THE UNIVERSITY OF MANITOBA

INHERITANCE OF RESISTANCE TO *Puccinia coronata avenae* IN FOUR COLLECTIONS OF *Avena sterilis*

by

FERDINAND ALBERT KIEHN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF PLANT SCIENCE

WINNIPEG, MANITOBA

May 1975

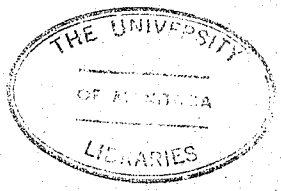
INHERITANCE OF RESISTANCE TO Puccinia coronata avenae IN FOUR COLLECTIONS OF Avena sterilis

by

FERDINAND ALBERT KIEHN

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE



ACKNOWLEDGEMENTS

The writer wishes to express his sincere appreciation to Dr. R. I. H. McKenzie, for suggesting the field of study and for his helpful guidance and encouragement throughout the study and in the preparation of the manuscript. The author is also indebted to Drs. J. W. Martens and D. E. Harder for their suggestions and assistance. Grateful thanks is also due to Mr. W. L. Timlick for his assistance with techniques and rust collections.

In addition to those mentioned, the author is grateful to the many others who provided suggestions and assistance throughout this study.

ABSTRACT

INHERITANCE OF RESISTANCE TO *Puccinia coronata avenae* IN FOUR COLLECTIONS OF *Avena sterilis*

F. A. Kiehn

The inheritance of resistance to oat crown rust *Puccinia coronata* Corda f.sp. *avenae* Erikss. was studied in four collections of *Avena sterilis* L., three of these were from Israel (CAV 4963, CAV 1358, and CAV 1376) and one from Algeria (CAV 1964). Tests with crown rust races 264 (3 isolates), 203 (2 isolates), 295 (2 isolates), 211, 239, 259, 305 and 326 (one isolate each) on F_2 backcross families, indicated a single recessive gene (Pc-55) in CAV 4963 conditioned resistance to all crown rust isolates tested. Pc-55 conditioned resistance in adult plants to four of the five rust cultures used, but was susceptible to race 305. A single dominant gene (Pc-56) in CAV 1964 conditioned resistance to all the crown rust isolates except race 239, while a second dominant gene conditioned resistance to only two of the twelve cultures used. Pc-56 tested to five rust cultures conditioned the same resistance in the adult plants as in the seedling. The inheritance of resistance in CAV 1358 and CAV 1376 was complex. From field studies and seedling tests it appeared that the resistance in these collections was conditioned by a number of recessive minor additive genes.

The genes Pc-55 and Pc-56 were not allelic with the genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-47, Pc-48, and Pc-50.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Crown rust, *Puccinia coronata* Corda. f.sp. *avenae* Erikss. has long been considered the most important disease attacking cultivated oats *Avena byzantina* C. Koch., and *Avena sativa* L., in North America (Coffman *et al.* 1961). It occurs to some extent almost everywhere oats are grown, but is most serious in humid areas. Control of crown rust has been of great economic importance in the major oat producing areas of Canada and the United States. At present the most feasible means of control appears to be the development of resistant cultivars.

Breeding oats for resistance to crown rust has been very difficult because of the high degree of specialization and the broad virulence spectrum exhibited by the pathogen. The prevalence and distribution of different crown rust race groups in North America has been influenced by the change-over from susceptible to resistant cultivars. The release of cultivars with new crown rust resistance resulted in selection pressure for new or previously unidentified rust races capable of aggressively attacking the new previously resistant hosts. As the acreage of these cultivars increased so did the new races that could attack them.

Stevens and Scott (1950) pointed out that a given oat cultivar had an average life of four to five years and ranged from one to 12 years individually. This, therefore, creates a recurring need for new resistant cultivars (Murphy *et al.* 1967). Oat cultivars with single gene crown rust resistance have remained resistant for only a limited number of years when grown over a large area. Therefore, different ways of using resistance genes have been proposed and some have already been put into effect. Multiline and multigene cultivars have been suggested for the conservation

of resistance genes. Regional deployment of genes has also been proposed for oat crown rust and wheat stem rust (Browning and Frey 1969; Browning *et al.* 1969; Knott 1971). These programs would require a substantial number of resistance genes to be effective.

It has been recognized for many years that noncultivated species of oats might furnish new sources of crown rust resistance. Therefore, it was necessary to search among the wild relatives of oats in order to build up a supply of genes for resistance to crown rust. Crown rust resistance has been found in diploid and tetraploid species of *Avena* (Murphy *et al.* 1958; Simons *et al.* 1959; Marshall and Myers 1961). The crosses between ploidy levels, to transfer rust resistance of diploid and tetraploid species to hexaploid oats, were easily obtained, but often the resulting F_1 and later generations were highly sterile (Sadanaga and Simons 1960). Gene transfer to higher ploidy levels has usually not been successful.

Avena sterilis L., indigenous to the Mediterranean region, is widespread and comprises many different ecotypes (Simons *et al.* 1962). *A. sterilis* is believed to be the wild or primitive form of hexaploid oats from which the cultivated oats were derived. It should have some rust resistance since at least three species of *Rhamnus*, which serve as alternate hosts of *P. coronata*, are present in the area. The presence of *Rhamnus* spp. permits the occurrence of sexual recombination with the resulting production of a variety of physiological races and the consequent accumulation of resistance genes in the general host as a result of natural selection (Wahl *et al.* 1960; Dinoor and Wahl 1963). Good crown rust resistance has been found in many *A. sterilis* (wild oat) collections (Wahl *et al.* 1960). McKenzie and Fleischmann (1964) and others have

conducted genetic studies on the inheritance of crown rust resistance in *A. sterilis*, and have isolated and described useful genes.

The present study was undertaken to investigate the inheritance of crown rust resistance in each of four *A. sterilis* collections. These four were among the very best of several hundred collections screened in Puerto Rico, Texas and in Manitoba for resistance to crown rust, particularly to race 305, which is virulent on most of the known sources of resistance. Crosses were made to study the mode of inheritance and to determine if resistance genes present in these collections were similar to or allelic to others previously isolated from *A. sterilis*. It was hoped that additional useful crown rust resistance genes would be found. Observations were also made on some of the undesirable characteristics present in *A. sterilis*, to determine if they are linked to the resistance genes.

CHAPTER 2

LITERATURE REVIEW

2.1 Rust Physiologic Race Differential Sets and Host-Parasite Interaction Descriptions

The phenotype or 'infection type', ranging from immunity to full susceptibility, produced in a host-parasite interaction is determined by the genotypes of the interactants. Stakman and Levine (1922) established a uniform system of classification of reaction types for *Puccinia graminis* f.sp. *tritici* Erikss. and Henn. Murphy (1935) adopted their classification for the purpose of identifying *Puccinia coronata* var. *avenae* races. The infection type designations used by crown rust workers are:

(I) or (0) - immune - no indication of infection,

(0;) - nearly immune - no uredia, hypersensitive flecks present,

(1) - highly resistant - uredia small, distinct necrotic areas surround pustules,

(2) - moderately resistant - uredia small to medium surrounded by distinct chlorotic or necrotic borders,

(3) - moderately susceptible - uredia medium in size, some chlorosis may be present, no necrosis,

(4) - very susceptible - abundant large uredia without necrosis or chlorosis.

Murphy (1935), had designated 13 cultivars as the first standard set of differential cultivars for the identification of oat crown rust races. This set included Raukura, Green Russian, Hawkeye, Anthony, Sunrise, Victoria, Green Mountain, White Tartar, Appler, Sterisel, Belar, Bond and Glabrota. It was used to identify crown rust races 1 to 113. (Murphy

1935; Simons and Murphy 1955). The set lost much of its usefulness because it did not relate adequately to the host population and did not differentiate new important races. In 1955 Simons and Murphy (1955) introduced the use of a new set which consisted of Anthony, Victoria, Appler, Bond, Landhafer, Santa Fe, Ukraine, Trispernia, Bondvic and Saia. Races differentiated by this set were given numbers starting with race 201 to prevent confusion with the original race numbers on the old set.

Simons (1954, 1955) found that oat cultivars which showed differences in degree of infection to crown rust with temperature, showed more infection at higher than at lower temperatures. Futrell and Rivers (1955) found that some varieties were more resistant when grown at 65°F than at 85°F. With some varieties susceptibility increased when higher light intensities and longer daylengths produced healthier plant growth.

Zimmer and Schafer (1961) showed that when the cultivar Glabrota inoculated with race 263 the reaction type changed from a resistant type 0 at 15°C to a type 3 at 27°C. Glabrota was uniformly resistant to races 203 and 295 at both temperatures. Saari and Moore (1962) tested several isolates of crown rust against 95 oat cultivars at temperatures (18°, 24° and 30°C) and resistance changed to susceptibility with one or more isolates on 41 of the 95 cultivars. Gassner (1927, as reviewed by Simons 1970) found that pustule formation on plants was greatly reduced at reduced light intensity. Therefore, during the winter it was necessary to supplement the natural daylight to secure normal reaction.

Until 1966 all the identified genes for crown rust resistance had been named in a haphazard fashion (Simons *et al.* 1966). Some genes were even designated with two different symbols by two different investigators and so, in 1966, a committee on Oat Gene Nomenclature, appointed by the

National Oat Conference, developed a standardized system of nomenclature for genes governing characters of oats. The symbol Pc, for *P. coronata*, followed by an Arabic numeral, was assigned to the different genes that had been identified in inheritance studies.

John H. Parker, at Cornell University in 1920, apparently was the first to present the results of a study of the inheritance of disease resistance in oats (Coffman *et al.* 1961). Parker inoculated the progeny of the resistant variety Burt crossed to the susceptible variety Sixty Day with unidentified races of crown rust (Murphy and Coffman 1961). The data did not easily fit any common genetic ratio, so he concluded that the resistance was conditioned by multiple factors, with susceptibility partly dominant.

2.2 Resistance Genes Present in Cultivated Oats

2.2.1 Pc-1

Davies and Jones (1927) reported on the inheritance of resistance in Red Rustproof. The F_2 and F_3 progeny of a cross with the susceptible Scotch Potato oats were tested to both a pure culture of rust and possible mixed races of rust. They found that resistance was conditioned by a single partially dominant factor. Dietz and Murphy (1930) using race 3 also determined that a single dominant gene in Red Rustproof, which they designated "S", conferred resistance. In 1966 the gene was assigned the standardized symbol of Pc-1 (Simons *et al.* 1966).

2.2.2 Pc-2, Pc-11, and Pc-12

Murphy and Stanton (1930) reported that Victoria C.I.2401, an introduction from South America had a high level of resistance to oat crown

rust. Murphy *et al.* (1937) in the cross Victoria x Lee obtained a ratio of 1 resistant:2 intermediate:1 susceptible using crown rust race 1 indicating that Victoria possessed a single partially dominant gene for resistance to this race. Weetman (1942), Cochran *et al.* (1945) and Litzenberger (1949a) also found the Victoria resistance to race 1 and 45 was simply inherited. Murphy and Meehan (1946) reported that a single gene conferred resistance to crown rust race 45 in eight different varieties, each of which derived its resistance from Victoria. They found that all the crown rust resistant progeny were susceptible to Victoria blight (*Helminthosporium victoria* M. and M.), while the crown rust susceptible progeny were resistant to *H. victoriae.* From this and other experiments it was believed that resistance to *H. victoriae* and susceptibility to crown rust were apparently controlled by the same single gene or two very tightly linked genes.

Poehlman and Kingsolver (1950) reported that they tested selected F_{10} lines of the cross Columbia x Victoria-Richland and the reciprocal cross and obtained an intermediate reaction type to races 1 and 45 on some lines that had good resistance to Victoria blight. No indication of broken linkage was found by Finkner (1953) between the Victoria type hypersensitive reaction to crown rust and susceptibility to *H. victoriae*, in F_3 populations of five crosses. His results also showed that non-allelic factors for resistance to crown rust, obtained from crosses with other resistant varieties, had no effect on the susceptibility to Victoria blight.

Welsh *et al.* (1954) selected plants from a Garry cross with resistance derived from the variety Victoria which fell into three disease reaction classes.

The first class was the "Victoria" type hypersensitive resistance in

which the lines were resistant to all the races of crown rust studied but were susceptible to Victoria blight. Simons *et al.* (1966) gave this resistance gene the symbol Pc-2.

In the second class were the lines resistant to Victoria blight and susceptible to crown rust races 4, 5, 34A and 57 but resistant to races 1, 2, 3, 6, 24, 34, 38 and 45. These lines had a dominant gene which was designated Pc-11 (Simons *et al.* 1966).

The third class contained lines resistant to Victoria blight and susceptible to all crown rust races studied. It is not clear why this was considered to be due to anything other than the absence of genes Pc-2 and P-11, but this susceptibility was designated the symbol Pc-12 by Simons *et al.* (1966).

According to Welsh *et al.* (1954) Pc-11 was epistatic to Pc-12 which in turn was epistatic to Pc-2.

2.2.3 Pc-24, Pc-25, Pc-26, Pc-27, and Pc-28

Upadhyaha and Baker (1960) also studied the inheritance of crown rust resistance in Garry. Their studies have shown that Garry comprised a heterogeneous mixture of resistant genotypes. Results with races 203, 226, 237 and 286 showed that six factor pairs were concerned with crown rust resistance and these were in three linkage groups. In one group Vca and Vcb were complementary dominant genes conferring seedling resistance and have been reassigned the standardized symbols Pc-24 and Pc-25 by Simons *et al.* (1966). Vc_1, reassigned Pc-27, conditioned only adult plant resistance. In group 2, Vc_2 conditioned seedling and adult plant resistance but this gene was inhibited by IVc_2 which was linked 10 cross-over units from Vc_2, These genes were assigned Pc-26 and I-Pc-26 respectively. Vc_3 later assigned the number Pc-28 was an independent dominant

gene for adult plant resistance.

2.2.4 Pc-3, and Pc-4

Bond, produced in Australia from the cross Red Algerian x Gold Rain, was introduced into the United States in 1929 (Welsh *et al.* 1953) and has been studied by several investigators to obtain information on the inheritance of its crown rust resistance.

Hayes *et al.* (1939) studied the crown rust reaction of unidentified races in crosses of several susceptible oat varieties with Bond. On the basis of a 9 resistant:7 susceptible segregation they concluded that Bond possessed two dominant complementary genes for resistance. Weetman (1942) obtained similar results using race 1. The two genes have been designated Pc-3 and Pc-4 (Simons *et al.* 1966).

Torrie (1939) tested the progeny of the cross Iowa 444X Bond with races, 1, 7, 46 and a mixture of these races on both seedlings and adult plants. The results suggested two genes, one being an inhibitor which partly masked the effect of the resistance gene. The resistance gene appeared to be inhibited to a greater degree in the mature plant stage than in the seedling stage. The seedling reaction indicated a partial dominance of resistance whereas the mature plant reaction in the field showed a partial dominance for susceptibility.

2.2.5 Pc-3c, Pc-4c, Pc-6c, and Pc-9

Ukraine (Russia No. 7, Mutica Ukraine), introduced into the United States in 1930, was found to be highly resistant to some biotypes of crown rust that parasitized Bond (Murphy 1938). Weetman (1942), found that the Ukraine resistance to race 1 was due to two dominant complementary genes which are probably allelic to the complementary Bond genes for crown rust resistance. These genes were assigned the symbols Pc-3c

and Pc-4c (Simons *et al.* 1966).

Finkner (1954) concluded that Ukraine resistance to race 57 is controlled by duplicate dominant linked genes when he tested the progenies of the cross Clinton x Ukraine. Each of these genes was capable of producing the Ukraine immune type reaction. The genes were designated 'M' and 'V' which were designated Pc-6c and Pc-9 by Simons *et al.* (1966).

Rust tests by Sanderson (1960) indicated that a single dominant gene in Ukraine governed resistance to races 202, 202A and 213, while a different dominant gene controlled resistance to race 263. Sanderson explained the difference in his results compared to those of Finkner on the basis that the original Ukraine stock was not homogeneous for crown rust reaction. Therefore, two genetically different plants could have been used as parents in the two investigations.

2.2.6 Pc-5, Pc-6, Pc-7, Pc-8, Pc-9c, and Pc-21

Landhafer and Santa Fe were introduced from South America into the United States in 1938 and 1945, respectively. Litzenberger (1949b) conducted a genetic study of crown rust resistance in these varieties with crown rust races 1 and 45. The data indicated one dominant gene present in each of the two varieties. These genes were designated Pc-5 in Landhafer which gave a 0 to 1 reaction and Pc-6 in Santa Fe which gave a 0 reaction to crown rust.

Finkner (1954) and Upadhyaya and Baker (1962), obtained results with other rust races which confirmed Litzenberger's results.

Osler and Hayes (1953) obtained results indicating that three genes in Santa Fe conferred resistance to race 45 and 57. Two of the genes were complementary and were designated as Pc-7 and Pc-8 (Simons *et al.*

1966). Simons and Murphy (1954) reported the Santa Fe type of resistance to races 45 and 101 was controlled by two linked genes with a recombination value of about 23%. Linked to Pc-6, the second gene 'U' has been assigned the symbol Pc-9c.

Chang (1959) observed a gene in Santa Fe, designated 'S', which conferred resistance to crown rust races 203, 216 and 253; this was later renamed Pc-21 (Simons *et al.* 1966).

2.2.7 Pc-6d, and Pc-2c

Finkner (1954) described one partially dominant gene in Trispernia and Anthony-Bond x Boone that conferred resistant to race 54, which had originally been designated as 'M_2', which has since been redesignated Pc-6d. A second partially dominant gene in Anthony-Bond x Boone, conferring resistant to race 57, was designated Pc-2c (Finkner 1954; Simons *et al.* 1966). The resistance reaction type in Trispernia is more often 1 or 2 while in Landhafer and Santa Fe it is 0 or 1.

2.2.8 Pc-10, Pc-13, and IPC-10

The inheritance of reaction to crown rust race 57 was studied in the cross Klein 69B x Clinton and the results indicated one dominant gene for resistance, Pc-10 from Klein 69B and one dominant inhibitor gene I-Pc-10 from Clinton which was epistatic to Pc-10 (Finkner 1954; Simons *et al.* 1966). Finkner *et al.* (1955) found resistance to race 109 in Clinton was conditioned by a single dominant gene Pc-13 (Simons *et al.* 1966).

Finkner (1954) found allelism between the gene or genes in Ukraine and the gene or genes in Santa Fe, Trispernia and Anthony-Bond x Boone. It was also observed that the Ukraine gene Pc-6c was independent of the genes in Landhafer, Klein 69B and Victoria. The Ukraine resistance allele

was also dominant and epistatic to the alleles in Santa Fe, Trispernia and Anthony-Bond x Boone.

2.2.9 Pc-14

The variety Ascencao from South America is characterized by near-immune reactions to most available isolates of crown rust along with its susceptible reaction to *H. victoriae* (Simons 1956). Ascencao x Markton F_2 seedlings tested with race 202 and 263 indicated that Ascencao carried the Victoria gene or gene complex. It also possessed a dominant gene 'E' which was epistatic to the Victoria gene as far as crown rust reactions were concerned and which conditioned a near-immune reaction to all the races tested. Gene "E" has been assigned the symbol Pc-14 by Simons *et al.* (1966), and was not allelic to any of the genes carried by Victoria, Landhafer, Trispernia or Santa Fe (Simons 1956).

2.2.10 Pc-22

McKenzie (1961) studied crosses of RL2461, a Ceirch dubach derived line, for crown rust resistance to three races of crown rust 264, 279 and 290. A single gene which was either incompletely dominant or modified by minor genes, governed resistance to all three races. This gene has been designated Pc-22 (Simons *et al.* 1966).

2.2.11 Pc-44

Crosses involving Kyto oats (C.I.8250) from Yugoslavia were tested for the inheritance of crown rust resistance by Martens *et al.* (1968). Resistance to five crown rust races was conferred by a single dominant gene assigned the symbol Pc-44. The crown rust resistance in Kyto appeared to be similar to that found in Anthony since both hosts reacted in the same way to all races tested. Resistance was associated with general chlorosis

of the leaf followed by necrosis.

2.3 Resistance Genes Present in Strains of *Avena strigosa* Schreb.

2.3.1 Pc-15, Pc-16, and Pc-17

Murphy *et al.* (1958) studied the inheritance of crown rust resistance in C.D. 3820, believed to be Saia, which is resistant to most of the virulent races attacking Landhafer, Santa Fe, Trispernia, Bond, Ukraine and Bondvic. When the F_2 plants from the cross C.I. 4748X x C.D. 3820 were tested with races 202 and 258, a 3 resistant:1 susceptible ratio indicated the presence of a single dominant gene. In a second cross the results indicated the presence of three dominant genes which were assigned the symbols Pc-15, Pc-16 and Pc-17 by Simons *et al.* (1966). In another strain of Saia (C.I. 4639) Marshall and Myers (1961) described two independent dominant genes, Pc-15 and Pc-16, either or both giving resistance to race 276.

Dyck and Zillinsky (1963) found two genes in C.D. 3820 conferring resistance to race 264 but only one gene conferring resistance to race 294. Pc-15, one of the two genes conferring resistance to race 264, must be the same as, or closely linked with the gene conferring resistance to race 294. The gene conditioning resistance to race 264, but not to race 294, was not fully dominant. Pc-23 was the symbol assigned to this gene by Simons *et al.* (1966). Simons *et al.* (1959) observed that resistance to race 264 in C.I. 7010, a reselection of Saia, was conditioned primarily by a single major gene, but a minor second gene was also present which conditioned a type 3 reaction.

2.3.2 Pc-18, Pc-19, Pc-29, and Pc-30

Crosses involving Glabrota (C.I.2630) were studied for the inheritance of crown rust resistance to races 205, 216 and 264. Its very high level of resistance was conditioned by a single almost completely dominant gene (Simons *et al.* 1959). Marshall and Myers (1961) tested the progeny of the cross Glabrota C.I. 2524 x C.I. 2837 to races 216 and 276, and obtained results similar to those of Simons *et al.* (1959) which indicated one dominant gene for resistance to both races in C.I. 2524, plus a second gene conferring resistance to race 276. These two genes were designated Pc-18 and Pc-29, respectively (Simons *et al.* 1966).

A. strigosa, C.I. 3815 possessed resistance to crown rust races 205, 227 and 294 (Simons *et al.* 1959). Studies with crown rust races 205 and 227 were made with the progeny of the cross C.I. 3815 x C.I. 7010, where C.I. 7010 was susceptible to both races. The progeny of C.I. 3815 when crossed to susceptible C.I. 2630 were tested to race 294. Results showed that the resistance of C.I. 3815 was conditioned by a single dominant or nearly dominant gene (Simons *et al.* 1959), which has been designated Pc-19 (Simons *et al.* 1966). In the cross C.I. 3815 x C.I. 2837, Marshall and Myers (1961) found that one gene in C.I. 3815 conditioned resistance to race 203, and that this gene plus another near dominant gene conditioned resistance to race 216 and 276. The second gene was named Pc-30 by Simons *et al.* (1966).

Saia C.I. 7010, Glabrota C.I. 2630 and another diploid C.I. 3815 were intercrossed in all combinations and the resistance genes were found to be non-allelic (Simons *et al.* 1959).

2.3.3 Pc-31, Pc-32, and Pc-33

Marshall and Myers (1961), used crown rust races 203, 216 and 276 in inoculating the F_2 progeny of the cross C.I. 4746 x C.I. 2837 and reported that one dominant gene in *A. strigosa* C.I. 4746 conditioned resistance. This gene has been assigned the symbol Pc-31. The F_2 progeny of Ceirch Llwyd x C.I. 2837 were tested with crown rust races 203, 216 and 276. One dominant gene in Ceirch Llwyd conditioned resistance to races 203 and 216 (Marshall and Myers 1961). This gene, plus an additional dominant gene, conferred resistance to race 276 and have been assigned designations Pc-32 and Pc-33 respectively (Simons *et al.* 1966).

2.3.4 Pc-37

Dyck (1966) crossed two resistant *A. strigosa* collections C.D. 3820 and C.D. 7994. C.D. 3820 has genes Pc-23 conferring resistance to race 264 and Pc-15 conferring resistance to races 264 and 294. The F_3 lines of the cross were tested to race 294 and a second gene for resistance was found. This gene came from C.D. 7994 and was assigned the symbol Pc-37.

2.4 Resistance Genes Present in *Avena abyssinica* Hochst.

2.4.1 Pc-20

Simons *et al.* 1959 found the resistance to crown rust races 202, 203, 205, 216 and 264 in *Avena abyssinica* Hochst. strain C.I. 7233 was due to an incompletely dominant gene which has been assigned the symbol Pc-20 by Simons *et al.* (1966).

2.5 Genes for Crown Rust Resistance Derived from *Avena sterilis* L.

Shown in Table 1 is a brief summary of the major Pc genes derived from *A. sterilis* indicating the place of origin of each gene, the names

TABLE 1

Major Crown Rust Resistance (Pc) Genes Isolated from *Avena sterilis*

Gene No.	Investigated by	Gene Expression	Original Number	CAV* Number	Country of Origin
Pc-34	McKenzie & Fleischmann 1964	Incompletely recessive	D 60	-	Israel
Pc-35	McKenzie & Fleischmann 1964	Incompletely recessive	D 137	-	Israel
Pc-36	Simons 1965	Incompletely dominant	C.I. 8081	-	Portugal
Pc-38	Fleischmann & McKenzie 1968	Dominant	CW 491-1	(CAV 2468)	Algeria
Pc-39	Fleischmann & McKenzie 1968	Dominant	F 366	(CAV 5165)	Israel
Pc-40	Fleischmann & McKenzie 1968	Dominant	F 83	(CAV 4992)	Israel
Pc-45	Fleischmann *et al.* 1971a	Dominant	F 169	(CAV 5050)	Israel
Pc-46	Fleischmann *et al.* 1971a	Dominant	F 290	(CAV 5115)	Israel
Pc-47	Fleischmann *et al.* 1971b	Partially dominant	C.I. 8081	-	Portugal
Pc-48	Fleischmann *et al.* 1971b	Dominant	F 158	(CAV 5041)	Israel
Pc-50	Fleischmann *et al.* 1971b	Dominant	CW 486	(CAV 2643)	Tunisia

* Canadian *Avena*.

of the investigators and gene expression.

2.5.1 Pc-34, and Pc-35

D 60 and D 137, two Israeli collections of *A. sterilis*, were found to have resistance to a number of races of crown rust (Dinoor and Wahl 1963). McKenzie and Fleischmann (1964) tested F_2 backcross seedlings from the D 60 x Victory^2 amd D 137 x Victory^2 crosses and found there was one incompletely recessive gene in each wild oat for seedling resistance to crown rust races 203, 205, 264, 276 and 279. The resistance genes in D 60 and D 137 were designated Pc-34 and Pc-35, respectively (Simons *et al.* 1966). Fleischmann *et al.* (1971a) tested D 137 x Pendek^2 F_2 families in the seedling stage to races 264, 290 and 326, and obtained results that one dominant gene believed to be Pc-35 conferred resistance to these races.

In a 1963 field test, McKenzie and Fleischmann (1964) obtained data suggesting that adult plant resistance in each of D 60 and D 137 was governed by one seedling resistance gene and one or more genes for adult plant resistance. It was assumed that all these genes must be present for the expression of the full parental resistance. Fleischmann *et al.* (1971a) conducted adult plant greenhouse tests on D 137 progeny with crown rust races 264 and 332. No differences in rust reaction were noted between plants in the seedling and adult stages.

2.5.2 Pc-36, and Pc-47

C.I. 8081, a selection from the *A. sterilis* P.I. 267989 collection showed a very high degree of resistance and Simons (1965) stated that it was "apparently immune" to several crown rust races. Crown rust races 203, 216, 264, 290, and 321 were used for the test on the F_2 of C.I. 8081 x Clinton and C.I. 8081 x Markton. F_2 tests indicated that with race 203

C.I. 8081 had a single, nearly dominant gene conferring resistance to all the races tested. This gene was assigned Pc-36 by the Committee on Oat Gene Nomenclature.

An inheritance of crown rust resistance study was also carried out on C.I. 8081 by Fleischmann *et al.* (1971b). The C.I. 8081 x Pendek[2] F_2 backcross data indicated that a single incompletely dominant gene designated Pc-47 conditioned resistance to all eight races tested.

The two independent studies with C.I. 8081 each obtained results of one incompletely dominant gene, but Pc-36 conditioned near immunity while Pc-47 conditioned a type (2) reaction. These results could be explained on the basis that the designation C.I. 8081 was assigned to two different wild oats or that the original C.I. 8081 collection was heterogeneous.

2.5.3 Pc-38, and Pc-39

CW 491-4 (CAV* 2468), an *A. sterilis* collection from Algeria, was tested against crown rust races 216, 264, 290, 294 and was resistant in all the tests (Zillinsky and Murphy 1967).

Fleischmann and McKenzie (1968) used 30 crown rust cultures to study the inheritance of resistance of CW 491-4 and of an Israeli *A. sterilis* collection, F 366 (CAV 5165). Results obtained from testing F_2 backcross families indicated that a single dominant gene in each collection conferred a fleck type reaction to all the races tested. These two genes were not linked and were assigned the symbols Pc-38 and Pc-39, respectively.

---

* Canadian *Avena* number.

2.5.4 Pc-40, Pc-41, Pc-42, and Pc-43

The inheritance of crown rust resistance in F 83 (CAV 4997), another Israeli *A. sterilis* collection was also studied by Fleischmann and McKenzie (1968). Results obtained from testing F_2 backcross families using race 446, indicated that a single dominant gene confers resistance against this race. This gene, designated Pc-40, conditioned a fleck reaction to 28 other isolates of crown rust and was susceptible only to two isolates of race 264. This gene generally appeared to give the Trispernia-Bondvic spectrum of crown rust resistance but conditioned a fleck reaction, whereas Trispernia and Bondvic conditioned a one or two type reaction to a number of the same crown rust isolates.

A second dominant gene in F 83 was named Pc-41, and conferred a type 2 reaction to a number of races.

A third dominant gene conferring a fleck reaction only to race 332 was present in F 83 and was designated Pc-42.

A fourth incompletely dominant gene Pc-43 conferred resistance only to race 290, with a type 2 reaction.

2.5.5 Pc-45

F 169 (CAV 5050), another collection of *A. sterilis* from Israel was also found to be resistant to a number of races of crown rust (Fleischmann *et al.* 1971a). Results of testing F_2 backcross families of crosses to Pendek with races 264, 290 and four other races indicated that a single dominant gene conferred resistance to the six crown rust races in the form of a "standard" crown rust fleck reaction. The gene has been assigned the number Pc-45.

A second gene in F 169 also conditioned resistance to races 326, 239,

330 and 332. This gene was designated as F 169B (Fleischmann *et al.* 1971a).

2.5.6 Pc-46

Another *A. sterilis* collection F 290 (CAV 5115) had a single dominant gene for resistance to races 239, 264, 290, 326, 330 and 332 (Fleischmann *et al.* 1971a). The resistance reaction was in the form of large blotchy white lesions on the leaves. Pc-46 was the symbol assigned to the resistance gene. A second gene in F 290 was found to confer resistance to four races of crown rust (326, 239, 330, and 332), and was designated as F 290B.

2.5.7 Pc-48, and Pc-49

Inheritance studies were conducted on F 158 (CAV 5041) another *A. sterilis* collection from Israel by Fleischmann *et al.* (1971b). Tests of F_2 backcross families with races 264, 295 and five other races gave results which indicated that two dominant genes were responsible for the resistance in F 158. One designated Pc-48 conferred resistance to all seven races while the second, designated Pc-49* conferred resistance only to five races (216, 326, 330, 332 and 446).

2.5.8 Pc-50

CW 486 (CAV 2643), an *A. sterilis* collection from Tunisia was found by Fleischmann *et al.* (1971b), to have one dominant gene designated Pc-50, for crown rust resistance. This gene conferred a fleck reaction to five of the eight races tested.

---

* Pc-40 and Pc-49 are believed to be the same gene. (R. I. H. McKenzie, unpublished data).

2.6 Allelism

Several cases of allelism of oat crown rust resistance genes have been reported earlier in this Literature Review. Allelism tests conducted in crosses of lines with resistance genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-47, Pc-48 and Pc-50, indicated that all the genes were independent except Pc-46 and Pc-50 which were assumed to be closely linked genes or alleles (Fleischmann *et al.* 1971b).

Some association between crown rust resistance and other diseases have been reported. Crown rust resistance gene Pc-2 is either pleiotropic or closely linked in the coupling phase with the gene for susceptibility to *H. victoriae* (Litzenberger 1949a; Finkner 1953). Martens *et al.* (1968) obtained results which suggested Pc-44 and stem rust resistance gene Pg-9 are alleles or are linked in repulsion. McKenzie *et al.* (1968) reported that the stem rust resistance gene Pg-3 was associated with crown rust resistance to race 273. McKenzie *et al.* (1965) reported that crown rust resistance to rust races 293 and 325 in the cultivars Rosen's Mutant and Ukraine were associated in the coupling phase to the stem rust resistance gene Pg-9.

2.7 Inheritance of Seed Characters in *Avena sterilis* L.

Jensen (1961), in an extensive review of literature on the inheritance of black lemma color in oats notes that in some varieties color is conditioned by a single gene, in others two genes are responsible. McKenzie and Fleischmann (1964) also found black lemma color in D 60 was controlled by two genes. Grey color has been found to be controlled by one gene (Jensen 1961). In the presence of a gene for black color, the gene for grey color is not expressed.

The inheritance of weak and strong awns has been studied by many investigators. Two strong awns, one each on the primary and secondary kernels and a basal type abscission producing a suckermouth scar, go together and are inherited as a complex (Jensen 1961). This complex appears to be controlled by a single gene. McKenzie and Fleischmann (1964) found that one gene controlled awn expression in each of two *A. sterilis* collections.

CHAPTER 3

MATERIALS AND METHODS

3.1 Parents

One crown rust resistant *A. sterilis* collection made in 1966 and three collections made in 1970 (Baum *et al.* In Press) were used in this study. Descriptions of each collection used are given in Table 2.

These collections were selected for several reasons:

(a) They were of relatively diverse origin and therefore might possess rust resistance genes differing from each other and from those previously identified from *A. sterilis*.

(b) Each collection possessed a moderate to very high degree of greenhouse seedling and field adult plant resistance to some of the most widely virulent North American crown rust races.

TABLE 2

Origin of the Four Selected Collections of *Avena sterilis*

Identification Number*	Collected Year	Country of Origin	Site
CAV 4963	1966	Israel	Geyala
CAV 1964	1970	Algeria	Algiers (10KM-SW)
CAV 1358	1970	Israel	Nahariya
CAV 1376	1970	Israel	Haifa University

* CAV - Canadian *Avena*.

Pendek, a common *A. sativa* cultivar developed in Holland was used as the susceptible parent to which the *A. sterilis* selections were crossed and backcrossed. Pendek was chosen because:

(a) It is considered to be universally susceptible to crown rust and has been successfully used in other genetic studies (Fleischmann and McKenzie 1968; Fleischmann *et al.* 1971a, b). It has become the common genetic background for the genes previously isolated from *A. sterilis*, which are now used as crown rust race differentials (Fleischmann and Baker 1971).

(b) It is a strong strawed high yielding variety easily crossed with *A. sterilis*. If the resistance factors present in the four *A. sterilis* parents should prove to be useful they would be in a desirable background for use in breeding better oats.

The genetic homogeneity of each collection was ascertained through consistency of infection types or lack of segregation within each collection. CAV 4963 and CAV 1964 were both uniform and crosses were made with a few plants tested for rust reaction. CAV 1358 and CAV 1376 were both single plant selections and, after further tests with crown rust, were found to be uniform.

3.2 Crown Rust Races Used

Test races of *P. coronata* were chosen from cultures collected in some of the recent yearly Canadian crown rust surveys (Fleischmann 1967; Fleischmann 1968; Fleischmann 1969; Fleischmann 1971). Many of the races have been used in previous genetic work involving *A. sterilis*. The rust

cultures which ranged from widely virulent to widely avirulent were selected for the purpose of identifying the presence of major and minor genes. Cultures of races 326, 305, 295, 264, 259, 239, 211 and 203 were used. The reactions of the differential host varieties to the 12 cultures of crown rust used in this study are presented in Table 3.

All the rust cultures used were obtained from the Agriculture Canada Research Station, Winnipeg, and were taken from stored material which had been verified and assigned a Vacuum Dried (VD) storage reference number. Each culture was removed from the vacuum dried tube and a concentrated suspension of urediospores in Amsco* (an odorless insecticide base oil) was sprayed on 10-20 pots of Victory seedlings and on both the standard differential set (Simons and Murphy 1955) and nine substituted single gene resistance lines (Harder and McKenzie 1974). The excess oil on the plants was allowed to evaporate off for approximately one hour before the plants were placed into moist incubation chambers. The plants were fogged with a fine spray of water and sealed in the chamber for 24 hours at a temperature of 60^{o} - 65^{o}F.

After the incubation period the plants were all transferred to an isolated compartment where the temperature was maintained at 60^{o} - 70^{o}F and natural lighting was supplemented with fluorescent lighting for 18 hours a day.

Two weeks later when the rust pustules had developed to a maximum size, the sets were scored and if the race keyed out on the differential set with little or no contamination, then the increase on the Victory plants was used. The urediospores were collected and used within a few days.

---

* Amsco - Chemical trade name, Union Oil Co. of California.

TABLE 3

Infection Type[1] of the Standard[2] Cultivars and Substituted Single Gene Lines to the Twelve Crown Rust Cultures Uses

Lines or Cultivars	Crown Rust Race and Accession (VD) Number											
	264 (VD-1269)	326 (VD-1713)	305 (VD-1479)	239 (VD-1714)	259 (VD-1669)	295 (VD-1687)	203 (VD-1676)	211 (VD-1679)	264 (VD-1784)	264 (VD-1700)	203 (VD-1689)	295 (VD-1692)
Anthony	4	4	4	;	4	4	4	;	4	4	4	4
Victoria	4	4$^-$	4	;	4	;1	;1	;1$^+$	4	3$^+$	2	;1
Appler	4	4	4	;	4	4	3$^+$	4	4	4	4	4
Bond	4	4	;	;	;	4	4	4	4	4	4	4
Landhafer	4	4	4	;	;1	4	2	;	3$^+$	4	2$^+$	3$^+$
Santa Fe	4	3$^+$	4	;	;1	4	;1$^+$	;	4	3$^+$	2	3
Ukraine	3$^+$	4	;1	;	4	3$^+$	4	3$^+$	4	4	3$^+$	3
Trispernia	4	;1$^-$	4	;	;1	;1$^+$	;1$^-$	;	4	4	1$^+$	;1
Bondvic	3$^+$	;	4	;	1$^+$	;2	1$^+$	;	4	3$^+$	1$^+$	1
Saia	;	;	;	0;	;	0;	;	0;	;N*	0;	;	;
Pc-35**	;1	;	;1	;1	;	4	;1$^+$	4	;N	4	4	3$^-$
Pc-38	;	4	;	;1	;	;	;	;	;	;	;	4
Pc-39	;	;	4	;	;	0;	;	;	4	;	;	;
Pc-40	4	;1$^-$	4	;	;1$^-$	1$^+$	;	;	4	4$^-$	2$^+$	;
Pc-45	;1	0;	4	;	0;	;	;	;	4	;	;	;1
Pc-46	;	;	4	;N*	;	;	;2	;	4	;	;C*	;
Pc-47	2$^+$	2$^-$	4	;1$^+$	3	;	3$^-$	3	4	2	2	2
Pc-48	;1	;	3$^+$	;	;	0;	0;	;	3	;	;	;
Pc-50	0;	0;	0;	;	;	0;	0;	;	0;	;	0;	0;

[1] 0 = immune, ; = fleck, 1 = very resistant, 2 = moderately resistant
3 = moderately susceptible, 4 = susceptible.

[2] Ten cultivars used as crown rust differentials by Simons and Murphy (1955).

* N - necrotic C = chlorotic

** Single gene lines used as differentials by Harder and McKenzie (1974).

Pc-39 was used instead of Victory for the increase of race 305 and race 264 (VD-1784). This insured purity since these were the only two races known to attack Pc-39.

3.3 Method of Seedling Inoculation in Greenhouse Beds

The method of inoculation used for the rust increases, was also used on the greenhouse beds to inoculate the hybrid populations with freshly collected urediospores of a pure rust culture. After inoculation the bed was covered with a polyethylene sheet which served as the rust incubation chamber.

3.4 Recording of Rust Reactions

Recording infection types on the test seedlings and differential sets was in accordance with the system proposed by Stakman and Levine (1922) and adopted for crown rust by Murphy (1935). Infection types ranged from Type 0; very resistant, to a type 4 highly susceptible reaction.

3.5 Crosses Made

The four rust resistant *A. sterilis* parents CAV 4963, CAV 1964, CAV 1358, and CAV 1376 were each crossed to the susceptible parent 'Pendek', in the spring of 1972. Four seeds of each cross were planted in a growth cabinet, one seed to a 6-inch pot. In December, 1972, these F_1 plants were crossed again to Pendek, to produce approximately one hundred and fifty seeds from each backcross. The backcross F_1 plants were grown in greenhouse beds spaced four inches apart. Adequate seed was produced on most of these F_1 plants to conduct the inheritance studies.

3.6 Seedling Rust Tests

In September 1973, F_2 seedlings of 105 backcross families from each cross were tested to crown rust. Approximately 15 seeds from each family were planted about one-half inch apart in rows four inches apart in greenhouse beds. The seedlings were inoculated with race 264(VD-1269) at the full one leaf stage, using the procedure described previously. Race 326 (VD-1713) was applied one week later when the plants were at the two to three leaf stage and the first rust was flecking on the first leaf. The second inoculation could be easily distinguished from the first, when the two separate readings were recorded. Race 305(VD-1479) and race 239 (VD-1714) were applied respectively to the first and second leaf of a second planting. After the two seedling tests were recorded on the second planting, the plants were thinned to eight plants per family and allowed to continue growing. At a stage just before flowering, the flag leaves were inoculated in the same manner as the seedlings with race 305 (VD-1479). Rust reactions were recorded 14 days later.

A number of families with adequate seed from each cross were selected for further rust tests. From the CAV 4963 backcross, 14 backcross families were selected, eight of which had been susceptible and six that had been segregating in the previous tests. From the CAV 1964 backcross 26 families were selected. Six families which segregated in reaction to three of the four rust cultures used; six families which segregated in reaction to only one culture of rust; six families which segregated to all four cultures of rust and eight families that were susceptible to all four cultures. CAV 1358 and CAV 1376 each had 14 of their backcross families chosen for more rust tests including the most resistant and the

most susceptible. The additional crown rust cultures used were races: 259(VD-1669), 295(VD-1687), 264(VD-1784), 264(VD-1700), 203(VD-1676), 211(VD-1679), 203(VD-1689) and 295(VD-1692).

3.7 Adult Plant Rust Tests

Studies were undertaken on a small scale, to determine if plants resistant in the seedling stage gave a resistance reaction in the adult plant stage.

Six F_3 plants from each resistant F_2 backcross plant which previously had been grown to maturity, were grown in each of five six-inch pots. Eight F_2 plants from each of the corresponding backcross families were also grown in each of five pots. Four backcross lines from the CAV 4963 cross and five lines from the CAV 1964 cross were grown in this manner, along with a total of five pots of each wild oat parent. When the flag leaves had emerged on the plants each of the five lots were inoculated in the usual way with one of the five different rust cultures. The cultures used were races 295(VD-1692), 264(VD-1269), 264(VD-1700), 305(VD-1479) and 326(VD-1713). Rust reactions were recorded 13 days later.

3.8 Selection and Selfing

From the backcrosses involving CAV 1358 and CAV 1376, F_2 plants rusted in the adult stage with race 305, which showed the least susceptible reaction (type 3^+-4^-) and a fully susceptible plant from the same family were grown out to maturity and the seed from each was planted in the greenhouse for further rust tests. Race 264(VD-1700) was applied at the one to two leaf stage. Race 305 was not used for further tests

in order to prevent spore escape and its establishment in commercial fields. From each susceptible line, the most susceptible plant was selected and from each resistant line the plant which showed the most resistant reaction was selected. All the selected F_3 plants were grown to maturity and each was harvested separately. In August 1974 the progeny of these F_3 plants were retested to race 264(VD-1269) in the seedling stage along with the progeny of resistant F_2 plant from the same crosses selected in the 1974 rust nursery.

3.9 Field Rust Nursery 1974

In 1974 F_2 backcross families from all four backcrosses along with all the parents and the Pc differential lines were sown in a crown rust nursery, in Winnipeg. The nursery was artificially inoculated with a mixture of crown rust races 264(VD-1269), 264(VD-1700), 259(VD-1669), 295(VD-1692) and 326(VD-1713). Because of the dry season, crown rust developed slowly and was only moderately heavy when the leaves began to senesce.

3.10 Test for Allelism (or Close Linkage) of Rust Resistance Genes

In February 1973 the *A. sterilis* collections CAV 4963, CAV 1964, CAV 1358, CAV 1376, were each crossed with lines of oats containing *A. sterilis* derived resistance genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-47, Pc-48 and Pc-50. The pedigree of the lines containing the Pc genes are shown in Table 4 and future reference in this study to these lines will often only refer to the gene to identify the oat line.

TABLE 4

Pedigree of *Avena sterilis* Resistance Derived Lines

Crown Rust Rust Resistant Gene	Pedigree
Pc-35	D 137 x Pendek[2]
Pc-38	CAV 2468 x Pendek[2]
Pc-39	CAV 5165 x Pendek[2]
Pc-40	CAV 4992 x Pendek[2]
Pc-45	CAV 5050 x Pendek[2]
Pc-46	CAV 5115 x Pendek[2]
Pc-47	C.I. 8081 x Pendek[2]
Pc-48	CAV 5041 x Pendek[2]
Pc-50	(Pendek x CAV 2463) x Pendek

Four seeds from each cross, two per six-inch pots, were planted in growth cabinets in May 1973. As the panicles of the F_1 plants emerged they were covered with crossing bags to insure pure selfed seed for each cross.

One hundred to 200 F_2 seeds per cross, involving CAV 4963 and CAV 1964, were planted in greenhouse beds. The crosses involving Pc-40 were inoculated with race 295(VD-1692). All the remaining crosses were inoculated with race 264(VD-1269).

3.11 Classification for Awn Type and Kernel Color

Seed color was determined visually on the progeny of the F_1 backcross plants and the seeds were classified as white, grey or black. Backcross families were classified in the field as either segregating for the strong awn abscission kernel base complex or as uniform for the awnless, tame kernel base complex present in Pendek.

3.12 Test for Goodness of Fit

The Chi-square goodness of fit method was used to obtain the probability value to test the validity of the ratios obtained. Yates' correction factor was used when the smallest expected population class was less than 30.

CHAPTER 4

RESULTS

4.1 Greenhouse Seedling Rust Tests

The parental reactions to the crown rust races used in this study are presented in Table 5. Seedling tests were conducted on the parents with the same crown rust races at the same time and place as the tests on the F_2 backcross families.

4.1.1 CAV 4963

In the Pendek[2] x CAV 4963 cross 46 families segregated for resistance to races 264(VD-1269), 326(VD-1713), 305(VD-1479), and 239(VD-1714) and 59 families were susceptible (1:1 ratio, P = .20-.30), indicating the presence of a single major gene conditioning resistance to these races. Individual backcross families that segregated to one race segregated to the other three races while the susceptible families were always susceptible.

Counts of resistant and susceptible plants in the segregating families gave a good fit to a 1 resistant:3 susceptible ratio to three of the four races (Table 6) indicating that the resistance gene was recessive. However, the gene was not completely recessive since there were intermediate types which were almost susceptible and were therefore classed with the susceptible plants. With race 239 there was an excess of resistant plants and therefore it was not possible to determine whether the gene for resistance behaved as a dominant or recessive to this race. The heterozygous plants in segregating families may have given a slightly higher, although still variable, reaction to race 239 either due to changes of light, temperature or some other unknown factors, which made

TABLE 5

Reaction Types Produced by Crown Rust Infection of Four *Avena sterilis* Collections

Crown Rust Test Race	CAV* 4963	CAV 1964	CAV 1358	CAV 1376
		Reaction Types		
203(VD-1676)	;	;	2+ - 3^{-}	1
203(VD-1689)	0; - ;	;	2	1^{+}
211(VD-1676)	;	;	;1^{+}	;1
239(VD-1714)	0; - ;	0;	;1	;1
259(VD-1669)	;	;1^{+}	3	3
264(VD-1269	;	;	;1	;1
264(VD-1700)	;	;	;1	;1
264(VD-1784)	;1**	0; - ;	2^{+}	;2^{+}
295(VD-1687)	;	;	2 - 3	2^{+} - 3
295(VD-1692)	;N	;	1^{+}	;1
305(VD-1479)	;1 - 2^{+}	0; - ;	3^{-}	2^{+}
305(VD-1479)***	4	;	;2	;2
326(VD-1713)	;1	;	2	1^{+}

* CAV - Canadian *Avena*.

** Type 4 reaction on some upper leaves.

*** Adult plant test.

TABLE 6

Results of Crown Rust Tests on Segregating F_2 Backcross Populations Involving *Avena sterilis* Collection CAV[1] 4963

Crown Rust Races	Plant Stage Inoculated	Number of Plants — Reaction Types				Ratio	P. Value
		R*	MR	MS	S		
264(VD-1269)	1st Leaf	145		202**	254	1:3	.50-.70
326(VD-1713)	2-3 Leaf	150		66**	393	1:3	.70-.90
305(VD-1479)	1st Leaf	46	120***		517	1:3	.50-.70
239(VD-1714)	2-3 Leaf	125	99***	50**	440	1:3	< .001

1 CAV - Canadian *Avena*.

* R = Type ;1^- resistant, MR = type $1:2^-$ moderately resistant, MS = type 2^+3^- moderately susceptible, S = type 4 susceptible.

** Included with susceptible class.

*** Included with resistant class.

it difficult to determine in which class they should be placed. A modifier gene or genes may also have affected the reaction of heterozygous plants to race 239. These plants were inoculated at the two to three leaf stage and therefore the age of the plant may have had some effect on the expression of the gene in the heterozygous plants as was found by McKenzie *et al.* (1968), and McKenzie *et al.* (1970) with recessive oat stem rust resistance genes.

Six segregating and eight susceptible F_2 backcross families were tested against eight other isolates of crown rust. All of the families tested gave the same results as they had to the first four races. This indicated that the single gene conditioned resistance to all 12 cultures. This gene conditioned a fleck reaction to all rust cultures except race 305 where the reaction was a (;1) to type (2), similar to that of the CAV 4963 parent.

4.1.2 CAV 1964

In the Pendek[2] x CAV 1964 cross, 57 F_2 backcross families segregated to races 264, 326 and 305, while 48 were susceptible and this is a good fit to a 1:1 ratio (P:.30-.50). Thirty-one of the families that segregated to races 264, 326 and 305, also segregated to race 239 (Table 7) while 26 families that were susceptible to the first three races segregated for resistance to race 239. Twenty-six families that segregated to the first three races were susceptible to race 239. Twenty-two F_2 backcross families were susceptible to all the races tested.

These results fit a 1:1:1:1 ratio (P:.7-.9) which indicates independent assortment of two genes for crown rust resistance. A major gene conditioned resistance to races 264, 326 and 305, while a second gene conferred

TABLE 7

Crown Rust Reaction of CAV[1] 1964 F_2 Backcross Families and Probable Resistance Genotypes

Possible Genotypes	Reaction of Families to Rust Races				
	Race 264	Race 326	Race 305	Race 239	No. of Families*
AABB) AABb) AaBB) AaBb)	Seg.**	Seg.	Seg.	Seg.	31
AAbb) Aabb)	Seg.	Seg.	Seg.	S	26
aaBB) aaBb)	S	S	S	Seg.	26
aabb	S	S	S	S	26

1 Canadian *Avena*.

* P value for fit to 1:1:1:1 ratio is .70-.90.

** Seg. = segregating; S = susceptible.

resistance to race 239. Both genes conditioned a (;) reaction to the race or races against which they were effective.

Counts of resistant and susceptible plants in the segregating F_2 backcross families to race 305 gave a good fit to a 3:1 ratio (Table 8), where plants with intermediate infection types were included with the resistant. It appears that the gene conferring resistance is nearly dominant. There was a poor fit to a 3 resistant:1 susceptible ratio with the tests involving crown rust races 264 and 326. Both of these rust races were applied to the same plants, race 264 to the first leaf and race 326 to the second leaf.

The test with race 239 gave a good fit to a 3 resistant:1 susceptible ratio of plants within the segregating families (Table 8), which indicates that this second gene in CAV 1964 is also nearly dominant. The moderately resistant intermediate plants were classed with the resistant ones.

Selected F_2 backcross families which segregated for the major gene only, families which segregated for the second gene only, families with both genes, and families with neither gene were tested with eight more rust cultures. With seven of the eight remaining crown rust cultures there was segregation in only those families which contained the major gene. With race 203(VD-1676) there was segregation in the families which contained either and both of the genes. There was no segregation for resistance within any of the susceptible lines and therefore it appears there are no other seedling crown rust resistance genes present.

The major gene in CAV 1964 confers resistance to eleven of the twelve rust cultures while the second gene confers resistance to only two of the twelve rust cultures.

TABLE 8

Results of Crown Rust Tests on Segregating F_2 Backcross Populations Involving CAV[1] 1964

Crown Rust Cultures Used**	Number of Plants: Reaction Types: Resistant*	Susceptible	Ratio	P. value
264(VD-1269)	542	258	3:1	< .001
326(VD-1713)	537	273	3:1	< .001
305(VD-1479)	661	240	3:1	.20-.30
239(VD-1714)	634	196	3:1	.30-.50

1 CAV - Canadian *Avena*.

* Moderately resistant types (;1-1) included.

** Races 264 and 326 were inoculated on the same plants.
Races 205 and 239 were inoculated on the same plants.

4.1.3 CAV 1358 and CAV 1376

The Pendek^2 x CAV 1358 and Pendek^2 x CAV 1376, F_2 backcross families were tested to four races of crown rust. The resistant parents' reactions are shown in Table 5. In both crosses most of the F_2 backcross families showed a fully susceptible type of reaction, but within some of the families there were a few plants which appeared to exhibit less susceptibility. There was no consistency from test to test as to which families had a few plants with slight resistance. From these tests it was not possible to determine any genetic ratios.

4.2 Greenhouse Adult Plant Tests

One hundred and five F_2 backcross families from each of the four crosses, plants previously tested in the seedling stage to races 305 and 239, were inoculated with crown rust race 305 after the flag leaves had emerged.

4.2.1 CAV 4963

All the Pendek^2 x CAV 4963 F_2 plants in the test were susceptible including the plants which had shown very good for seedling resistance. Since it appeared that the seedling resistance of CAV 4963 did not continue through into the adult plants, a small rust test using five rust cultures was conducted to determine reaction of adult plants in four Bc_1F_2 segregating families and four corresponding resistant F_3 lines. Inoculated at the flag leaf stage, the F_3 lines were all homozygous for resistance to races 264, 295, 326 and to a second culture of 264. But with race 305, all of the plants were susceptible.

It appears that the seedling resistance gene confers resistance in the adult plant stage to some races but appears to lose its effectiveness

against race 305.

4.2.2 CAV 1964

The same Pendek^2 x CAV 1964 F_2 families which segregated for resistance to race 305 in the seedling stage also segregated for resistance in the adult plant stage to this race.

Additional adult plant tests with five crown rust cultures on three segregating F_2 backcross families and three selected F_3 lines gave the same results as in the seedling stage. Within the F_2 families there was segregation for resistance while all the F_3 lines showed a homozygous resistant reaction in all the tests. This indicates that it was possible to recognize plants homozygous for the resistance factor and select for them successfully, again indicating that the gene is not completely dominant.

4.2.3 CAV 1358 and CAV 1376

Most of the Pendek^2 x CAV 1358 and Pendek^2 x CAV 1376 backcross families inoculated in the flag leaf stage with race 305 were completely susceptible. Within each of 38 families from the two crosses there were some plants which showed some degree of resistance. The most resistant and the most susceptible plants from each of 14 families were selected and grown to maturity. The Bc_1F_3 seedlings derived from these 14 families were inoculated with race 264(VD-1700) and the most resistant plant from each resistant selection along with the most susceptible plant from each susceptible selection were again selected and grown to maturity. This procedure was repeated again in the Bc_1F_4.

In the F_2 families the plants showing resistance to race 305 were in the moderately susceptible range. After two generations of selfing

the most resistant plant selections showed from a fleck to a type (1) reaction to race 264(VD-1700). While in most of the lines there was a complete range of infection types, a few lines showed only the more resistant types. The susceptible selections were consistently less resistant than the resistant selections and ranged from a (2) type to completely susceptible type. The most resistant plant from each of the ten best backcross families were selected in the field rust nursery, five from the cross involving CAV 1358 and five from the cross involving CAV 1376. The progeny of these plants were tested in the seedling stage at the same time as the selected Bc_1F_4 seedlings. The best resistance level obtained among the progeny of these ten plants was a $(1)^+$ infection type.

Further tests are needed to determine the mode of inheritance of the resistance present in these two wild oat collections. It would appear that a number of minor additive genes are conferring resistance. As more of these genes become stabilized in a homozygous condition, they produce greater resistance to crown rust.

4.3 The Field Rust Nursery

The CAV 4963 F_2 backcross material seeded in the artificially inoculated field nursery was scored for resistance to crown rust. The same Pendek[2] x CAV 4963 families that segregated for resistance in the seedling greenhouse tests also segregated in the field. The most resistant plants to the mixture of races, ranged from very resistant in some families to moderately resistant in other families. However, eleven families which expressed no resistance in the seedling greenhouse tests had some plants which were scored as moderately resistant.

The gene that conditioned greenhouse seedling resistance also conditioned field resistance. The eleven greenhouse seedling susceptible families which showed moderate resistance in the field possibly contained factors for adult plant resistance which went unnoticed in the greenhouse adult plant tests.

Field rust readings on Pendek^2 x CAV 1964 F_2 material indicated that the major resistance gene did not condition as high a degree of resistance to crown rust as was observed in the greenhouse. In the greenhouse a fleck reaction was observed and the best comparable field reaction appeared as a (;1) type. There also did not appear to be any sign of resistance conditioned by the minor gene, within families which segregated, in greenhouse tests, for only the minor gene. This was not too surprising since some of the same cultures virulent on this gene in the greenhouse were used in the field mixture of races. The races used, however, were all avirulent on the major gene.

Pendek^2 x CAV 1358 and Pendek^2 x CAV 1376 F_2 backcross families with about 20 plants in each family were tested in the rust nursery even though seedling and adult plant greenhouse tests did not indicate the presence of resistance. Of the one-hundred and four families in the CAV 1358 backcross there were four families which showed an almost uniform moderately resistant-moderately susceptible reaction within each family, with one or two plants showing slightly better resistance. Of the 113 CAV 1376 backcross families, five families were scored moderately resistant-moderately susceptible, with a few plants in each family showing a higher degree of resistance.

As there were only a few families with a moderate type of resistance,

when compared to the immune type resistance of the wild oat parents CAV 1358 and CAV 1376, and since most of the families conditioned no resistance, would again indicate that the resistance in the parents could be conditioned by a number of genes producing an additive or complementary effect, as has been described by Sharp and Volin (1970), for wheat stripe rust.

4.4 Intercrosses with Strains Containing Other *A. sterilis* Derived Crown Rust Resistance Genes

Results of rust tests on F_2 populations of crosses of CAV 4963 and CAV 1964 with lines possessing crown rust resistance genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-47, Pc-48 and Pc-50, are shown in Table 9. The tests were conducted on the progeny of three F_1 plants from each cross. Several hundred seeds were expected from each of the F_1 plants, but due to high sterility there were less seeds produced than had been expected. Poor germination of some of this seed further reduced some of the already small populations.

The crosses involving Pc-40 were tested with race 295(VD-1692) and the remaining crosses were tested with race 264(VD-1269). Crown rust susceptible plants were obtained in every cross and therefore there was no evidence of allelism of the major gene in CAV 4963 and CAV 1964 with any of the Pc genes studied.

Homogeneity Chi-square tests were conducted on each of the crosses involving CAV 4963. The progeny of the three F_1 plants within each cross were found to be homogeneous and as a result, the data within each cross was pooled (Table 9).

The tests on crosses of CAV 4963 with lines possessing Pc-35, Pc-38,

TABLE 9

Results of Seedling Tests on Crosses Between CAV[1] 4963 and CAV 1964 and Nine Lines Possessing *Avena sterilis* Derived Resistance Genes

Cross	Crown Rust Race	Number of Plants		Ratio	P. Value
		Resistant	Susceptible		
Pc-35 x CAV 4963	264	55	4	15:1	.95
Pc-38 x CAV 4963	264	99	9	15:1	.30-.50
Pc-39 x CAV 4963	264	77	2	15:1	.20-.30
Pc-40 x CAV 4963	295	137	7	15:1	.50-.70
Pc-45 x CAV 4963	264	93	28	13:3	.20-.30*
Pc-46 x CAV 4963	264	99	12	15:1	.10-.20
Pc-47 x CAV 4963	264	50	7	15:1	.05-.10**
Pc-48 x CAV 4963	264	111	16	13:3	.05-.10*
Pc-50 x CAV 4963	264	126	13	15:1	.10-.20
Pc-35 x CAV 1964	264	118	6	15:1	.90
Pc-38 x CAV 1964	264	127	7	15:1	.70-.90
Pc-39 x CAV 1964	264	27	1	15:1	.70-.90
Pc.40 x CAV 1964	295	138	7	15:1	.50-.70
Pc-45 x CAV 1964	264	90	11	15:1	.05-.10
Pc-46 x CAV 1964	264	112	7	15:1	.95
Pc-47 x CAV 1964	264	113	8	15:1	.95
Pc-48 x CAV 1964	264	113	11	15:1	.20-.30
Pc-50 x CAV 1964	264	155	11	15:1	.95

1 CAV - Canadian *Avena*.

* Would not readily fit a 15:1 ratio.

** 13:3 ratio P. value = .20-.30.

Pc-39, Pc-40, Pc-46, Pc-47 and Pc-50, all gave a good fit for a 15:1 ratio, demonstrating the expression of the CAV 4963 gene and the Pc genes as dominant genes for crown rust resistance. In the cross involving the Pc-47 gene, which is incompletely dominant (Fleischmann *et al.* 1971b), a good fit was obtained to a 13:3 ratio, indicating independent segregation of a dominant and a recessive gene. In the crosses with the lines containing Pc-45 and Pc-48 there was also a good fit to a 13:3 ratio, from which it appeared that one of the genes possibly the one from CAV 4963 expressed resistance as a recessive while Pc-45 and Pc-48 were dominant. The apparent inconsistency in dominance of the resistance gene in CAV 4963 cannot be explained.

The rust tests on the F_2 progeny of crosses of CAV 1964 with lines possessing the nine Pc-genes, all fit a 15:1 ratio (Table 9) indicating that the CAV 1964 gene and each Pc gene acted as dominant genes and that the gene in CAV 1964 was not closely linked to any of the Pc genes.

The F_1 progenies of the cross involving Pc-39 x CAV 1964 were extremely small but each of the three plant progenies when inoculated with race 264(VD-1269) produced results as follows: one gave 3 resistant and 1 susceptible; a second gave 8 resistant; the third gave 16 resistant plants. Because the total population and especially the susceptible population was so small, further tests were conducted to obtain more proof of gene segregation. The progeny of the susceptible F_2 plant were tested with race 264 and were all susceptible. The progeny of six of the resistant F_2 plants were also tested with race 264 and segregation for susceptibility occurred in two of the F_3 lines, which is close to what would be expected when two dominant genes are segregating.

The progeny of the lines containing the Pc-genes used in the intercrosses with the two *A. sterilis* collections were tested for purity. The Pc-35, Pc-38, Pc-40, Pc-45, Pc-46, Pc-47, Pc-48 and Pc-50 sources were all pure, as was the progeny of the Pc-39 plants used in the CAV 4963 cross. The progeny of the Pc-39 used in the cross with CAV 1964; was the bulk of seeds from two plants grown in the same pot. When race 305 was applied, approximately one-half of the plants showed the susceptible reaction expected of Pc-39. The resistant plants could not have Pc-39 and could be any one of Pc-35, Pc-38 or Pc-50. Due to a shortage of this probably mixed Pc seed, a test was conducted with the F_3 plants of the Pc-39 x CAV 1964 cross, to determine if Pc-35, Pc-38, Pc-50 or if the Pc-39 gene was actually used in the cross.

The seed from seven resistant F_2 plants involving the line containing Pc-39 x CAV 1964 cross was bulked and 36 F_3 seedlings were tested to race 305 which is virulent on Pc-39 but not on CAV 1964. The fifteen susceptible plants were divided into a group of seven and a group of eight. The group of seven were then tested on the fourth leaf to race 326 and the group of eight were tested to race 264(VD-1700). There were three resistant plants and four susceptible plants to race 326, and three resistant plants and five susceptible plants to race 264(VD-1700). All plants susceptible to race 305 cannot have the gene from CAV 1964, Pc-35, Pc-38 or Pc-50 which are all resistant to 305. The fact that these same plants segregated for resistance to races 326 and 264 proves the presence of a gene for resistance which could not be Pc-35, Pc-38 or Pc-50. It therefore appears most probable that the gene was Pc-39 and that the cross involved the line with Pc-39 and CAV 1964.

4.5 Seed Color and Awn Type

The inheritance of seed color was studied in crosses involving three of the four *A. sterilis* collections. CAV 1964 was a white seeded strain. The inheritance of the strong geniculate awn, abscission spikelet separation complex was also looked at in the crosses with all four wild oat collections. Future references to the complex of strong geniculate awns always present in those plants where the spikelet separated by abscission, for simplicity sake, the author will refer to it as segregation for awns.

Pendek[2] x CAV 4963 F_2 backcross families segregated for color in a ratio of two black:one grey:one white, as shown in Table 10. This indicates the presence of two genes for color, one gene for black hull and one gene for grey hull color. Grey and white families were present in both the resistant and susceptible families indicating that the genes for hull color are not closely linked to the gene for crown rust resistance.

TABLE 10

Results of Classification for Hull Color of F_1 Progenies from Backcrosses of Four *Avena sterilis* Collections to Pendek

Crosses	Number of F_1 Progenies			Ratio	P. Value
	Black	Grey	White		
Pendek[2] x CAV*4963	74	27	30	2:1:1	.30-.50
Pendek[2] x CAV 1964		ALL WHITE			
Pendek[2] x CAV 1358		49	73	1:1	.01-.05
Pendek[2] x CAV 1376		63	61	1:1	.90

* CAV - Canadian *Avena*.

The CAV 4963 F_2 backcross families shown in Table 11 gave a good fit to a ratio of one family segregating for awns to one family homozygous for a fracture type of spikelet separation or awnless character. This indicates the presence of one gene segregating for awns. A good fit was also obtained for independent segregation for awns and crown rust resistance. There were 30 awned susceptible: 25 awned resistant:28 awnless susceptible:21 awnless resistant (1:1:1:1 ratio, P = .50-.70, Table 12).

The Pendek[2] x CAV 4963 F_2 backcross families segregating for the awned character appeared to segregate independently of black seed color (Table 12) with a good fit to a one black awned:one black awnless ratio (P = .10-.20). The gene for grey color and awn type appeared to be closely linked with only 2.04% (Standard error $\pm$ 2.00%) crossover occurrence.

TABLE 11

Results of Classification for Awns on F_2 Families from Backcrosses of Four *Avena sterilis* Collections to Pendek

Crosses	Number of Families		Ratio	P. Value
	Seg. for Awns	Awnless		
Pendek[2] x CAV* 4963	55	49	1:1	.50-.70
Pendek[2] x CAV 1964	53	52	1:1	.90-.95
Pendek[2] x CAV 1358	44	60	1:1	.10-.20
Pendek[2] x CAV 1376	52	61	1:1	.50

* CAV - Canadian *Avena*.

TABLE 12

Results of Classification for Crown Rust Resistance, Hull Color and Presence of Awns, of Progenies from Backcrosses of Four *Avene sterilis* Collections to Pendek

Crosses	*Rust Class	Seg. Awned Color			Awnless Color		
		Black	Grey	White	Black	Grey	White
Pendek^2 x CAV**4963	Seg.	16	8	1	7	0	12
	Susc.	17	13	0	16	0	12
Pendek^2 x CAV 1964	Seg. all Races			13			18
	Seg. 264			16			10
	Seg. 239			12			14
	Susc.			12			10
Pendek^2 x CAV 1358	--		31	13		11	49
Pendek^2 x CAV 1376	--		45	7		13	48

* Seg. - segregating; Susc. - susceptible; - all families.

** CAV - Canadian *Avena*.

In CAV 1964 the awned character was also conditioned by a single gene as was evident from the good fit to a ratio of one segregating awned:one awnlesss among the F_2 backcross families (Table 11). There was also a good fit for independent segregation of the major rust resistance gene and the gene for awns (28 resistant-awnless, 29 resistant-awned, 24 susceptible awnless, 24 susceptible awned, 1:1:1:1 ratio P = .50-.70, Table 12).

Although the Pendek^2 x CAV 1358 backcross F_1 backcross progenies did not give a very good fit to a 1:1 ratio for grey versus white hull color, there is most probably only one gene segregating as shown in Table 10. The awned character was controlled by one gene as was evident by the good fit of the F_2 backcross families to one segregating for awns to one awnless ratio shown in Table 11.

Awned seed in the CAV 1358 backcross was found which had white hulls and awnless seed was obtained which had grey hulls. The data from the small population in the CAV 1358 backcross showed that awns and grey color appeared to be linked with 23.07% (Standard error $\pm$ 4.11%) crossing over (Table 12). The presence of only white, awnless seed was observed on the selected resistant F_4 lines, and so it appears that rust resistance is inherited independently of the other two characters.

The Pendek^2 x CAV 1376 backcross F_2 families, shown in Table 10 gave an excellent fit to a 1:1 ratio for hull color. It is evident that one gene controls grey seed color in this wild oat. A good fit to a ratio of one F_2 backcross family segregating for awns to one awnless family, indicates one gene controls the presence of this character in CAV 1376 (Table 11). Linkage between grey color and awn type in CAV 1376 was 17.69% (Standard error 3.59%).

Seed from crown rust resistant CAV 1376 backcross F_4 plants was obtained which was white and awnless also indicating that resistance can be inherited independently of both of the other characters.

CHAPTER 5

DISCUSSION

The inheritance of crown rust resistance present in four *A. sterilis* collections was studied using F_2 backcross families. Knott and Anderson (1956) found that the study of F_2 backcross families had advantages over the study of F_2 plants and F_3 lines since in backcrosses the ratios are simpler, it is easier to separate genes for resistance and study their effects singly; and it is easier to separate segregating families from non-segregating families than it is to accurately determine ratios of plants within families.

The results obtained on the inheritance of resistance of CAV 4963 and CAV 1964 conformed to a Mendelian manner of inheritance. One major gene in each collection conditioned resistance to a large number of races; such results are similar to those reported for other genetic studies with *A. sterilis* (Fleischmann and McKenzie 1968; Fleischmann *et al.* 1971a, b).

Many investigators have described oat varieties which reacted similarly to specific crown rust races in both seedling and mature stages and other varieties which were susceptible as seedlings but resistant as adults. Dinoor and Wahl (1963), while screening wild oat collections, found that some plants which were highly resistant in the seedling stage became susceptible as the plant matured. This is similar to results obtained in this study with race 305 on CAV 4963. Upadhyaya and Baker (1962) found seedling resistance in Ukraine due to a single incompletely dominant factor pair, which conferred no resistance to the adult plant. A similar situation occurred with the Kyto stem rust resistance gene Pg-12 (Martens *et al.* 1968). Duff (1954) reported finding wheat with seedling resistance and mature plant susceptibility to *P. graminis*, in Kenya.

Crown rust resistance in CAV 4963 was conditioned in the form of an incompletely recessive major gene, which is similar to results obtained by McKenzie and Fleischmann (1964) on the *A. sterilis* collections D60 and D137. The recessiveness of the gene appeared to change to incomplete dominance with some rust races, as the leaves grew older. This is similar to the findings on the stem rust resistance gene Pg-13 by McKenzie *et al.* (1970).

The rust test with race 305 on CAV 4963 produced results where the resistance gene was effective in the seedling stage but appeared to become completely ineffective as the plants matured. One possible explanation why the CAV 4963 gene could have been ineffective is that the gene is perhaps part of a complex gene locus and that portion of the locus which conditioned resistance to this race may have been deactivated by some control system, as the plant grew older.

The seedling reaction type was similar to all races and therefore did not predict adult reaction in any way. It is not known how widely resistant the CAV 4963 gene may be since it was only tested to five rust cultures in the adult stage. More adult tests should be conducted to learn more about this resistance gene. The resistance of CAV 4963, when crossed with the lines containing the Pc-genes, was governed by one gene which appeared to be dominant in some crosses and recessive in others. This type of expression could have been due to different genetic backgrounds. Dyck and Samborski (1968) found similar results with the Lr_2 gene in wheat behaving as a dominant in one genetic background and as a recessive in another.

The cross CAV 4963 x CAV 1964 was not made and consequently it is not known if the major resistance genes in these wild oats are allelic.

The two genes are clearly distinct because they are differentiated by different crown rust races. The CAV 4963 gene appeared to be recessive or incompletely recessive, while the CAV 1964 gene appeared to be dominant.

The major genes of both CAV 4963 and CAV 1964 were inherited independently of the nine Pc genes previously isolated and presents no barrier in producing a combination of one or more of the Pc genes with either one of the newly described genes.

Test results from the CAV 1358 and CAV 1376 inheritance studies did not fit any obvious genetic ratio. They did not contain any major resistance genes. Based on selection for rust resistance for several generations it appeared as if several minor additive or complementary genes behaving mainly as recessives, could be responsible for conditioning resistance in CAV 1358 and CAV 1396. Sharp and Volin (1970) have shown a similar type of gene action for resistance to stripe rust in wheat.

In the field ten families from these two crosses were scored in the moderately resistant-moderately susceptible range with one or two plants conditioning better resistance. These families should have had some plants that were completely susceptible assuming that several recessive genes in the homozygous condition were required for resistance, but none were noted. Possibly environmental conditions, which caused many leaves to senesce shortly after the rust infected them resulted in difficulties of classification. Subsequent seedling tests of the best plant progenies from nine of these families showed considerable resistance.

Unfortunately, due to limited seed quantities only 105 F_2 backcross families from the CAV 1358 and the CAV 1376 crosses were tested for rust resistance. Hypothetically, if a plant required four homozygous recessive

genes to produce the parental resistant reaction, the chance is extremely small with the size of population used for the seedling rust tests, that such a plant would be found in a population of only 30 plants resulting from the two seedling plantings.

If CAV 1358 and CAV 1376 have the same resistance genes, intercrossing the best segregates from both would not improve the resistance, but if they have some genes that are different then an intercross could result in even better resistance.

Extensive, complicated work is still required to positively determine the mode of inheritance of resistance in CAV 1358 and CAV 1376. Use of resistance from the wild oats in a breeding program would be very difficult since it would behave as a quantitative character. The use of large populations would help in the selection of the good parental *A. sterilis* resistance in the F_2. The minor additive gene type resistance to crown rust in these or other collections of wild oats may well be an answer to the continuing problem of lasting resistance as this type of resistance should be more resistant to breakdown by any rust race than major gene resistance.

In the crosses between lines possessing the Pc-genes with CAV 4963 and CAV 1964 there was a very small amount of seed produced on the F_1 plants. This could be due to environmental conditions or due to chromosome interchanges resulting in sterility as was found by McKenzie *et al.* (1970). This resulted in conducting allelism and linkage tests with a minimum size of population. However, the presence of susceptible plants in all crosses despite the small populations indicates that close linkage probably did not occur.

The 11 F_2 backcross families in the Pendek[2] x CAV 4963 cross susceptible in the seedling stage, but with some resistance in the field nursery was similar to results obtained by McKenzie and Fleischmann (1964). This resistance was either overlooked in the seedling stage or was due to genes for adult resistance. These 11 families may possess resistance of a type similar to that found in the CAV 1358 and CAV 1376 crosses.

CHAPTER 6

SUMMARY

The inheritance of crown rust resistance in four *A. sterilis* collections was investigated. CAV 4963 contained one recessive or incompletely recessive resistance gene which conditioned resistance in the seedling stage to all cultures of rust tested. The gene appeared to be ineffective to one of the five cultures of rust tested, race 305, in the adult plant stage. This gene was not allelic to any of the nine resistance genes to which it was tested.

CAV 1964 contained two incompletely dominant genes for resistance to crown rust. One gene conditioned resistance to 11 of the 12 cultures tested while the second gene conditioned resistance to only two of the rust cultures. Reaction in the adult plant stage was similar to that obtained in the seedling stage when tested to five crown rust cultures. This gene was not allelic to any of the nine genes tested.

No major crown rust resistance genes were found in CAV 1358 and CAV 1376. There was good field resistance which appeared to be conditioned by a number of additive or complementary minor genes.

Seed color was conditioned by two genes in CAV 4963, one for black color and one for grey color. In CAV 1358 and CAV 1376 one gene conditioned grey seed color. The strong awn basal abscission complex appeared to be controlled by one gene or one gene complex in all four *A. sterilis* collections.

The genes for seed color and awn character did not appear to be linked to the crown rust resistance genes in any of the four *A. sterilis* lines. The gene for grey seed color in CAV 4963 appeared to be almost completely linked to the gene for awn production. In CAV 1358 and

CAV 1376 the genes for grey color and awns appeared to be linked at about 23 and 18 units, respectively.

LITERATURE CITED

Baum, B. R., T. Rajhathy, J. W. Martens, and H. Thomas. 1974. Wild Oat Gene Pool. Can. Dept. of Agric. (In Press)

Browning, J. A., and K. J. Frey. 1969. Multiline cultivars as a means of disease control. Ann. Rev. Phytopath. *7*: 355-382.

Browning, J. A., M. D. Simons, R. J. Frey, and H. C. Murphy. 1965. Regional deployment for conservation of oat crown rust resistance genes. Iowa State Univ. Agr. and Home Ec. Exp. Stat. Spec. Rept. No. 6A, pp. 49-56.

Chang, T. T. 1959. Analysis of genes conditioning resistance of oat varieties to races of *Puccinia coronata* Cda. var. *avenae* F. and L. Diss. Abs. 20: 1133. [Ph.D. Thesis, University of Minnesota, St. Paul, Minnesota, 1959].

Cochran, G. W., C. O. Johnston, E. G. Heyne, and E. D. Hansing. 1945. Inheritance of reaction to smut, stem rust and crown rust in four oat crosses. J. Agr. Res. *70*: 43-61.

Coffman, F. A., H. C. Murphy, and W. H. Chapman. 1961. Oat breeding. *In* F. A. Coffman (Ed.), Oats and Oat Improvement, pp. 263-329. American Society of Agronomy, Madison, Wisc.

Davies, D. W., and E. T. Jones. 1927. Further studies on the inheritance of resistance to crown rust (*P. coronata* Corda) in F_3 segregates of a cross between Red Rustproof (*A. sterilis*), and Scotch Potato oats (*A. sativa*). Welsh, J. Agr. *11*: 232-235.

Dietz, S. M., and H. C. Murphy. 1930. Inheritance of resistance to *Puccinia coronata avenae* p.f. III. Phytopath. *20*: 120. (Abstract)

Dinoor, A., and I. Wahl. 1963. Reaction of non-cultivated oats from Israel to Canadian races of crown rust and stem rust. Can. J. Plant Sci. *43*: 263-270.

Duff, A. D. S. 1954. Seedling resistance and mature plant susceptibility of wheat to *P. graminis* found in Kenya. Nature *173*: 779.

Dyck, P. L. 1966. Inheritance of stem rust resistance and other characteristics in diploid, *Avena strigosa*. Can. J. Genet. Cytol. *8*: 444-450.

Dyck, P. L., and F. J. Zillinsky. 1963.
Inheritance of crown rust resistance transferred from diploid to hexaploid oats. Can. J. Genet. Cytol. *5*: 398-407.

Dyck, P. L., and D. J. Samborski. 1968.
Genetics of resistance to leaf rust in the commom wheat varieties Webster, Loros, Brevit, Corina, Malakof and Centenaria. Can. J. Genet. Cytol. *10*: 7-17.

Finkner, R. E., R. E. Atkins, and H. C. Murphy. 1955.
Inheritance of resistance to two races of crown rust in oats. Iowa State Col. J. of Sci. *30*: 211-228.

Finkner, V. C. 1953.
Inheritance of susceptibility of *Helminthosporium victoriae* in crosses involving Victoria and other crown rust resistant oat varieties. Agron. J. *45*: 404-406.

Finkner, V. C. 1954.
Genetic factors governing resistance and susceptibility of oats to *Puccinia coronata* Corda var. *avenae*, F. and L. race 57. Iowa Agr. Exp. Sta. Bull. 411: 1040-1063.

Fleischmann, G. 1967.
Crown rust of oats in Canada in 1966. Can. Plant Dis. Surv. *47*: 11-13.

Fleischmann, G. 1968.
Crown rust of oats in Canada in 1967. Can. Plant Dis. Surv. *48*: 14-16.

Fleischmann, G. 1969.
Crown rust of oats in Canada in 1969. Can. Plant Dis. Surv. *49*: 91-94.

Fleischmann, G. 1971.
Crown rust of oats in Canada in 1970. Can. Plant Dis. Surv. *51*: 14-16.

Fleischmann, G., and R. I. H. McKenzie. 1968.
Inheritance of crown rust resistance in *Avena sterilis*. Crop Sci. *8*: 710-713.

Fleischmann, G., and R. J. Baker. 1971.
Oat crown rust race differentiation: replacement of the standard differential varieties with a new set of single resistance gene lines derived from *Avena sterilis*. Can. J. Bot. *49*: 1433-1437.

Fleischmann, G., R. I. H. McKenzie, and W. A. Shipton. 1971a.
Inheritance of crown rust resistance in *Avena sterilis* L. from Israel. Crop Sci. *11*: 451-453.

Fleischmann, G., R. I. H. McKenzie, and W. A. Shipton. 1971b.
Inheritance of crown rust resistance genes in *Avena sterilis* collections from Israel, Portugal, and Tunisia. Can. J. Genet. Cytol. *13*: 251-255.

Futrell, M. C., and G. W. Rivers. 1955.
The effect of temperature on the response of oats to race 216 of crown rust. Plant Dis. Reptr. *39*: 853-858.

Harder, D. E., and R. I. H. McKenzie. 1974.
Crown rust of oats in Canada in 1973. Can. Plant Dis. Surv. *54*: 16-18.

Hayes, H. K., M. B. Moore, and E. C. Stakman. 1939.
Study of inheritance in crosses between Bond, *Avena byzantina* and varieties of *A. sativa*. Minn. Agr. Expt. Sta. Tech. Bull. 137.

Jensen, N. F. 1961.
Genetics and inheritance in oats. *In* Coffman, F. A., (Ed.). Oats and Oat Improvement. pp. 125-206. American Society of Agronomy, Madison, Wisc.

Knott, D. R. 1971.
Can losses from wheat stem rust be eliminated in North America. Crop Sci. *11*: 97-99.

Knott, D. R., and R. G. Anderson. 1956.
The inheritance of rust resistance. I. The inheritance of stem rust resistance in ten varieties of common wheat. Can. J. Agr. Sci. *36*: 174-175.

Litzenberger, S. C. 1949a.
Nature of susceptibility of Helminthosporium *victoriae* and resistance to *Puccinia coronata* in Victoria oats. Phytopath. *39*: 300-318.

Litzenberger, S. C. 1949b.
Inheritance of resistance to specific races of crown and stem rust, to Helminthosporium blight, and of certain agronomic characters of oats. Iowa Agr. Expt. Sta. Res. Bull. 370: 453-496.

Marshall, H. G., and W. M. Myers. 1961.
A cytogenetic study of certain interspecific *Avena* hybrids and the inheritance of resistance in diploid and tetraploid varieties to races of crown rust. Crop Sci. *1*: 29-34.

Martens, J. W., R. I. H. McKenzie, and G. Fleischmann. 1968.
The inheritance of resistance to stem and crown rust in Kyto oats. Can. J. Genet. Cytol. *10*: 808-812.

McKenzie, R. I. H. 1961.
Inheritance in oats of reaction to race 264 of oat crown rust. Can. J. Genet. Cytol. *3*: 308-311.

McKenzie, R. I. H., and G. Fleischmann. 1964.
The inheritance of crown rust resistance from selections from two Israeli collections of *Avena sterilis*. Can. J. Genet. Cytol. *6*: 232-236.

McKenzie, R. I. H., G. Fleischmann, and G. J. Green. 1965.
A close association of stem and crown rust resistance in 'Ukraine' and ' Rosen's Mutant' oats. Crop Sci. *5*: 551-552.

McKenzie, R. I. H., J. W. Martens, G. Fleischmann, and D. J. Samborski. 1968.
An association of stem rust and crown rust resistance in Jostrain oats. Can. J. Genet. Cytol. *10*: 190-195.

McKenzie, R. I. H., J. W. Martens, and T. Rajhathy. 1970.
Inheritance of oat stem rust resistance in a Tunisian strain of *Avena sterilis*. Can. J. Genet. Cytol. *12*: 501-505.

Murphy, H. C. 1935.
Physiologic specialization in *Puccinia coronata avenae*. U. S. Dept. Agr. Tech. Bull. 433: 1-48.

Murphy, H. C. 1938.
Parasitism of smuts, rusts, and minor diseases affecting oats. Iowa Agr. Expt. Sta. Ann. Rept. 1938.

Murphy, H. C., and T. R. Stanton. 1930.
Oat varieties highly resistant to crown rust. J. Amer. Soc. Agron. *22*: 573-574.

Murphy, H. C., T. R. Stanton, and H. Stevens. 1937.
Breeding winter oats resistant to crown rust, smut and cold. J. Amer. Soc. Agron. *29*: 622-637.

Murphy, H. C., and F. Meehan. 1946.
Reaction of oat varieties to a new species of *Helminthosprium*. Phytopath. *36*: 407. (Abstract)

Murphy, H. C., F. J. Zillinsky, M. D. Simons, and R. Grindeland. 1958.
Inheritance of seed color and resistance to races of stem and crown rust in *Avena strigosa*. Agron. J. *50*: 339-541.

Murphy, H. C., and F. A. Coffman. 1961.
Genetics of disease resistance. *In* F. A. Coffman (Ed.). Oats and Improvement. pp. 207-226. American Society of Agronomy, Madison, Wsic.

Murphy, H. C., I. Wahl, A. Dinoor, J. D. Miller, D. D. Morey, H. H. Luke, D. Sechler, and L. Reyes. 1967.
Resistance to crown rust and soilborne mosaic virus in *Avena sterilis*. Plant Dis. Rptr. *51*: 120-124.

Osler, R. D., and H. K. Hayes. 1953.
Inheritance studies in oats with particular reference to the Santa Fe type of crown rust resistance. Agron. J. *45*: 49-53.

Poehlman, J. M., and C. H. Kingsolver. 1950.
Disease reaction and agronomic qualities of oat selections from a Columbia x Victoria-Richland cross. Agron. J. *42*: 498-502.

Saari, E. E., and M. B. Moore. 1962.
The effect of temperature on crown rust reactions. Phytopath. *52*: 749-750. (Abstract)

Sanderson, K. E. 1960.
Inheritance of reaction to several races of crown rust *Puccinia coronata avenae* Erikss., in two crosses involving Ukraine oats. Can. J. Plant Sci. *40*: 345-352.

Sharp, E. L., and R. B. Volin. 1970.
Additive genes in wheat conditioning resistance to stripe rust. Phytopath. *60*: 1146-1147.

Simons, M. D. 1954.
The relationship of temperature and the stage of growth to the crown rust reaction of certain varieties of oats. Phytopath. *44*: 221-223.

Simons, M. D. 1955.
The use of pathological techniques to distinguish genetically different sources of resistance of crown rust of oats. Phytopath. *45*: 410-413.

Simons, M. D. 1956.
The genetic basis of the crown rust resistance of the oat variety Ascencao. Phytopath. *46*: 414-416.

Simons, M. D. 1965.
Seedling resistance to *Puccinia coronata avenae* race 264 found in *Avena sterilis*. Phytopath. *55*: 700-701.

Simons, M. D. 1970.
Crown Rust of Oats and Grasses. Mono. #5. American Phytopathological Society, Worcester, Mass.

Simons, M. D., and H. C. Murphy. 1954.
Inheritance of resistance to two races of *Puccinia coronata* Cda. var. *avenae* Fraser and Led. Iowa Acad. Sci. Proc. *61*: 170-176.

Simons, M. D., and H. C. Murphy. 1955.
Comparison of certain combinations of oat varieties as crown rust differentials. U.S.D.A. Tech. Bull. No. 1112. pp. 1-22.

Simons, M. D., K. Sadanaga, and H. C. Murphy. 1959.
Inheritance of resistance of strains of diploid and tetraploid species of oats to races of the crown rust fungus. Phytopath. *49*: 257-259.

Simons, M. D., I. Wahl, and Ady Raul da Siva. 1962.
Strains of noncultivated *Avena* spp. resistant to important races of the crown rust fungus. Phytopath. *52*: 585-586.

Simons, M. D., F. J. Zillinsky, and N. F. Jensen. 1966.
A standardized system of nomenclature for genes governing characters of oats. Crops Research U.S.D.A., ARS Bull. 34: 85, pp. 22.

Stakman, E. C., and M. N. Levine. 1922.
The determination of biologic forms of *Puccinia graminis* on Triticum spp. U. of Minn. Agr. Expt. Sta. Tech. Bull. 8.

Stevens, N. D., and W. O. Scott. 1950.
How long will present spring oat varieties last in the central corn belt. Agron. J. *42*: 307-309.

Torrie, J. H. 1939.
Correlated inheritance in oats of reaction to smuts, crown rust, stem rust and other characters. J. Agr. Res. *59*: 783-802.

Upadhyaya, Y. M., and E. P. Baker. 1960.
Studies on the mode of inheritance of Hajira type stem rust resistance and Victoria type crown rust resistance as exhibited in crosses involving the oat variety Garry. Linn. Soc. N.S. Wales, Proc. *85*: 157-179.

Upadhyaya, Y. M., and E. P. Baker. 1962.
Studies on the inheritance of rust resistance in oats. II. The mode of inheritance of crown rust resistance in the varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia, and Victoria in their crosses with susceptible varieties. Linn. Soc. N.S. Wales, Proc. *87*: 200-219.

Wahl, I., A. Dinoor, J. Halperin, and S. Schreiter. 1960.
The effect of *Rhamnus palaestina* on the origin and persistence of oat crown rust races. Phytopath. *50*: 562-569.

Weetman, L. M. 1942.
Genetic studies in oats of resistance to two physiologic races of crown rust. Phytopath. *32*: 19. (Abstract)

Welsh, J. N., R. B. Carson, W. J. Cherewick, W. A. F. Hagborg, B. Peturson, and H. A. H. Wallace. 1953.
Oat Varieties - past and present. Can. Dept. Agr. Publ. 891.

Welsh, J. N., B. Peturson, and J. E. Machacek. 1954.
Associated inheritance of reaction to races of crown rust, *Puccinia coronata avenae* Erikss., and to Victoria Blight, *Helminthosporium victoriae* M. and M., in oats. Can. J. Bot. *32*: 55-68.

Zillinsky, F. J., and H. C. Murphy. 1967.
Wild oat species as sources of disease resistance for the improvement of cultivated oats. Plant Dis. Reptr. *51*: 391-395.

Zimmer, D. E., and J. F. Schafer. 1961.
Relation of temperature to reaction-type of *Puccinia coronata* on certain oat varieties. Phytopath. *51*: 202-203.