resistant to this race became urgent. Extensive work along this line has been done at the North Dakota Agricultural Experimental Station by Heermann and his associates. In 1956, Heermann et al. (19) reported inheritance studies of resistance to race 15B of a number of durum varieties. Three of these varieties, St.464, P.I.192179, and C.I.7805 were also studied in the present project. Results obtained by Heermann et al. from seedling tests indicated that P.I.192179 and St. 464 have two factors for resistance in common. One factor produces a type 1. reaction and the other an X reaction. The combination of the two factors gives a 0; type reaction. There was evidence for the presence of additional factors which modify the reaction in the adult stage. On the basis of mature plant reaction they concluded that C.I.7805 has one or two factors in common with St.464.

The results of studies with a number of other durum varieties were also reported in the same paper. The varieties, C.I.3255, P.I.94701, R.L.1714 (Golden Ball x Iumillo - Mindum) and P.I.168906 all produced a type 3⁻ reaction in seedling tests with race 15B. In crosses with Stewart, evidence was obtained to show that C.I.3255, P.I.94701 and R.L.1714 had one factor for resistance in the seedling stage. From seedling and mature plant tests, it appeared that these varieties, including P.I.168906, possessed factors for resistance that were allelic. All four varieties possess the resistance of Golden Ball to race 15B and are susceptible to strain 15B-4 which is rapidly increasing in prevalence.

In addition, evidence from tests using race 15B in the adult stage showed that C.I.7780 and C.I.8155 had either one or two factors in common with St.464. These three varieties and C.I.7805 all originated in Ethiopia.

In the same year Heermann and Stoa (18) reported the development of four durum varieties which possessed good resistance to race 15B. These varieties, Langdon, Yuma, Towner and Ramsey, were the result of crosses involving rust resistant durum introductions and durum varieties which derived their resistance from Triticum dicoccum.

Langdon was developed from the following crosses; an F_3 selection of [LD.194 (Mindum x Carleton)] x Khapli (Triticum dicoccum) was crossed with LD.308. [(Heiti x Stewart) x (Mindum x Carleton)]; an F_2 derivative of this combination was crossed with Stewart; finally an F_1 plant from this third cross was crossed with Carleton. Langdon is only moderately resistant to race 15B, but has a high degree of resistance to other races.

Yuma is a selection from the second cross made in the development of the variety Langdon. This cross involved an F_3 selection of LD.194 x Khapli which was crossed with LD.308. The variety is nearly as resistant to race 15B as its Khapli emmer parent.

Ramsey and Towner were derived from a cross of Carleton x P.I. 94701, the latter being an introduction from Palestine. Both varieties are characterized by the production of small size pustules, but the resistance decreases at high temperatures. In addition, the varieties are susceptible to 15B-4, a virulent strain of race 15B.

MATERIAL AND METHODS

Parent Varieties.

Initially, three varieties of durum wheat, Arabian, Camadi and St.464, were selected for this study. These varieties, reported to be resistant to stem rust in the 1953 report of the International Rust Nursery, were introduced by the Field Husbandry Department, at Saskatoon. Field tests, using race 15B, showed that Camadi and St.464 were almost immune, while Arabian carried a considerable number of moderately resistant pustules. Nugget and Stewart, both of which are severely attacked by race 15B, were also included in the study.

In the summer of 1955, a number of other durum varieties, selected on the basis of their performances in the International Rust Nursery, were tested for mature plant resistance to race 15B. Six of these introductions, C.I.8133, C.I.7875, C.I.7870, C.I.7805, P.I.192179 and P.I. 191194, were added to the three original varieties. All six varieties showed good resistance to race 15B in the field.

All nine varieties which are resistant are introductions from foreign countries (table 1). Five of the varieties St.464, C.I.8133, C.I. 7870, C.I.7875 and C.I.7805, originated in Ethiopia. Camadi and P.I.192179 are Portugese varieties. Arabian was obtained from Arabia, while P.I.191194 originated in Spain.

With respect to agronomic characteristics, Camadi, C.I.8133, C.I.7870, C.I.7875 and C.I.7805, are similar. All five varieties have short, weak straw and are poor yielders. A desirable agronomic characteristic of these varieties is their early maturity. In addition, all the varieties, except C.I.7875, have deep purple seeds.

Table 1. Varieties Used in this Study and their Origin.

Name	Designation	Country of origin
St.464	P.I.191365	Ethiopia
Arabian	P.I.145720	Arabia
Camadi Abdu tipo 103	P.I.192168	Portugal
Amerai bianco tipo 142	P.I.192179	Portugal
Rojal de Almerai	P.I.191194	Spain
-	C.I.8133	Ethiopia
-	C.I.7875	Ethiopia
-	C.I.7870	Ethiopia
-	C.I.7805	Ethiopia
Nugget	CAN.3872	North Dakota
Stewart	CAN.3599	North Dakota

The varieties, St.464 and P.I.192179, are also early maturing and have weak stems. P.I.192179 is characterized by pubescent glumes, while St.464 has black awns and glumes.

Arabian, a red seeded durum,and P.I.191194 are good yielding varieties, but are late in maturity, especially P.I.191194.

Nugget and Stewart were both developed by the North Dakota Agriculture Experimental Station in cooperation with the United States Department of Agriculture. Nugget was obtained from a cross (Mindum x Carleton) x (Heiti x Stewart). This amber seeded variety has short, weak straw and is early maturing. The macaroni quality of Nugget is considered excellent. The variety.Stewart, was produced by crossing Mindum with

Vernel emmer, and backcrossing twice to Mindum. Stewart is late maturing and has long, medium straw strength. Since its release in 1946, Stewart has been extensively grown in Southern Manitoba and Eastern Saskatchewan.

Crosses

In the spring of 1955, diallel crosses involving St.464, Arabian and Camadi were made in the greenhouse. In addition the three varieties were crossed with Stewart and Nugget. The F_1 of these crosses were grown in the field the following summer. A large number of the F_1 plants were backcrossed to Stewart or Nugget. Furthermore, the six introductions, C.I.8133, C.I.7875, C.I.7870, C.I.7805, P.I.192179 and P.I.191194, were crossed initially with Stewart and Nugget.

The F_1 generation of the initial crosses and backcrosses were grown in the greenhouse the following winter. Many of the F_1 plants of crosses involving the six introductions, were backcrossed to Stewart or Nugget. In addition, diallel crosses were made between the nine resistant varieties, giving a total of 36 crosses.

During the summer of 1956, the F_1 of diallel crosses and backcrosses were grown in the field. At this time, backcrosses from which poor seed set was obtained were repeated. The F_1 of these backcrosses were later grown in the greenhouse.

Rust Study

In the summer of 1955 and 1956, F_1 plants of diallel crosses and the F_2 plants of all available diallel crosses and backcrosses were tested for mature plant reaction in the field. Plants were space seeded in continuous rows in the rust nursery. At maturity, the plants were pulled, the families kept separate and later classified for percentage stem rust infection.

In addition, seedling tests, to determine the reaction to race 15B of F_2 generation of the diallel crosses and backcrosses, were made in the greenhouse.

Method of Inoculation

In field tests, spreader rows composed of very susceptible varieties such as, Marquis, Garnet and Lemhi, were seeded at intervals in the rust nursery. When the plants in the spreader rows were 6-8 inches high, they were inoculated with a suspension of race 15B spores in water by means of a hypodermic needle. A detergent,"Tween 80", was used to insure suspension of the spores in water. Inoculation was carried out at one foot intervals in the spreader rows. Irrigation, by means of an overhead sprinkler system, was used to maintain an optimum moisture condition in the rust nursery.

Inoculation in the greenhouse was performed by dusting with a mixture of talc and dry spores of race 15B, when the seedlings were in the 2-3 leaf stage. The waxy bloom was first removed by rubbing the leaves. A film of water was then formed on the leaves by spraying with a weed spray nozzle attached directly to a water line. After the seedlings were dusted with the talc-rust spore mixture, a canvas hood was put over the inoculation bed. This canvas and the seedlings were kept moist for 24 hours to insure uniform infection.

Classification of Rust Reaction

An arbitrary scale, from 0-70, was used for classifying the plants for mature plant reaction to race 15B. A system of classifying described by Peterson et al.(26), was followed closely. An attempt was made to place in the 50-70% classes only those plants which were as susceptible as the parents, Nugget and Stewart.

In seedling tests, symbols described by Stakman et al.(33), were used to indicate the type of infection produced by race 15B.

RESULTS

Reaction of Parent Varieties.

The reactions of eleven durum varieties to race 15B, obtained from seedling and field tests, are given in tables 2 and 3, respectively. A close agreement was found between the reaction of the parent varieties to race 15B at the two stages of growth. Varieties which showed resistance in the seedling stage, also possessed mature plant resistance.

The varieties, St.464, C.I.8133, C.I.7870, C.I.7875 and C.I.7805 are highly resistant to race 15B. The resistance of St.464 and C.I.7805 is characterized by hypersensitive flecking at both stages of growth. The other three varieties gave a type 1^- reaction in the seedling tests, while in the field tests from 0-1% stem rust infection was typical.

P.I.192179 is very similar to St.464 and C.I.7805 in reaction to race 15B at both stages of growth.

In seedling tests, the resistance of Camadi is characterized by a 1^-- 1 reaction, while in field tests, from 0-1% stem rust infection is typical of the variety.

Arabian and P.I.191194 are moderately resistant to race 15B. In the mature plant stage, the varieties gave up to 10% infection, while in the seedling stage Arabian gave a 2^- reaction, and P.I.191194 a 2^+ reaction.

Stewart and Nugget are both very susceptible to race 15B. In seedling tests, the varieties gave a type 4 reaction and in field tests from 50-70% infection was common.

Greenhouse and Field Studies.

The seedling and mature plant reaction obtained when the F_1

Table 2. Reaction of Parent Varieties to Race 15B in the Field.

Variety	Stem rust infection in per cent.										Total
	0;	1	5	10	20	30	40	50	60	70	
St.464	32	18	1								51
Arabian		23	8	3							34
Camadi	40	13	2								55
C.I.8133	25	5									30
C.I.7870	17	4									21
C.I.7875	11	4	1								16
C.I.7805	26	10	1								37
P.I.192179	18	11	2								31
P.I.191194		12	6	4							22
Nugget								3	23	10	36
Stewart								5	20	15	40

Table 3. Seedling Reaction of Parent Varieties to Race 15B in the Greenhouse.

Variety	Type of reaction.															Total
	;	$1^{=}$	1^{-}	1	1^{+}	x^{-}	2^{-}	2	2^{+}	x	3^{-}	3	x^{+}	3^{+}	4	
St.464	105	34														139
Arabian					2		133									135
Camadi	6	81	39	13	5											144
C.I.8133	1	16	25	11												53
C.I.7875		19	21	2												42
C.I.7870	2	24	14	24												64
C.I.7805	33	16	4													53
P.I.192179	28	22	3													53
P.I.191194							5	36	21							62
Nugget															157	157
Stewart														2	133	135

generation of crosses with Stewart and Nugget were tested to race 15B, are shown in tables 4 and 5, respectively. The reaction of the F_2 generation of a number of crosses to race 15B, in the seedling and mature plant stages of growth, is given in tables 6 and 7, respectively. The seedling reaction of the F_2 generation of diallel crosses to race 15B is given in table 8.

The F_1 results serve only to indicate the over-all dominance of factors entering into the genotype of the F_1 plants. The F_2 results are used primarily to establish the presence or absence of common factors in the parents of a particular cross. It was difficult in most of the crosses to separate the F_2 populations into definite reaction classes. It was possible, however, to distinguish the fully susceptible plants in the F_2 segregation. The plants which gave a 4 reaction in the seedling tests and from 50-70% stem rust infection in the field tests were classified as susceptible as Nugget and Stewart. In this way a ratio of resistant to susceptible F_2 plants was obtained which was used to estimate the number of factors for resistant carried by the parent varieties.

The genetic analysis of a variety was mainly based on backcross data obtained from seedling tests. In the backcross, Arabian x Nugget^2, results were obtained from field tests as well as seedling tests.

A system of nomenclature was used to obtain more clarity in describing and distinguishing the resistant factors present in the nine varieties. Each factor for resistance was given the symbol "Sr", followed by a subscript which was a letter of the alphabet. The author wishes to stress that the nomenclature of the rust resistance factors in this study is not permanent, but was used for sake of convenience.

Table 4. Reaction of F_1 Plants to Race 15B in the Field.

Cross	Stem rust reaction in per cent.										Total
	0;	1	5	10	20	30	40	50	60	70	
St.464 x Stew.	2	7	32	5							46
St.464 x Nug.	1	5	20	8	1						35
Arab. x Stew.		1	14	11	1						27
Arab. x Nug.		4	17	16							37
Cam. x Stew.						22	19	11	1		53
Cam. x Nug.						5	10	1			16
C.I.7805 x Stew.	2	15	3								20
C.I.7870 x Stew.		3	12								15
C.I.7875 x Stew.		2	15	1							18
C.I.8133 x Stew.		5	20								25
P.I.192179 x Stew.		5	10	1							16
P.I.191194 x Stew.		10	5	5							20

Table 5. Seedling Reaction of F_1 Plants to Race 15B in the Greenhouse.

Cross	Type of reaction.														Total
	;	$1^=$	1^-	1	1^+	X^-	2^-	2	2^+	X	3^-	3	X^+	3^+	4	
St.464 x Stew.				3		7										10
Arab. x Stew.							1	10	2							13
Cam. x Stew.												2	5	4	1	12
C.I.7805 x Stew.				7		10										17
C.I.7870 x Stew.					3	9				8						20
C.I.7870 x Nug.						2				17						19
C.I.7875 x Stew.							1	5		10						16
C.I.8133 x Stew.										21						21
P.I.192179 x Stew.				1		2				1						4
P.I.192179 x Nug.				7		15										22
P.I.191194 x Stew.							2	12								14

Table 6. Reaction of F_2 Plants to Race 15B in the Field.

Cross	Stem rust reaction in per cent.										Total
	0;	1	5	10	20	30	40	50	60	70	
St.464 x Stewart	36	58	66	32	32	32	24	10	4		299
St.464 x Nugget	42	50	64	49	40	14	23	8	6		296
Arabian x Stewart	1	6	53	61	24	43	54	20	4		269
Arabian x Nugget	2	39	110	56	27	32	31	19	4		359
Camadi x Stewart		5	13	10	29	68	75	43	28	5	276
Camadi x Nugget		10	53	37	54	145	168	182	98	44	791
St.464 x Arabian	118	42	111	38	16	12	12	1			349
Camadi x Arabian	68	102	57	9	11	6	1				255
St.464 x Camadi	89	28	14	5	6		6	2			152

Table 7. Reaction of F_2 Seedlings to Race 15 in the Greenhouse.

Cross	Type of reaction.															Total
	;	$1^=$	1^-	1	1^+	x^-	2^-	2	2^+	x	3^-	3	x^+	3^+	4	
St.464 x Stewart	129	208	50	11	19	56	52	2	7	5	11	5	40	-	50	665
St.464 x Nugget	111	61	29	8	10	1	59	3	7	2	23	3	2	1	21	340
Arabian x Stewart							234	-	33	-	5	9	-	1	21	310
Arabian x Nugget							214	2	50	-	10	5	-	1	19	306

Table 8. The Range in Seedling Reaction to Race 15B of F_2 Plants from Diallel Crosses.

Parents	St. 464	Arab.	Camadi	C.I. 8133	C.I. 7875	C.I. 7870	C.I. 7805	P.I. 192179	P.I. 191194
St.464	-	;-2^{+}	;-4	;-2^{-}	;-2^{-}	;-2	;-1	;-1^{-}	;-4
Arabian	;-2^{+}	-	;-4^{-}	;-2	;-2	;-2	;-2	;-2	1^{-}-2^{+}
Camadi	;-4	;-4^{-}	-	;-4	;-4	;-4	-	-	;-4
C.I.8133	;-2^{-}	;-2	;-4	-	1$^{=}$-2	;-2	;-2	;-2	;-4
C.I.7875	;-2^{-}	;-2	;-4	1$^{=}$-2	-	1$^{=}$2^{-}	;-2^{-}	;-2^{-}	;-4
C.I.7870	;-2	;-2	;-4	;-2	1$^{=}$-2	-	;-2^{-}	;-2^{+}	1$^{=}$-X^{+}
C.I.7805	;-1	;-2	-	;-2	;-2^{-}	;-2^{-}	-	;-1	;-4
P.I.192179	;-1^{-}	;-2	-	;-2	;-2^{-}	;-2^{+}	;-1	-	;-4
P.I.191194	;-4	1^{-}-2^{+}	;-4	;-4	;-4	1$^{=}$-X^{+}	;-4	;-4	-

St.464, P.I.192179 and C.I.7805.

The three varieties, St.464, P.I.192179 and C.I.7805 are very similar in both their seedling and mature plant reaction to race 15B. All three gave ;-1= pustules in the seedling stage and from 0-1% infection under field tests.

The reaction of F_1 plants to race 15B in the seedling and field tests (tables 4 and 5) showed that the factor or factors in each of the varieties was dominant. The results of rust tests on plants from crosses and backcrosses involving, St.464, P.I.192179 and C.I.7805 are given in tables 9 and 10.

Backcross data obtained from seedling tests indicated that two factors are present in each variety. In backcross, St.464 x Stewart^2, 87 F_2 families were tested for seedling reaction. The observed ratio of 66 segregating : 21 susceptible families is a good fit to a 3:1 or a 2 factor backcross ratio. Additional evidence was obtained from the backcross with Nugget. Of 54 F_2 families tested, 41 segregating and 13 were susceptible. This segregation will also fit a 3:1 ratio and supports the hypothesis that St.464 has two factors for resistance.

Table 9. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
St.464 x Stew.^{2}	87	66	21	3:1	.50-.95
St.464 x Nug.^{2}	54	41	13	3:1	.50-.95
P.I.192179 x Stew.^{2}	29	24	5	3:1	.20-.50
C.I.7805 x Stew.^{2}	35	27	8	3:1	.20-.50
C.I.7805 x Nug.^{2}	18	15	3	3:1	.20-.50

With P.I.192179, data are available only from the backcross to Stewart. The observed ratio of 24 segregating :5 susceptible F_2 families will fit a 3:1 ratio. A chi square test for goodness of fit gave a probability value of between .20 - .50. This strongly suggests the presence of two factors in the variety.

The presence of two factors for resistance in C.I.7805 was indicated by the results obtained from the backcrosses, C.I.7805 x Stewart^2 and C.I.7805 x Nugget^2. Of 35 F_2 families tested from the backcrosses with Stewart, 27 segregated and 8 were susceptible, while in the backcross with Nugget, the observed ratio of 15 segregating :3 susceptible families was obtained. In both backcrosses segregation will fit a 3:1 or a 2 factor backcross ratio.

Table 10. Results from Rust Tests on F_2 Populations from the Crosses Involving St.464, P.I.192179 and C.I.7805.

Cross or Type of Test.	Number of plants			Ratio	Probability
	Total	Resistant	Susceptible		
Seedling Tests					
St.464 x Stewart	665	615	50	15:1	.10-.20
St.464 x Nugget	340	319	21	15:1	.50-.95
P.I.192179 x St.464	150	150	0	0	-
C.I.7805 x St.464	110	110	0	0	-
C.I.7805 x P.I.192179	91	91	0	0	-
Field Tests					
St.464 x Stewart	299	285	14	15:1	.20-.50
St.464 x Nugget	296	282	14	15:1	.20-.50

The diallel crosses, C.I.7805 x St.464, P.I.192179 x St.464, and C.I.7805 x P.I.192179, were tested for seedling reaction to race 15B.

All F_2 plants obtained in each cross were as resistant as the parents indicating that the two factors for resistance in each variety are the same.

The two factors present in each of the varieties, St.464, P.I.192179 and C.I.7805, are independent and have an additive effect on resistance to race 15B. One factor, which will be designated $\underline{Sr_A}$, controls a type 1-X reaction and the other, which will be designated $\underline{Sr_B}$, a type 2 reaction. The combination of the two factors results in high resistance characterized by hypersensitive flecking.

Reactions within some F_2 families in each backcross indicated that one or two factors were segregating. In some families the reactions indicated that two independent factors were segregating. This was verified by the ratio of 15 resistant to one susceptible plant that was obtained within the families. In other families a 3:1 ratio was obtained indicating that only one factor was segregating. An examination of the reaction within the backcross families, suggested that some of the families segregated for the factor $\underline{Sr_A}$, while the rest segregated for the factor $\underline{Sr_B}$. The remainder of the families were fully susceptible.

In the cross, P.I.192179 x Stewart[2], of 29 F_2 families tested, 8 segregated for both factors, 7 segregated for the factor $\underline{Sr_B}$, 9 segregated for the factor $\underline{Sr_A}$ and 5 were susceptible. This is a satisfactory fit to a 1:1:1:1 ratio which is expected when two independent factors are segregating.

In the cross, C.I.7805 x Stewart[2], a total of 35 F_2 families were tested, 11 of which segregated for both factors, 10 segregated for the factor $\underline{Sr_B}$, 6 segregated for the factor $\underline{Sr_A}$ and 8 were susceptible. Here again the segregation fits a 1:1:1:1 ratio giving a probability value of between .10 and .20.

In only 16 F_2 families of the cross, St.464 x Stewart^2, was the reaction clear enough to determine the number of factors segregating on the basis of the ratios obtained. Of these 16 families, 5 segregated for both factors, 4 segregated for factor $\underline{Sr}_B$, 3 segregated for the factor $\underline{Sr}_A$ and 4 were susceptible. The segregation suggests a 1:1:1:1 ratio supporting the evidence for the presence of two factors for resistance in St.464. In the other backcross families, the seedling tests were run at a different time and the reaction obtained was not clear enough to separate the families which segregated for the factor $\underline{Sr}_A$, or for the factor $\underline{Sr}_B$, or for both factors.

The data from the tests on F_2 plants (table 10) corroborate the backcross results with St.464. In seedling tests, the cross, St.464 x Stewart, gave a ratio of 615 resistant :50 susceptible F_2 plants. Of 340 F_2 plants classified in the cross with Nugget, 319 were resistant and 21 were susceptible. In both crosses, segregation fits a 15:1 ratio which is expected when 2 independent factors are segregating.

In field tests, a total of 299 F_2 plants were classified for percentage infection in the cross, St.464 x Stewart. The observed ratio of 285 resistant :14 susceptible plants is a satisfactory fit to a 15:1 ratio. A chi square test for goodness of fit gave a probability value of between .20 and .50. Additional evidence was obtained from the cross with Nugget. The segregation obtained, 282 resistant :14 susceptible F_2 plants, fits a 15:1 ratio and supports the evidence for the presence of two factors for resistance in St.464.

The hypothesis that St.464, P.I.192179 and C.I.7805 have two common factors for resistance to race 15B agrees with results reported by Heermann *et al.*(19), but the presence of additional factors which modify the mature plant reaction of the varieties, is not supported by results obtained in this study.

Arabian

Tables 11 and 12 give the data obtained from the crosses and backcrosses involving Arabian.

The results from the backcrosses, Arabian x Stewart^2 and Arabian x Nugget^2, are conflicting. The presence of three or four factors is indicated in the backcross with Stewart. The observed ratio of 84 segregating :6 susceptible F_2 families will fit either a 7:1 or a 15:1 ratio. On the other hand, the results from the backcross with Nugget, seem to show that Arabian has only two factors for resistance. Of 129 F_2 families tested, 98 segregated and 31 were susceptible. This segregation is a good 3:1 ratio giving a probability value of between .50 and .95. The difference in reaction in the two backcrosses can not be explained. The presence of two factors, both of which give a 2 reaction is clear. One of the factors results in a poorer resistance than the other and is characterized by a 2^+ reaction. There is a possibility that Arabian possesses one or two factors which govern a 1-X reaction. This was not definitely established from backcross data, but was indicated in diallel crosses. The combination of the Arabian factors results in moderate resistance characterized by small pustules similar to a 1 reaction and the presence of definite "green islands" typical of a 2 reaction. The reaction of Arabian was designated by a 2^-.

Table 11. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
Arabian x Stewart^2	90	84	6	7:1 15:1	.05-.10 .95-.99
Arabian x Nugget^2	129	98	31	3:1	.50-.95

The presence of two factors in Arabian was also indicated by results obtained when the F_2 plants of crosses, Arabian x Stewart and Arabian x Nugget, were tested for seedling reaction to race 15B. In the cross with Stewart, a ratio of 289 resistant :21 susceptible was obtained, while in the cross with Nugget the ratio was, 282 resistant :19 susceptible F_2 plants. In both crosses, segregation fits a 15:1 ratio which is expected when two factors are segregating.

Table 12. Results from Rust Tests on F_2 Populations from the Crosses Involving Arabian.

Cross or Type of Test.	Number of plants.			Ratio	Probability
	Total	Resistant	Susceptible		
Seedling Tests.					
Arabian x Stewart	310	289	21	15:1	.20-.50
Arabian x Nugget	301	282	19	15:1	.95-.99
St.464 x Arabian	517	517	0	0	-
Field Tests.					
Arabian x Stewart	269	245	24	15:1	.05-.10
Arabian x Nugget	359	336	23	15:1	.50-.95
St.464 x Arabian	349	349	0	0	-

Results from field tests supported the hypothesis that Arabian has only two factors for resistance to race 15B. Thirty-one F_2 families of the backcross, Arabian x Nugget^2, were classified for reaction to race 15B. The observed ratio of 23 segregating :8 susceptible will fit a 3:1 or a 2 factor backcross ratio.

Of 269 F_2 plants classified from the cross, Arabian x Stewart, 245 were resistant and 24 were susceptible, while in the cross with Nugget, 282 were resistant and 19 susceptible. In both crosses, segregation

fits a 15:1 or a two factor ratio.

The F_2 results of the cross, Arabian x St.464, suggested the presence of a common factor in the two parents. Of 349 F_2 plants classified for mature plant reaction to race 15B, none was susceptible. In seedling tests the same cross gave a similar result. In the F_2 generation, the reaction of resistant plants ranged from a ; to a type 2^-. The absence of fully susceptible plants clearly indicates that the varieties, St.464 and Arabian, have one factor in common. Since the presence of a factor that conditions a 2 reaction has been established in both St.464 and Arabian on the basis of backcross results, it is logical to assume that the factor $\underline{Sr_B}$ is common to the two varieties. The factor that conditions a 2^+ reaction in Arabian was designated as $\underline{Sr_C}$.

P.I.191194

The results of rust tests from crosses and backcrosses involving P.I.191194 are given in tables 13 and 14.

The moderate resistance of P.I.191194 was found to be controlled by a single factor. Results were obtained only in the backcross with Stewart. The observed ratio of 18 segregating :16 susceptible F_2 families is a good fit to a 1:1 or a one factor backcross ratio. In a homozygous condition, the factor gives a 2^+ reaction.

The seedling reaction of the F_2 generation of the cross, Arabian x P.I.191194, indicated the presence of a common factor in the parents. No susceptible plants were found in a total of 80 F_2 plants examined. Segregation of resistant plants ranged from 1^- to 2^+ reaction. Although the results are limited, it appears that the factor which conditions a 2^+ reaction in P.I.191194 is identical with the $\underline{Sr_C}$ factor of Arabian.

Segregation was obtained in the diallel crosses, P.I.191194 x St.464, P.I.192179 x P.I.191194 and C.I.7805 x P.I.191194, indicating that P.I.191194 does not have a common factor with the other three parents.

Table 13. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
P.I.191194 x Stewart[2]	34	18	16	1:1	.50-.95

Table 14. Results from Seedling Tests on F_2 Population from the Crosses Involving P.I.191194.

Cross	Number of plants		
	Total	Resistant	Susceptible
P.I.191194 x St.464	117	112	5
P.I.192179 x P.I.191194	83	79	3
C.I.7805 x P.I.191194	55	53	2
P.I.191194 x Arabian	80	80	0

Camadi

The segregation of the F_2 generation of crosses and backcrosses involving Camadi is given in tables 15 and 16.

Evidence from backcrosses to Stewart indicates that only one factor for resistance to race 15B is present in Camadi. A ratio of 41 segregating :42 susceptible families was obtained in the F_2 backcross generation. This is a good 1:1 or a one factor backcross ratio. Further evidence was obtained from the backcross, Camadi x Nugget[2]. Of 28 families tested, 13 segregated and 15 were susceptible. This is a good 1:1 ratio

giving a probability value of between .50 and .95.

The reaction of the F_1 generation of the crosses, Camadi x Stewart and Camadi x Nugget (tables 4 and 5), suggested that the factor for resistance present in Camadi is incompletely dominant. In a homozygous condition the factor gives a 1⁻ - 1 reaction, while in a heterozygous condition a X-3 reaction is typical.

Table 15. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
Camadi x Stewart[2]	83	41	42	1:1	.50-.95
Camadi x Nugget[2]	28	13	15	1:1	.50-.95

The evidence for the presence of a single factor in Camadi was supported by field studies. In the cross, Camadi x Stewart, the ratio obtained, 200 resistant :76 susceptible plants is a good fit to a 3:1 ratio. In addition, 791 F_2 plants of the cross with Nugget were classified for per cent infection. The observed ratio of 467 resistant to 324 susceptible F_2 plants will not fit a 3:1 ratio. Difficulty was experienced in distinguishing the plants that were heterozygous for the Camadi factor and the plants that were susceptible. Misclassification of F_2 plants could explain the large number in the susceptible class.

Results obtained from seedling and field tests in the cross, Camadi x St.464, are similar. In seedling tests, 6 of 278 F_2 plants tested were susceptible, while in field tests, 2 of 152 F_2 plants classified were susceptible. In each of the two crosses, segregation fits a 63:1 ratio indicating a three factor difference between the two varieties.

This result agrees with the conclusions that Camadi has one factor and St.464 has two factors for resistance to race 15B.

Table 16. Results from Rust Tests on F_2 Populations from the Crosses Involving Camadi.

Cross or Type of Test.	Number of plants.			Ratio	Probability
	Total	Resistant	Susceptible		
Seedling Tests					
Camadi x Arabian	578	575	3	255:1	.50-.95
St.464 x Camadi	278	272	6	63:1	.20-.50
Camadi x P.I.191194	67	60	7	15:1	.10-.20
Field Tests					
Camadi x Stewart	276	76	200	3:1	.20-.50
Camadi x Nugget	791	467	324	3:1	.01
Camadi x Arabian	255	255	0	0	-
St.464 x Camadi	152	150	2	63:1	.50-.95

A total of 578 F_2 plants of the cross between Camadi x Arabian were tested for seedling reaction to race 15B. The observed segregation of 575 resistant :3 susceptible plants will fit a 255:1 ratio suggesting that in addition to the Camadi factor, three factors of Arabian were segregating. In field tests, segregation was not obtained in the F_2 generation of the same cross. However, the number of F_2 plants tested for mature plant reaction was too small to draw any definite conclusions. Of a total of 67 F_2 plants classified for mature plant reaction from the cross, Camadi x P.I.191194, 60 were resistant and 7 were susceptible. This segregation fits a 15:1 ratio giving a probability value of .10-.20. This result agrees with the hypothesis that each parent has a single factor for resistance to race 15B.

Since it has been established that Camadi does not possess the factors, $\underline{Sr}_A$, $\underline{Sr}_B$ or $\underline{Sr}_C$, the factor which controls the resistance of the variety was designated as $\underline{Sr}_D$.

C.I.7875

The data obtained from the crosses and backcrosses involving C.I.7875 are given in tables 17 and 18.

Results obtained from the backcross to Stewart suggested that the resistance of C.I.7875 is controlled by a single dominant factor. Of a total of 51 F_2 families tested, 27 segregated and 24 were susceptible. This is a good 1:1 ratio. A chi square test for goodness of fit gave a probability value of between .50-.95. In a homozygous condition the factor gives a $1^{=}$ - 1^{-} reaction, while in a heterozygous condition a X-2 reaction is obtained.

Table 17. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
C.I.7875 x Stewart^2	51	27	24	1:1	.50-.95

Crosses of C.I.7875 with P.I.192179, St.464 and C.I.7805 did not result in segregation in the F_2 generation. This is taken as an indication of the presence of a common factor in the four parents. Since C.I.7875 gives a 1^{-} reaction, it is logical to assume that the factor $\underline{Sr}_A$, which controls a 1 - X reaction, is present in all four varieties.

Table 18. Results from Seedling Tests on F_2 Population from the Crosses Involving C.I.7875.

Cross	Number of plants		
	Total	Resistant	Susceptible
C.I.7875 x St.464	101	101	0
C.I.7805 x C.I.7875	48	48	0
P.I.192179 x C.I.7875	84	84	0
C.I.7875 x Arabian	109	109	0
C.I.7875 x P.I.191194	68	66	2
C.I.7875 x Camadi	89	85	4

No segregation was obtained in the F_2 generation of the cross between Arabian and C.I.7875. This result can not be explained on the hypothesis basis that C.I.7875 has only the $\underline{Sr_A}$ factor. Assuming that Arabian has two factors and C.I.7875 has one factor for resistance, 1 in 63 plants should be susceptible in the F_2 generation. Since only 80 F_2 plants were tested, the chances of not obtaining a susceptible plant is great.

C.I.7870

Tables 19 and 20 give the segregation of the F_2 generation of crosses and backcrosses involving C.I.7870.

Backcross data indicated that 2 factors for resistance are present in C.I.7870. Of 63 F_2 families examined from the backcross C.I. 7870 x Stewart[2], 44 segregated and 19 were susceptible. This segregation fits a 3:1 or a two factor backcross ratio.

One of the factors of C.I.7870 appears to be the factor $\underline{Sr_A}$ that is also found in C.I.7875, C.I.7805, P.I.192179 and St.464. In

the cross, C.I.7870 x C.I.7875, no segregation was obtained in the F_2 generation indicating that the factor Sr_A of C.I.7875 is also present in C.I.7870. Supporting evidence was obtained from the crosses of C.I. 7870 with St.464, P.I.192179 and C.I.7805. No susceptible plants were obtained in the F_2 generation. The reaction of resistant plants ranged from ; to type 2. This suggests that C.I.7870 possesses only the Sr_A factor and not the factor Sr_B of St.464, P.I.192179 and C.I.7805.

Table 19. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
C.I.7870 x Stewart[2]	63	44	19	3:1	.20-.50

The results from the cross between C.I.7870 and Arabian indicated a common factor in the parents. Of 116 F_2 plants classified, none was fully susceptible. Reaction of resistant plants in the F_2 generation ranged from ; to type 2. Since it has been established that the Sr_B factor of St.464, C.I.7805, P.I.192179 and Arabian is not present in C.I.7870, the possibility that the Sr_C factor is common in C.I.7870 and Arabian is suggested. Supporting evidence for this hypothesis was given by the results of the cross, C.I.7870 x P.I.191194. Of 66 F_2 plants examined, none was fully susceptible suggesting that the factor Sr_C of P.I.191194 is also present in C.I.7870. In the two crosses, C.I.7870 x Arabian and C.I.7870 x P.I.191194, the number of F_2 plants tested is small. The conclusions made from these crosses, therefore, are not definite.

Segregation was obtained in the cross, C.I.7870 x Camadi , indicating that the two varieties do not have a common factor for resistance to race 15B.

Table 20. Results from Seedling Tests on F_2 Population from the Crosses Involving C.I.7870.

Cross	Number of plants		
	Total	Resistant	Susceptible
C.I.7870 x St.464	143	143	0
C.I.7870 x Arabian	116	116	0
C.I.7870 x C.I.7875	73	73	0
P.I.192179 x C.I.7875	56	56	0
C.I.7805 x C.I.7870	41	41	0
C.I.7870 x P.I.191194	66	66	0
C.I.7870 x Camadi	54	53	1

C.I.8133

The results of rust tests on plants from crosses and backcrosses involving C.I.8133 are given in tables 21 and 22.

The results obtained from the backcross, C.I.8133 x Stewart[2], are not clear. The observed ratio of 44 segregating :26 susceptible F_2 families does not fit either a 1:1 or a 3:1 ratio. In the segregating F_2 families, ratios of 15:1 and 3:1 were obtained suggesting that two factors were segregating. Supporting evidence for the presence of two factors for resistance in C.I.8133 was obtained from the backcross with Nugget. Of 10 F_2 families tested, 8 segregated and 2 were susceptible. This is a good fit to a 3:1 ratio giving a probability of between .50 and .95.

C.I.8133 was found to possess the factor $\underline{Sr_A}$ which conditions a 1-X reaction. This was established from the cross between C.I.8133 and C.I.7875. No segregation was obtained in the F_2 generation of this cross, suggesting that the factor $\underline{Sr_A}$ of C.I.7875 is also present in

C.I.8133. Further evidence was obtained from the crosses, C.I.8133 x St.464, C.I.8133 x P.I.192179 and C.I.8133 x C.I.7805. Of 227 F_2 plants tested for seedling reaction, none was fully susceptible, indicating that a common factor is present in all four varieties. Since the presence of the factor $\underline{Sr_A}$ was established in each variety, it is logical to assume that it is the common factor.

Table 21. Segregation of F_2 Backcross Families in Seedling Tests with Race 15B.

Cross	Number of families			Ratio	Probability
	Total	Segregating	Susceptible		
C.I.8133 x Stewart[2]	70	44	26	1:1 3:1	.02-.05 .01-.02
C.I.8133 x Nugget[2]	10	8	2	3:1	.50-.95

Table 22. Results from Seedling Tests on F_2 Population from the Crosses Involving C.I.8133.

Cross	Number of plants		
	Total	Resistant	Susceptible
C.I.8133 x St.464	150	150	0
P.I.192179 x C.I.8133	93	93	0
C.I.7805 x C.I.8133	84	84	0
C.I.8133 x Arabian	82	82	0
C.I.8133 x C.I.7875	66	66	0
C.I.8133 x P.I.191194	80	78	2
C.I.8133 x Camadi	117	115	2
C.I.7870 x C.I.8133	60	60	0

The identity of the second factor for resistance in C.I.8133 has not been established. Reaction of segregating F_2 families of backcrosses with Stewart and Nugget suggested that C.I.8133 possesses a

factor which conditions a 2 reaction in addition to a factor $\underline{Sr_A}$ which controls a 1-X reaction. The results from the cross between C.I.7870 and C.I.8133 showed that these two parents have only the factor $\underline{Sr_A}$ in common. No susceptible plants were obtained in the F_2 generation, but plants that were more susceptible than either of the parents were obtained. This indicates that the factor $\underline{Sr_C}$ which C.I.7870 possesses is not present in C.I.8133. This conclusion is supported by the results of the cross, C.I.8133 x P.I.191194. Segregation was obtained in the F_2 generation, definitely showing that the varieties do not possess a common factor for resistance to race 15B.

Of 82 F_2 plants examined from the cross, C.I.8133 x Arabian, none was susceptible. Reaction of resistant plants ranged from ; to type 2 indicating the presence of a common factor. This result can not be explained since it was established that C.I.8133 does not possess the $\underline{Sr_B}$ or $\underline{Src}$ factors of Arabian. The number of plants tested in the F_2 generation however, was far too small to allow any definite conclusions to be made.

DISCUSSION

The results obtained in this study are valuable to a plant breeder who is interested in using any of the varieties investigated in a breeding program. A number of factors for resistance to race 15B were found to be present in the varieties studied.

The varieties, St.464, P.I.192179 and C.I.7805 appear to be the best sources of resistance to race 15B. The combination of the factors, $\underline{Sr}_A$ and $\underline{Sr}_B$, results in near immunity to the rust in the seedling and mature plant stage. Individually, $\underline{Sr}_A$, which conditions a 1-X reaction, results in a better resistance than the factor $\underline{Sr}_B$, which controls a 2 reaction.

The value of the purple seeded varieties, Camadi, C.I.7805, C.I.8133 and C.I.7870, as parents in a breeding program, is questionable. An amber seeded durum is desirable for the manufacture of macaroni and related products. Preliminary study on the inheritance of the purple seed color of Camadi indicated that the character is dominant and is inherited in a complex manner. In the segregating generation of a cross between Camadi and Nugget or Stewart, a large number of plants would have to be grown to obtain the combination of amber seed color and rust resistance. In most breeding programs this would be impractical. By using a backcross program this problem can be avoided. After backcrossing to Nugget or Stewart for several generations and selecting for amber seed color, the purple seed character can be eliminated.

The resistance of Arabian is sufficient to be of value as a parent in a program to develop a high quality durum variety resistant to race 15B. In field tests, the variety gives from 5-10% stem rust infection. The variety, P.I.191194, which possesses only the $\underline{Sr}_C$ factor of Arabian, is inferior as a source of resistance to race 15B. Furthermore, the variety

is much later in maturity than Arabian.

The reactions obtained in seedling and field tests were comparable. The field tests, however, are not very reliable for determining the number of factors for resistance present in the parents of a particular cross. Plants in the segregating population usually, show a continuous variation from resistance to susceptibility. In addition, many environmental factors influence the rust reaction of individual plants so that their correct classification is difficult. Field tests, however, are useful in testing the reaction of diallel crosses and thereby, establish the presence or absence of common factors in the parents of a cross. In greenhouse tests, the number of plants that can be tested for seedling reaction is limited by the space available. This limitation is not present in field tests. In this study, most of the diallel crosses were tested for seedling reaction to race 15B in the greenhouse. As a result the number of F_2 generation plants tested from some of the diallel cross was far too small to indicate the relationship of the factors for resistance in the parents.

Rust tests are being continued to clarify the inheritance of resistance in some of the varieties. Additional F_2 families of the backcrosses, C.I.7870 x Stewart^2 and C.I.8133 x Stewart^2, are being tested for seedling reaction to race 15B in the greenhouse. Furthermore, critical diallel crosses are being tested for seedling reaction. The results of these tests are not available for this report. Additional field tests will be conducted to obtain more information on the mature plant reaction of the F_2 generation, of diallel crosses and backcrosses involving varieties of which the inheritance of resistance is not clear.

A limitation of this study is that only one race of stem rust was used. Race 15B was selected because it is the most prevalent and the

most virulent race attacking the commercially grown durum varieties in Western Canada. Originally, it was intended to use race 56 as well, but no variety susceptible to the race could be obtained. The possibility that the established factors in the variety investigated give resistance to other races was not studied.

SUMMARY

1. Nine varieties, St.464, Camadi, Arabian, C.I.8133, C.I.7805, C.I.7875, C.I.7870, P.I.192179 and P.I.191194, all of which were obtained from the International Rust Nursury, were studied for inheritance of resistance to race 15B.

2. Seedling and mature plant reaction of the varieties were obtained from field and greenhouse studies. All nine varieties showed good resistance to race 15B at both stages of growth.

3. Each variety was crossed and backcrossed to Nugget and Stewart, both of which are very susceptible to race 15B. In addition, diallel crosses were made between the resistant varieties, involving a total of 36 crosses.

4. The F_2 of all available diallel crosses and backcrosses was tested for mature plant reaction in the field. In addition, seedling tests with race 15B have been carried out on F_2 families from the majority of diallel crosses and backcrosses.

5. St.464, P.I.192179 and C.I.7805 were found to have two common factors for resistance. One factor, $\underline{Sr}_A$, conditions a 1-X reaction and the second factor $\underline{Sr}_B$, controls a 2 reaction in the seedling stage. The combination of the two factors results in high resistance characterized by a hypersensitive flecking at both stages of growth.

6. The presence of two factors for resistance was definitely established in Arabian. One factor is $\underline{Sr}_B$ which is also present in St.464, P.I. 192179 and C.I.7805. The other factor, $\underline{Sr}_C$, conditions a 2^+ reaction in the seedling stage. The combinations of the Arabian factors results in a 2^- reaction.

7. The moderate resistance of P.I.191194 is controlled by a single factor $\underline{Sr_C}$, which is also found in Arabian.

8. Camadi was found to possess an incompletely dominant factor which in a homozygous condition results in a 1^- - 1 reaction and in a heterozygous condition a X-3 reaction. The factor designated $\underline{Sr_D}$.

9. The presence of the factor $\underline{Sr_A}$ was established in C.I.7875.

10. The varieties, C.I.7870 and C.I.8133, have two factors for resistance to race 15B. Both varieties have the factor $\underline{Sr_A}$. Some evidence was obtained to show that the second factor of C.I.7870 is $\underline{Sr_C}$ which is also present in Arabian and P.I.191194. The identity of the second factor of C.I.8133 was not established. The variety appeared to possess a factor which conditions a 2 reaction, but is not $\underline{Sr_B}$ or $\underline{Sr_C}$.

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