THE INHERITANCE OF RESISTANCE TO *PUCCINIA CORONATA AVENAE* AND OF FLORET CHARACTERS IN *AVENA STERILIS*

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Linda Siu Ling Wong

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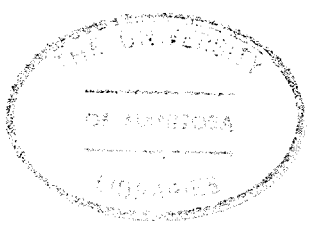

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ABSTRACT

Wong, Linda Siu Ling. M.Sc., The University of Manitoba, October, 1981. The Inheritance of Resistance to *Puccinia coronata avenae* and of Floret Characters in *Avenae sterilis*. Major Professor; Ronald I.H. McKenzie.

The inheritance of resistance to oat crown rust, caused by *Puccinia coronata* Cda. f. sp. *avenae* Eriks. was studied in *Avena sterilis* L. accessions CAV 4248, CAV 4656, and CAV 4904. These were collected in Tit-Mellil, Morocco; Tizi Ouzov, Algeria; and Algiers, Algeria, respectively. Seedling rust tests on BC_1F_2 families indicated the presence of three independent, partially dominant genes in CAV 4248, one partially dominant gene in CAV 4656 and a dominant gene in CAV 4904. The three genes in CAV 4248 were designated A, B and C. Gene A conferred resistance to all but one race tested, gene B conferred resistance to nine of the 15 races tested and gene C to six of them. In CAV 4656, the resistance gene conferred resistance to 13 of the races tested while the gene in CAV 4904 conditioned resistance to all of the races tested. All the resistance genes were operative throughout the life of the plant. The resistance gene in CAV 4904 was closely linked or allelic to gene Pc-46.

Awns and lemma pubescence were each inherited monogenically in the three crosses while grey lemma color was controlled by one gene in the cross involving CAV 4248 and by two genes in the cross involving CAV 4656. In the CAV 4904 x Sun II cross, the brown lemma color was controlled by one

gene which appeared to be completely linked with the gene for lemma pubescence. In the CAV 4656 x Sun II^2 cross, one of the two genes governing grey lemma was associated with the gene for lemma pubescence by a recombination value of 28.30 $\pm$ 4.87%. In the CAV 4248 x Sun II^2 cross, the gene for grey lemma and the gene for strong awns were linked with a crossover value of 4.58 $\pm$ 1.86%.

No significant association was found between crown rust reaction and the three floret characters studied.

Cytological observations on the frequencies and types of meiotic irregularities were conducted at metaphase I and subsequent stages. A low level of irregular meiosis was observed in the parents. A much higher frequency was found in F_1 plants. In addition to univalents and bridges observed in all the hybrids, multivalents were seen in F_1 plants of CAV 4248 x Sun II and CAV 4656 x Sun II. The variation observed appeared to be caused by a differentiation in chromosome structures.

INTRODUCTION

Oats is one of the major crops of the world. It ranks sixth among the cereal grains in world production, after wheat, corn, rice, barley and sorghum (FAO, 1980). In Canada, production of oats for grain was approximately 3 million metric tonnes in 1979 according to Statistics Canada (1980). In the United States, production was about 9.3 million metric tonnes (Long, 1980). The leading oat producing countries are Russia, United States, West Germany, Canada, Poland, France, Sweden and Australia (FAO, 1980).

Crown rust caused by Puccinia coronata Cda. f. sp. avenae Eriks. is probably the most widespread and destructive disease of oats (Simons and Murphy, 1961; Roelfs, 1978). It occurs in most regions of the world where oats are grown and causes striking reductions in yield and quality of grain and forage, and may cause severe lodging (Simons, 1970).

To protect the oat crops from crown rust damage, several means of controlling crown rust have been suggested. The main control measures include eradication of the alternate host, mainly Rhamnus cathartica L. (European buckthorn), development of resistant cultivars and application of fungicides. Complete eradication of buckthorn is not feasible since it has become very widespread. However, it is advocated that buckthorn should be eradicated in the vicinity of oat fields in order to reduce damage.

Fungicides have been used to control crown rust in various parts of the world. Dickson (1959) and Rowell (1968) reviewed the subject of

chemical control of cereal rusts. They concluded that chemicals do not appear to be an economic means to control rust. The successful use of chemicals requires reliable forecasts of impending rust epidemics (Rowell, 1968). The short duration of activity of fungicides, compared to the length of the rust epidemic, limits their effectiveness. Moreover, the ecological and human health consequences (Baker and Cook, 1974; Huisingh, 1974) preclude the use of chemical control as a routine practice.

The possibility of utilizing resistance to crown rust as a means of control was known before the end of the 19th century (Simons, 1970). While resistant cultivars constitute the only effective control of the disease, it has been shown repeatedly (Simons, 1970; Frey et al., 1977) that they are usually soon surpassed by the progress of breeding and concurrent changes in the spectrum of pathogen races prevailing in the area of cultivation. Consequently, the search for resistance genes to incorporate into oat cultivars is a continuing process (Harder et al., 1977).

For many years, it has been recognized that crown rust resistance may be found in the wild oat species. Recent investigations prove that populations of Avena sterilis L. constitute an extremely heterogeneous reservoir of genotypes for crown rust resistance (Wahl, 1970; Harder et al., 1980; Martens et al., 1980). The discovery of new resistance genes in A. sterilis has an immediate practical value in the improvement of oat cultivars. Since A. sterilis is a hexaploid species, it is highly compatible with cultivated hexaploid oats (Rajhathy and Thomas, 1974). Thus, there should be no difficulty in transferring resistance genes.

The present study was undertaken to investigate the inheritance of

crown rust resistance and floret characters (awns, lemma color and lemma pubescence) in three accessions of A. sterilis. The relationship between floret characters and crown rust reaction was also studied. In addition, the parents used in the crosses and the F_1 plants were examined cytologically in order to gain a better understanding of the chromosomal pairing in interspecific hybrids.

LITERATURE REVIEW

I. Nature of the Pathogen

Crown rust is the common name of the leaf rust disease of oats and refers to the causal agent, Puccinia coronata Cda. f. sp. avenae Eriks.. Both "crown" and "coronata" refer to the crown-like digitate projections at the teliospores apices.

A. Importance of Oat Crown Rust

Oat crown rust has the potential for causing severe epidemics in susceptible cultivars when environmental conditions are favorable. Roelfs (1978) stated that in the United States the greatest nationwide epidemic of crown rust probably occurred in 1938. Since 1970, oat crown rust probably caused the greatest loss of any of the cereal rusts. In many states, losses exceeded 20%. In an earlier study (Sherf, 1954), crown rust was found to cause an estimated loss of 30% of the Iowa oat crop of 6 million acres for 1953.

In Canada, oat crown rust epidemics are most severe in Manitoba, Ontario and eastern Saskatchewan. In Manitoba, losses caused by crown rust in oats have been monitored on a continuing basis since 1963. In a study by Martens et al. (1972), natural infections caused significant reductions in groat yield ranging from 6.8% to 30% in most years. Fleischmann and McKenzie (1965) found that 30% crown rust infection of oats at the flowering stage resulted in 25% yield losses. Similar results were obtained by Clark (1968). He reported that in Ontario heavy

natural infection of crown rust reduced yields by approximately 20%.

In a study on the effect of crown rust on the quantity and quality of oat yield, Sebesta (1972) found that the decrease of grain yield, of 1,000 kernel weight and of crude protein content caused by a mixture of crown rust races was about 18%, 20% and 18%, respectively. Furthermore, the content of nitrogen and the amount of starch were significantly decreased in the kernels. On the other hand, the fibre content in kernels as well as the percentage of hulls was significantly increased (Sebesta, 1974).

Similar results were reported by Harder and Clark (1981). Using six susceptible cultivars, they conducted a disease loss test in Ontario under a favorable rust-environment. They found that under natural infection, crown rust caused mean reduction of 40% in yield, 23% in kernel weight and a 31% increase in the amount of hull relative to the groat. In addition, the susceptible cultivars were badly lodged due to hastened maturity caused by the crown rust infection, which further reduced seed quality.

B. Biology and Life-Cycle of *P. coronata*

Descriptions of the life cycle of *P. coronata* have been given in numerous sources (Simons and Murphy, 1961; Simons, 1970; Manners, 1971). *P. coronata* is a heteroecious, heterothallic, macrocyclic rust fungus. The uredial and telial stage occur on oats and many other grasses; the spermagonial and aecial stages mainly on European buckthorn (*R. cathartica*). The uredial stage of *P. coronata* occurs mainly on the leaf blades of its gramineous hosts, but is not uncommon on the sheaths and floral structures. On susceptible varieties of oats, the uredia appear as bright

orange-yellow, round to oblong pustules.

Telia appear after the uredia are well established and sometimes form in rings around the uredia. They are black or dark brown and remain covered by the epidermis. Teliospores survive northern winters on host debris, and their germination in the spring may result in development of the sexual stage on Rhamnus. The aecial stage is conspicuous when the bright orange-yellow aecial cups are forming and discharging aeciospores; later when rust is building up on oats, buckthorn leaves show only necrotic lesions or shot-holes. Aeciospore infection of oats results in re-establishment of the uredial stage.

The urediospores of P. coronata are wind-borne. Thus, P. coronata can overwinter in the southern United States in the uredial stage and cycle between north and south independently of Rhamnus (Frey et al., 1977).

II. The Genetics of Resistance

Resistance to rust diseases can be described either in functional or in genetic terms (Day, 1974). The functional terms recognize that resistance may be either highly specific and effective against some rust races but not others, or non-specific and equally effective against a range of rust races. A large number of terms have been used to describe these two kinds of resistance (Hooker, 1967; Browning et al., 1977). At the present time, the most widely used terms are "specific" and "general" resistance (Day, 1974; Browning et al., 1977). While the nature of general resistance is not well understood, segregations for specific resistance are usually discrete and frequently fit simple genetic ratios.

The genetic terms describe the mode of inheritance for rust resis-

tance (Hooker and Saxena, 1971; Day, 1974). There are three classes: (a) oligogenic, (b) polygenic and (c) extrachromosomal. In this review, only oligogenic resistance will be discussed.

A. Oligogenic Inheritance

Biffen (1905) first showed, working with yellow rust of wheat, that inheritance of disease resistance followed Mendel's laws. Working in Cambridge, he showed that the resistance of Rivet wheat was determined by a single recessive gene. Fifteen years later, Parker (1920) presented data on the inheritance of crown rust resistance in oats. He reported that the resistance was due to the action of multiple genes. Subsequently, many genetic studies have been conducted on the inheritance of crown rust resistance in oats (Simons et al., 1978). Attempts will be made in the following sections to point out the different modes of inheritance encountered since the work of Parker.

1. Mode of Inheritance for Monogenic Resistance. The simplest form of inheritance involves single genes. Davies and Jones (1926) demonstrated that a single partially dominant gene conditioned resistance in the cross Red Rustproof (resistant) x Scotch Potato (susceptible). Further cases of resistance to crown rust controlled by a single gene were described by Litzenberger (1949). He found that both Landhafer and Santa Fe contained a single dominant gene effective against crown rust races 1 and 45.

The same mode of inheritance was established with resistance derived from A. sterilis. Fleischmann and McKenzie (1968) studied the inheritance of resistance in A. sterilis accessions CW 491-4 and F 366 to crown rust races 264, 290, 295, 332 and 446. They found that resis-

tance of CW 491-4 to these races was due to a dominant gene, designated Pc-38, while the resistance of F 366 was conditioned by gene Pc-39. For designation of genes refer to Simons et al. (1978).

Although genes for resistance to crown rust are usually dominant, there are cases where resistance is governed by single, incompletely recessive genes. Kiehn et al. (1976) found that resistance of A. sterilis accession CAV 4963 to 10 of 12 crown rust isolates tested was due to the incompletely recessive gene Pc-55. Similar results were reported by Martens et al. (1980). They found that the partially recessive gene Pc-54 conferred resistance to many of the crown rust races occurring in Canada.

It must be pointed out that dominance and recessiveness, just as resistance, are not, as such, absolute attributes of a host plant, but are only the expression of its specific interaction with a certain rust race. Accordingly, Fleischmann and McKenzie (1968) showed that the resistance gene Pc-39 reacted as a dominant against races 332, 295, 290 and 446, but manifested itself as an incompletely dominant gene against race 264. In other genetic studies, the degree of dominance was shown to be varied according to the genetic background upon which the resistance gene was functioning. For example, Smith (1934) found that resistance was dominant in some crosses involving Victoria, but dominance was lacking in others. In the case of the variety Landhafer, the resistance gene was recessive in the cross with Reselect Clinton, but dominant in others (Simons and Murphy, 1954).

Changes in dominance have been known to associate with growth stage. Although resistance to certain races of crown rust is generally dominant in the seedling stage, in the adult stage it may not be. In the cross

Iowa 444 x Bond, Torrie (1939) found that resistance was partially dominant in F_1 seedlings, but field reactions of mature plants showed a partial dominance of susceptibility.

2. Two or More Genes Acting Independently. It is not uncommon for genetic studies to reveal several genes for resistance to crown rust in one host. Marshall and Myers (1961) located two dominant genes in the diploid Ceirch Llwyd, conditioning resistance to race 276. The two genes were designated Pc-32 and Pc-33 (Simons et al., 1978). Murphy et al. (1958) reported that the high resistance of certain plants of the diploid C.D. 3820 to some races was conditioned by three independent dominant genes. Those genes were designated Pc-15, Pc-16 and Pc-17 (Simons et al., 1978). Similarly, Fleischmann and McKenzie (1968) tested F_2 families of A. sterilis accession CAV 4997 x Pendek[2] backcross using races 290, 295, 332 and 446. Their results indicated that four genes in A. sterilis accession CAV 4997 acting independently conferred resistance to crown rust isolates tested. These four resistance genes were designated Pc-40, Pc-41, Pc-42 and Pc-43.

3. Allelism, Linkage and Independent Assortment. Rieger et al. (1976) defined allelism as "the relationship between alleles" and linkage as "the association in inheritance of certain genes due to their being localized in the same chromosome". Allelism and linkage of genes for crown rust resistance have been reviewed by Kiehn (1975). Kiehn et al. (1976) revealed that genes Pc-39 and Pc-55 were either closely linked or allelic. Harder et al. (1980) reported that genes Pc-38, Pc-62 and Pc-63 were either closely linked or allelic. Furthermore, the incompletely recessive gene Pc-54 was shown to be either allelic or closely linked

with gene Pc-35 (Martens et al., 1980).

4. Gene Interaction. Disease resistance is not always simply inherited. There are many instances in which the expression of resistance is influenced by the interaction between allelic or non-allelic genes. Complementation, modification and epistasis are examples of gene interaction.

The term complementary gene action is used to describe the relationship of two or more genes, which are necessary for the full expression of resistance. Complementation among genes for crown rust resistance has been reported in several genetic studies. Hayes et al. (1939), Hayes (1941) and Weetman (1942) found that the resistance of Bond to races 1, 3 and 6 was conditioned by two dominant complementary genes. Weetman (1942) also reported that the resistance of Ukraine was due to two dominant complementary genes.

It is quite possible for the expression of a resistance gene to be affected by the action of another gene. The resistance may either be enhanced or reduced. So far, no modifier genes have been reported for crown rust resistance in oats, but some modifying genes have been noticed in connection with stem rust resistance. In wheat, Knott and Anderson (1956) observed that in the cross Kenya 117A x Red Egyptian, the resistance of the stem rust resistance gene Sr7, to race 15B of stem rust could be enhanced in the presence of genes Sr9 and/or Sr10, which are ineffective against race 15B.

According to Hooker (1967), the term epistasis is used when a gene at one locus superimposes its effect on a gene at another locus or inhibits its expression. Epistatic gene action has been reported for crown rust resistance in oats. Dietz and Murphy (1930) studied F_1, F_2

and F_3 generations of Sunrise (resistant) x Fulghum (susceptible) and found the F_1 susceptible and the F_2 segregated 13 susceptible:3 resistant, indicating two genes were involved; one acting as an inhibitor of resistance. The F_3 data indicated that the genotype of the resistant parent was SSii and that of the susceptible parent ssII. Torrie (1939) studied the inheritance of crown rust resistance in the cross Iowa 444 (susceptible) x Bond (resistant). The results suggested the presence of two genes: S, a gene for crown rust resistance and I, a gene which partly inhibited the expression of S. The masking effect of the inhibitor was greater in mature plants than in seedlings.

III. The Established Crown Rust Resistance Genes

In 1966, a set of rules for symbolization of genes governing characters and a list of genes were published by a committee appointed by the National Oat Conference (Simons et al., 1966). Since that publication, many new genes have been discovered. Thus, to make new changes and to reflect the latest developments and concepts in the field, a revised publication was issued by a second committee in 1978 (Simons et al., 1978).

The symbol for Puccinia coronata avenae resistance "Pc" followed by an Arabic numeral, was assigned to the different genes identified in the inheritance studies. The literature on the Pc genes from Pc-1 to Pc-50 was covered adequately by Kiehn (1975). No attempt will be made to duplicate Kiehn's review and only Pc genes isolated since the discovery of gene Pc-50 will be discussed.

A. Genes Pc-51 and Pc-52

Two dominant resistance genes Pc-51 and Pc-52 were isolated from

A. sterilis Wahl No. 8 and Wahl No. 2, respectively (Simons et al., 1978). Gene Pc-51 is in Iowa Midseason isoline X 270 and early isoline X 434, while Iowa Midseason isoline X 421 carried gene Pc-52.

B. Genes Pc-53 and Pc-57

Simons (Simons et al., 1978) identified two resistance genes from A. sterilis: Pc-53 and Pc-57. Gene Pc-53 is incompletely dominant. Gene Pc-57 conditions resistance at high temperature to crown rust 264A and other races.

C. Gene Pc-54

Gene Pc-54 is incompletely recessive. It confers resistance to many of the crown rust races occurring in Canada and was effective against over 95% of all isolates tested in Canada in 1978 (Harder, 1979). This gene was isolated from A. sterilis CAV 1830 and CAV 1832 and was the first crown rust resistance gene to be identified from Turkey. It is allelic or closely linked with gene Pc-35 (Martens et al., 1980).

D. Genes Pc-55 and Pc-56

Both genes Pc-55 and Pc-56 were identified by Kiehn et al. (1976). Gene Pc-55 is incompletely recessive. It confers resistance to crown rust races CR (Winnipeg crown rust accession) 11, CR 36, CR 37, CR 61 and many others. This gene occurs in A. sterilis CAV 4963 collected from Israel and is allelic or closely linked to gene Pc-39.

Gene Pc-56 is a partially dominant gene isolated in A. sterilis CAV 1964. It conditions resistance to races CR 11, CR 36, CR 61 and many others.

E. Genes Pc-58, Pc-59, Pc-60 and Pc-61

The crown rust resistance genes Pc-58, Pc-59, Pc-60 and Pc-61 were identified by McDaniel (Simons et al., 1978). Genes Pc-58 and Pc-59 were derived from A. sterilis P.I. 295919 and P.I. 296244, respectively. Both confer excellent field resistance to races 325 and 264B (McDaniel, 1974). Gene Pc-58 is incorporated into Tam 0-301 which is moderately resistant to many crown rust races. Tam 0-312 carries gene Pc-59 which is no longer effective due to a virulent race which developed in 1978 and has become prevalent in Texas (Dr. M.E. McDaniel, personal communication).

Coker 227 and Coker 234 carry genes Pc-60 and Pc-61, respectively (Simons et al., 1978). Both genes are derived from A. sterilis P.I. 287211 and confer resistance to many races of crown rust.

F. Genes Pc-62 and Pc-63

Genes Pc-62 and Pc-63 were identified from A. sterilis CAV 4274 and CAV 4540, respectively (Harder et al., 1980). Both are dominant genes, conferring resistance to many crown rust races including races CR 12, CR 37, CR 46, CR 50, CR 56 and CR 61. Gene Pc-62 is linked or allelic to gene Pc-38 and is possibly linked or allelic with gene Pc-63. Gene Pc-38, Pc-62 and Pc-63 are similar in resistance spectrum and are differentiated by races CR 102, CR 103 and CR 107.

IV. The Inheritance of Floret Characters in Oats

Reviews of the literature on the inheritance of floret characters in oats have been made a number of times, notably by Stanton (1955), Coffman and MacKey (1956) and Jensen (1961). In the present review, only floret characters related to the study will be mentioned, namely awns, lemma color and lemma pubescence.

A. Awns

Oats are generally awned. The development and shape of the awn depend on a multigenic system and the phenotypic expression is dependent on environment, ontogenetic sequence and genes with inhibiting effect (Coffman and MacKey, 1956). The different types of awns are generally classified under three headings (Fraser, 1919): (1) strong awns which are long, stiff, geniculate with the lower portion dark in color and twisted in a clock-wise direction; (2) medium-strong awns which lack the geniculation, are less stiff, generally twisted at the base, are dark in color on the twisted part and often curved; (3) weak awns which lack the tendency to twist and the dark color and are usually straighter. In cultivated oats, weak awns develop on the primary floret only and 40% to 95% of the spikelets may be completely awnless. Since the expression of the character is much influenced by environment, so-called awnless varieties are seldom completely awnless under all conditions (Jensen, 1961).

Due to the interfering action of an inhibitor gene (Fraser, 1919), monogenic segregation is generally reported for strong awns x awnless as well as for medium-strong or weak awns x awnless (Love and Fraser, 1917; Fraser, 1919; Torrie, 1939).

Strong awns have been reported to be completely linked with the wild-type articulate spikelet (Surface, 1916; Florell, 1931). Fraser (1919) noted strong linkage between A. sterilis base and the fully awned condition with about 4.14% crossovers. Middleton (1938) also obtained complete linkage of the A. sterilis base with the two strong awn characters.

B. Lemma Color

Oats are generally grouped into black (including brown), red, grey, yellow and white oats (Stanton, 1961). Incomplete epistasis in some cases and the existence of modifying and intensifying genes prevent distinct borderlines between each group (Coffman and MacKey, 1956). In addition, the expression of the color is greatly influenced and sometimes obscured by stage of maturity and by external conditions such as the degree of weathering (Jensen, 1961). Gross differences are usually distinguishable but the difficulty in classification arises between closely related shades of color, as between yellow and white (Coffman and MacKey, 1956; Jensen, 1961).

Genetic studies on the inheritance of lemma color reveal that there might be one (Nilsson-Ehle, 1909; Hayes et al., 1928; Torrie, 1939), two (Nilsson-Ehle, 1909; Welsh, 1931) or three (Nilsson-Ehle, 1909; Fraser, 1919) genes conditioning the expression of any one lemma color in oats. No evidence of linkage has been found between any of the genes for lemma color (Coffman and MacKey, 1956).

C. Lemma Pubescence

Lemma pubescence may vary from dense to scattered hairs on the lateral and dorsal surface of the lemma. This type of hairiness may be produced on the primary floret in each spikelet only or on the secondary floret as well and is rare in cultivated oats, but common in wild species (Coffman and MacKey, 1956; Stanton, 1961). Two independent genes (P_1, P_2) have been found regulating lemma pubescence which is dominant or semi-dominant to smooth lemma (Jensen, 1961). Monogenic segregation (Surface, 1916; Love and Craig, 1918; Philp, 1933) as well as segregation for two genes (Love and Craig, 1918; Nishiyama, 1937) have been reported.

V. Chromosome Pairing in Interspecific Hybrids

The cultivated oat, *Avena sativa* L, is an allohexaploid (2n = 6x = = 42) with the genomic formula AACCDD. The wild oat hexaploid species such as *A. sterilis* have the same basic chromosome structure as *A. sativa* (Rajhathy and Thomas, 1974). At the hexaploid level, species hybrids analyzed by Nishiyama (1929), Philp (1933) and Spier (1934) were all essentially normal in their chromosome pairing with 21 II forming regularly. The fertility of the F_1 hybrids were found equal to that of the parents (Aase, 1935). However, interchanges have been found in species hybrids (Ladizinsky, 1970) and the occurrence of univalents in some hybrids were reported by Joshi and Howard (1955). Obviously, some minor structural differences exist between species. According to several investigators (Rajhathy and Thomas, 1974; Thomas and Bhatti, 1975), chromosomal differentiation is apparently a common feature at all levels of ploidy in the genus *Avena*.

MATERIALS AND METHODS

I. Plant Materials

A. sterilis is a wild hexaploid oat species, very common in the Mediterranean area (Rajhathy and Thomas, 1974). Numerous good crown rust resistance genes have been found in A. sterilis (Simons et al., 1978). The A. sterilis accessions used in this study were selected through preliminary screening tests of A. sterilis materials from numerous collecting expeditions (Martens et al., 1980). These accessions all showed excellent seedling resistance to isolates of more than eight crown rust races used in the screening tests.

In addition to their seedling resistance, the three A. sterilis accessions were chosen on the basis of their relatively diverse origin. CAV (Canadian Avena) 4248 was collected from Tit-Mellil, Morocco; CAV 4656 was from Tizi Ouzov, Algeria and CAV 4904 originated from Algiers, Algeria. Thus, these accessions may possess crown rust resistance genes differing from each other and from those previously isolated from A. sterilis.

All three accessions have the typical floret characters of A. sterilis: the lemma is covered with a dense growth of hairs and both florets of the spikelet bear long, strong, twisted and geniculate awns. The lemma color of CAV 4248, CAV 4656 and CAV 4904 is dark grey, light-medium grey and dark brown, respectively.

Sun II is a Swedish variety released in 1940. This oat variety was produced from a cross between Star and Eagle (Akerman, 1948). Sun II

is susceptible to all known isolates of crown rust. It has been used as genetic background in many genetic (Mattsson, 1975) and cytogenetic studies (Hacker, 1965; Lin, 1968; Leggett, 1977).

Sun II is a white-seeded variety with infrequent, weak, non-twisted awns. The lemmas are glabrous.

Descriptions of the three A. sterilis accessions and Sun II are summarized in Table I. Their reactions to 15 races of crown rust are presented in Table II.

The susceptible variety Sun II was used as the male parent in crosses with each of the A. sterilis accessions. It was used as the male parent again to cross with the F_1 plants to produce at least 130 backcross seeds from each combination. The backcross F_1 plants were grown in growth cabinets (18 h photoperiod; 13°C night and 18°C day) to produce sufficient F_2 seeds for conducting genetic studies. To avoid outcrossing between the backcrosses, the F_1 plants of each backcross were grown in separate growth cabinets. Some seeds failed to germinate while a few others failed to produce much seed, thus reducing the number of families that could be used in this study.

II. Pathological Tests

To investigate the inheritance of crown rust resistance in the A. sterilis accessions used in this study, rust tests were conducted on the F_2 backcross families at the seedling stage. The same progenies were tested at the flowering stage in both the greenhouse and in the field in order to determine the adult stage resistance to crown rust. For all rust tests, the parental lines, the standard international differential varieties (Simons and Michel, 1964) and the Pc lines (Puccinia coronata

TABLE I. Origin and characteristics of parental lines of *Avena sterilis* and *A. sativa* cv. Sun II.

Parent	2n	Origin	Floret character		Awns
			Lemma color	Lemma pubescence	
CAV[a] 4248	42	Tit-Mellil, Morocco	dark grey	thick hairs present	strong, twisted, geniculate
CAV 4656	42	Tizi Ouzov, Algeria	light-medium grey	thick hairs present	strong, twisted, geniculate
CAV 4904	42	Algiers, Algeria	dark brown	thick hairs present	strong, twisted, geniculate
Sun II	42	Sweden	white	absent	infrequent, weak, non-twisted

[a]CAV refers to "Canadian *Avena*" accession number.

TABLE II. Infection types produced on seedlings of parental lines by 15 races of Puccinia coronata avenae.

Parent	Race (CR[b] No.)														
	11	12	13	20	25	36	46	56	106	109	116	120	123	124	136
CAV[a] 4248	;	;1⁻	;	;	;	;	;	;	;	;	;	;	;	;	4
CAV 4656	;N	;N	1⁺	;N	;	4	;N	;	;-2	4	;N	;N	;N	2N	1N
CAV 4904	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;
Sun II	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4

[a]CAV refers to "Canadian Avena" accession number.

[b]CR refers to "Winnipeg crown rust accession".

differential lines) were planted along with the test progenies.

All rust tests were conducted in the greenhouses from August, 1980 to May, 1981 except for the field rust tests which took place in the summer of 1980.

III. Test Rust Cultures

Crown rust races were chosen that represent a wide range of virulence on the standard set of differential varieties (Simons and Michel, 1964) and on the Pc- genes previously isolated from A. sterilis. The virulence characteristics of the races used are given in Table III. The rust isolates originated from field rust surveys, and are maintained at the Agriculture Canada Research Station, Winnipeg. The races are identified by CR (Winnipeg crown rust accession) numbers. The purity of races was tested on the differential hosts both before and during rust tests.

All rust tests conducted in the greenhouse were done by spraying the plants with a concentrated suspension of urediospores of the desired race in Shell Insecticide Base Oil 50. After spraying, the oil was allowed to evaporate off for about 30 minutes. Then the plants were incubated at high relative humidity under a polyethylene cover for about 24 h. During this time, the greenhouse lights were turned off and the temperature was set at 15°C. After 24 h incubation, temperature was maintained at about 20°C. Natural lighting was supplemented with fluorescent lighting for 18 h per day. The plants were scored for rust reaction 12 to 14 days after inoculation.

IV. Classification for Reaction to Crown Rust

Rust reactions were recorded according to pustule type, using the method described by Murphy (1935). The F_2 backcross families were

TABLE III. Isolates of *Puccinia coronata avenae*$_2$ used to test segregating populations of *Avena sterilis* x *Avena sativa* crosses.

Winnipeg accession no.	Standard[a] race no.	Effective/ineffective host resistance (Pc) genes
CR 11	264a	35, 38, 39, 45, 46, 47, 48, 50, 54, 55, 56/40
CR 12	264b	38, 39, 45, 46, 47, 48, 50, 54, 55, 56/35, 40
CR 13	264c	35, 38, 50, 56/39, 40, 45, 46, 47, 48, 54, 55
CR 20	295	35, 38, 39, 40, 45, 46, 47, 48, 54, 55/50, 56
CR 25	305	35, 38, 50, 56/39, 40, 45, 46, 47, 48, 54, 55
CR 36	326	35, 39, 40, 46, 47, 48, 50, 54, 55, 56/38, 40
CR 46	326	35, 38, 39, 40, 45, 46, 47, 48, 50, 54, 55, 56/
CR 56	210	35, 38, 39, 40, 45, 46, 47, 48, 50, 54, 55, 56/
CR 106	203	35, 39, 40, 45, 46, 47, 48, 50, 54, 55, 56/38
CR 107	295	35, 38, 39, 45, 47, 48, 50, 54, 55, 56/40, 46
CR 109	326	35, 39, 45, 46, 47, 48, 50, 54, 55, 56/38, 40
CR 116	345	35, 38, 39, 45, 47, 48, 54, 55, 56/40, 46, 50
CR 120	326	35, 38, 39, 40, 45, 47, 48, 54, 55/46, 50, 56
CR 123	303	35, 38, 50, 55, 56/39, 40, 45, 46, 47, 48, 54
CR 124	263	38, 39, 45, 47, 48, 50, 54, 55, 56/35, 40, 46
CR 126	-	35, 38, 39, 48, 50, 55, 56/40, 45, 46, 47, 54
CR 127	-	38, 39, 55, 56/35, 40, 45, 46, 47, 48, 50, 54
CR 136	326	35, 38, 39, 45, 46, 47, 48, 50, 54, 55, 56/40

[a]Simons and Michel (1964)

classified as either segregating or susceptible to crown rust.

V. Greenhouse Rust Tests

From each of the three backcrosses, 109 to 141 F_2 families were tested for seedling rust reactions with five races of crown rust. The races were CR 12, CR 13, CR 20, CR 25 and CR 36. Approximately 15 seeds of each backcross family were sown in a greenhouse bed for each planting. Two crown rust races were employed on the first two plantings. At each planting, the seedlings were inoculated with one race at the one- to two-leaf stage and with another race at the two- to three-leaf stage (about 6 days later).

On the third planting, the plants were thinned to about eight plants per family after the fifth seedling test was recorded. The remaining plants were allowed to grow and were inoculated with two more races at the flowering stage, one race after another 6 days apart. The inoculum used for the first inoculation was CR 36 and for the second, CR 13.

In order to learn more about the inheritance of resistance in the three *A. sterilis* accessions, selected segregating and susceptible F_2 backcross families were further tested with more crown rust races. Five segregating and 11 susceptible F_2 families were selected from the backcrosses involving CAV 4656 or CAV 4904. From the backcross involving CAV 4248, 17 families segregating for crown rust resistance and 11 susceptible families were selected. The plantings and inoculations were performed as described previously, each time using different rust races, to obtain the reactions to a total of nine additional races (CR 11, CR 46, CR 56, CR 109, CR 116, CR 120, CR 123, CR 124 and CR 136).

VI. Field Rust Tests

In the summer of 1980, all the F_2 backcross families were tested at Glenlea for adult-stage resistance in two isolated sites about 400 meters apart. About 15 seeds of each family were sown per row. An epidemic of the desired race was induced artificially by inoculating susceptible plants in spreader rows. Race CR 13 was applied to one site and race CR 36 to the other site. Inoculation with a hypodermic syringe was done by injecting an aqueous suspension of urediospores into the hollow stem of the susceptible plant at the five- to six-leaf stage.

Adult plants were classified as resistant, moderately resistant, moderately susceptible or susceptible to crown rust and the families were then classified as either segregating or uniformly susceptible. The crown rust classification was based primarily on the reaction of the flag leaf.

VII. Test for Allelism

To determine the identity and linkage characteristics of the resistance genes present in the three accessions, lines of Pendek (Table IV) carrying the single genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-48 and Pc-56 were used as the male parents in crosses with each of the *A. sterilis* accessions. The F_1 plants from these crosses were grown to maturity in the greenhouse beds. As the panicles of the F_1 plants emerged, they were bagged to obtain selfed F_2 seeds. Progenies of the crosses involving genes Pc-35 and Pc-40 and of CAV 4248 x Pc-38 were inoculated with race CR 106. The rest were inoculated with race CR 12. All the F_2 seedlings were grown in sterilized soil to avoid the presence of volunteer plants.

TABLE IV. Pedigrees of lines containing single crown rust resistance genes derived from *Avena sterilis* used as parents in crosses.

Crown rust resistance gene	Pedigree	Origin
Pc-35	Pendek^4 x D 137	Israel
Pc-38	CAV 2648-4 x Pendek^4	Algeria
Pc-39	CAV 5165 x Pendek^4	Israel
Pc-40	Pendek^2 x CAV 4997	Israel
Pc-45	Pendek^4 x CAV 5050	Israel
Pc-46	Pendek^4 x CAV 5115	Israel
Pc-48	Pendek^2 x CAV 5041	Israel
Pc-56	CAV 1964 x Pendek^4	Algeria

VIII. Floret Characterization

The floret characters studied were awns, lemma pubescence and lemma color. Each of the Bc_1F_1 plants was classified visually for these floret characters. At least six F_2 plants from each Bc_1F_1 plant were classified on the basis of either segregating or uniform for each floret character.

IX. Genetic Analysis of the Data

The Chi-square method was used to test the validity that the observed population segregation ratios fit a theoretical ratio. The Bc_1F_2 families were also tested for linkage of the various characters using a Chi-square test for independence. The recombination values were determined by the product method as outlined by Stevens (1939).

X. Cytological Techniques

Only the three A. sterilis accessions, Sun II and their F_1 hybrids were observed cytologically. For chromosome counts, root tips were collected from seedlings germinated on moist filter paper. The excised root tips were pretreated in ice chilled water ($+1^{o}$ to $+2^{o}C$) in a refrigerator for approximately 24 h and afterwards fixed in Farmer's fixative (3 parts 85% ethyl alcohol:1 part glacial acetic acid) for about 2 days. The fixed root tips were hydrolyzed in 1N HCl for 7 minutes and then transferred to Fuelgen's solution for staining. After 30 minutes. the stained root tips were ready for squashes in proprionic carmine. The chromosome number was recorded from observations of cells at the mitotic metaphase stage.

For meiotic studies, immature panicles were fixed in Carnoy's fluid (6 parts 85% ethyl alcohol:3 parts chloroform:1 part glacial acetic acid)

for about 2 days. Anthers were squashed in a drop of iron-acetocarmine and the chromosomes were examined. Meiosis was observed at most of the stages with emphasis on metaphase I, anaphase I, telophase I and tetrad stages. Chromosomal variation was examined by a comparison of meiosis behavior between parental lines and their hybrids.

RESULTS

I. The Inheritance of Crown Rust Resistance

For the purpose of clarity, results obtained with each cross will be discussed separately, under the heading of the resistant A. sterilis parent used.

A. CAV 4248

The F_2 backcross families of CAV 4248 x Sun II^2 were tested with races CR 12, CR 13, CR 20, CR 25 and CR 36. Results of the rust tests are shown in Table V. With race CR 12, the segregation of F_2 backcross families fitted a single gene ratio (1:1 ratio, P = 0.20 - 0.30). When backcross families were tested with race CR 20, 101 families segregated, including all 63 families which segregated to race CR 12, while 40 families were susceptible. The results give a satisfactory fit to a ratio of 3 segregating:1 susceptible (P = 0.30 - 0.50), indicating the presence of two genes conferring resistance to race CR 20, one of which also confers resistance to race CR 12.

All 63 families segregating to race CR 12, as well as 39 families susceptible to this race, segregated to race CR 36, while 39 families were susceptible to race CR 36. The ratio of 102 segregating to 39 susceptible families (3:1 ratio, P = 0.30 - 0.50) indicates that two genes conferred resistance to race CR 36, one of which also conferred resistance to race CR 12.

When tested with race CR 13 and CR 25, backcross families that segre-

TABLE V. Segregation for crown rust resistance in F_2 backcross families of CAV 4248 x Sun II[2].

Crown rust race	Plant stage inoculated[a]	No. of families		Ratio	P
		Segregating	Susceptible		
CR 12	1st leaf	63	78	1:1	0.20 - 0.30
CR 13	1st leaf	123	18	7:1	0.90 - 0.95
CR 20	1st leaf	101	40	3:1	0.30 - 0.50
CR 25	2-3 leaf	123	18	7:1	0.90 - 0.95
CR 36	2-3 leaf	102	39	3:1	0.30 - 0.50

[a]Races CR 13 and CR 25 were applied to the same planting.
Races CR 20 and CR 36 were applied to the same planting.

gated for resistance to races CR 12, CR 20 or CR 36 also segregated for resistance to these two races, while 18 families remained susceptible. The results obtained gave a good fit to a ratio of 7 segregating:1 susceptible, indicating the presence of three genes conferring resistance to races CR 13 and CR 25.

From these results, it was concluded that there were three genes in CAV 4248 conferring resistance to five races tested. The probable genotype for crown rust resistance in CAV 4248 is presented in Table VI. The three resistance genes in CAV 4248 will be referred as A, B and C. Gene A conferred resistance to all races tested. When tested with race CR 12, the rust reactions of plants within segregating families indicated that the gene is not completely dominant. A large class of plants showing a moderately resistant reaction was obtained. By combining the moderately resistant class with the resistant class, a good fit to a 3:1 ratio of resistant to susceptible plants was obtained.

Gene B conferred resistance to races CR 13, CR 20 and CR 25, but not to races CR 12 and CR 36. When tested with race CR 20, within segregating families lacking gene A, the rust reaction of plants indicated that gene B is not completely dominant. There were a large number of plants showing moderate resistance. However, when the same families were tested with races CR 13 and CR 25, a ratio of 209 resistant:72 susceptible was obtained (3:1 ratio, $P = 0.80 - 0.90$), indicating that resistance is conditioned by a single dominant gene. Apparently, the degree of dominance may vary with the rust races used and/or the conditions of the test.

While gene C conditioned resistance to races CR 13, CR 25 and CR 36, it was susceptible to races CR 12 and CR 20. Within segregating families

TABLE VI. Reaction of F_2 backcross families of CAV 4248 x Sun II[2] and probable resistance genotypes.

Bc_1F_1 genotypes	Reaction of families to races[a]					No. of families observed
	CR 12	CR 13	CR 20	CR 25	CR 36	
Aa Bb Cc Aa Bb cc Aa bb Cc Aa bb cc	Seg.[1]	Seg.	Seg.	Seg.	Seg.	63
aa Bb Cc	S	Seg.	Seg.	Seg.	Seg.	17
aa Bb cc	S	Seg.[4]	Seg.[2]	Seg.[4]	S	21
aa bb Cc	S	Seg.[5]	S	Seg.[6]	Seg.[3]	22
aa bb cc	S	S	S	S	S	18

[a]The ratio within segregating families were as follows:

[1]race CR 12 631 R:149 MR:278 S plants P for a 3:1 ratio = 0.30 - 0.50

[2]race CR 20 199 R:266 MR:172 S plants P for a 3:1 ratio = 0.20 - 0.30

[3]race CR 36 86 R: 77 MR:101 S plants P for a 3:1 ratio < 0.001

[4]race CR 13 or CR 25 209 R: 0 MR: 72 S plants P for a 3:1 ratio = 0.80 - 0.90

[5]race CR 13 165 R: 22 MR:126 S plants P for a 3:1 ratio < 0.001

[6]race CR 25 137 R: 50 MR:126 S plants P for a 3:1 ratio < 0.001

containing gene C only, there was a poor fit to a 3 resistant:1 susceptible ratio with the tests involving races CR 13, CR 25 and CR 36 (Table VI).

The reaction of the CAV 4248 x Sun II[2] backcross families to the five races tested gives a good fit to a 4:1:1:1:1 ratio (P = 0.50 - 0.70), indicating that genes A, B and C segregate independently.

The same F_2 backcross families were tested for adult-stage resistance. Tests with races CR 13 and CR 36 were conducted in the greenhouse and in the field. It was found that there were no differences in rust reactions among seedling and adult stage tests. Thus, all three genes condition resistance throughout the life of the plant.

In order to learn more about the inheritance of resistance in CAV 4248, selected families segregating to five races, four races (aaBbCc) or three races (aaBbcc or aabbCc) and 11 susceptible families were inoculated with nine additional races (CR 11, CR 46, CR 56, CR 109, CR 116, CR 120, CR 123, CR 124 and CR 136). None of the susceptible families segregated to any of the nine races tested, indicating that there are only three resistance genes in CAV 4248: genes A, B and C. As shown in Table VII, gene A conditions resistance to all races tested except for race CR 136. Gene B confers resistance to races CR 11, CR 46, CR 56, CR 116 and CR 123, but not to races CR 109, CR 120, CR 124 and CR 136. Gene C confers resistance to races CR 46, CR 109 and CR 123, but not to races CR 11, CR 56, CR 116, CR 120, CR 124 and CR 136.

The infection types produced by each gene to the races tested may not be consistent as they are presented in Table VII. Further rust tests on homozygous Bc_1F_3 families will be required to accurately ascertain the infection type conditioned by each gene to a particular race.

Results of rust tests on the F_2 population of crosses of CAV 4248 and

TABLE VII. Seedling infection types conditioned by genes isolated from CAV 4248, CAV 4656 and CAV 4904 and by known Pc- genes to races of Puccinia coronata avenae.

Resistance gene		Races (CR No.)															
		11	12	13	20	25	36	46	56	106	107	109	116	120	123	124	136
CAV 4248	A	;	;1$^-$	;1$^-$	;	;	;	;	;	;	;1	;1$^+$	;	;	;1	;	4
	B	2$^-$	4	;	;1	;	4	;	;	;	–	4	;	4	;	4	4
	C	4	4	;	4	;	;	;	4	4	–	;	4	4	;	4	4
CAV 4656		;N	;N	1$^+$	;N	;	4	;N	;	;-2	–	4	;N	;N	;N	2N	1N
CAV 4904		0;	0;	0;	0;	0;	0;	0;	0;	0;	–	0;	0;	0;	0;	0;	0;
Pc-35		;	4	;	;2$^-$	;	0;	;	;	;1$^+$	;	0;	;	0;	;	4	;
Pc-38		;	;	;	;	;	4	;	;	3$^+$	;	4	;	;	;	;	;
Pc-39		;	;	4	;	4	;	;	;	;	;	;	;	;	4	;	;
Pc-40		4	4	4	;	4	3$^+$	;	;1$^+$	;2$^+$	4	4	4	;	4	4	3$^+$
Pc-45		;	0;	4	;	3	0;	;	;	;	;	;	;1$^-$	;	4	;2	;
Pc-46		;	;1$^+$	4	2	3	;	;	;	;	4	;	3	3$^+$	4	4	;
Pc-47		2	;1$^+$	4	2	3	;1$^-$	1$^+$	2	;2	;2	2$^+$	;2	;2$^-$	4	2$^+$	;2$^-$
Pc-48		;	;	4	;	3$^+$	;1$^-$	;	;	;	;	;	;	0;	4	;	;
Pc-50		;	0;	;	4	;	0;	;	;	0;	;	0;	4	4	;	;	;
Pc-54		2	;1	4	;	3	;1$^-$	;	;	;	;	;	;	;	4	;1	;
Pc-55		;	;	3	;	3$^+$	;	;	;	;	;	;	;	;	2$^+$	;	;
Pc-56		;	;	;	4	;	;1	;	;1$^+$	;1	;	;	;	3$^+$	;	;	;1
Pc-58		;	;	;	;	;	0;	;	;	;	;	0;	;	0;	;	;1	;
Pc-59		;	2	;	;	;	;	;	;	;	;	0;	;	0;	;	4	;
Pc-60		;2	;1$^+$	;	;	;	;	;	;	;2$^-$	;	;	;	;	0;	;	;
Pc-61		;	;	;	;	;	;1$^-$	;	;	;	;	;	;	0;	;	;	;
Pc-62		;	;	;	;	;	;1$^-$	;	;2$^-$	;1	4	;1	;	;	;	;	4
Pc-63		;	0;	;	0;	0;	4	;	;	4	;	4	;	0;	;	;	;

lines possessing crown rust resistance genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-48 and Pc-56 are shown in Table VIII. For various reasons including shrivelled crossed seeds and the high sterility of some F_1 plants, the F_2 population size obtained was not as large as desired. Moreover, when rust tests were conducted on the test progenies, the exact nature of the inheritance of crown rust resistance in CAV 4248 was still unknown, resulting in the use of inappropriate rust races. Gene C does not confer resistance to both races CR 12 and CR 106, while gene B confers resistance only to race CR 106. Gene A confers resistance to both races. Thus, of the three resistance genes in CAV 4248, only gene A was fully tested and gene B was partly tested with respect to the interrelationship with the Pc-genes.

As shown in Table VIII, a good fit to 63:1 ratio was obtained for crosses involving genes Pc-35 and Pc-38, indicating that genes A, B and the two Pc-genes acted as dominant genes and that they were independent of each other.

With the cross involving Pc-40, a small F_2 population was tested. The insufficient number of seeds obtained was largely due to two factors. The endosperms of almost all crossed seeds failed to develop normally. Also, due to high sterility of the only F_1 plant, seed set was very poor. Thus, although a good fit to a 63:1 ratio ($P = 0.30 - 0.50$) was obtained, it was not possible to conclude that genes A and B are independent of Pc-40. Further tests are required.

When the crosses were tested with race CR 12, a good fit to a ratio for two genes was obtained, indicating that gene A and the Pc-genes are independent of each other. A good fit to a 13:3 ratio of resistant to susceptible seedlings was obtained in crosses involving genes Pc-48 and

TABLE VIII. Segregation of F_2 seedling population from intercrosses between CAV 4248 and lines of Pendek possessing *Avena sterilis* derived resistance (Pc) genes.

Cross	Crown rust race	No. of plants			Ratio	P
		Resistant	Moderately resistant	Susceptible		
CAV 4248 X Pc-35	CR 106	405	0	5	63:1	0.50 - 0.70
CAV 4248 X Pc-38	CR 106	228	0	6	63:1	0.20 - 0.30
CAV 4248 X Pc-38	CR 12	27	4	3	15:1	0.50 - 0.70
CAV 4248 X Pc-39	CR 12	41	6	3	15:1	0.90 - 0.95
CAV 4248 X Pc-40	CR 106	34	0	0	63:1	0.30 - 0.50
CAV 4248 X Pc-45	CR 12	101	14	10	15:1	0.30 - 0.50
CAV 4248 X Pc-46	CR 12	273	72	31	15:1	0.10 - 0.20
CAV 4248 X Pc-48	CR 12	101	14	29	13:3	0.50 - 0.70
CAV 4248 X Pc-56	CR 12	183	70	75	13:3	0.05 - 0.10

Pc-56, while crosses involving other Pc-genes gave a good fit to a 15:1 ratio. The 13:3 ratio obtained could be due to the fact that either gene A or genes Pc-48 and Pc-56 must act as a recessive in those crosses. This excess of susceptible plants clearly demonstrates that these genes are independent of each other.

Unfortunately, the interrelationships of genes B and C and Pc-genes generally remain unknown. Crosses with homozygous Bc_1F_3 plants of desirable genotypes (aaBBcc and aabbCC) and the Pc-genes will be required before further rust tests can be conducted to determine the relationship between these genes. Nevertheless, it is still possible to postulate that genes B and C are distinct from known Pc-genes previously isolated from A. sterilis. From Table VII, it is clear that genes B and C are distinct genes, based on the infection types and the spectrum of their resistance to 15 different races.

Compared to the Pc-genes previously isolated from A. sterilis, gene A seemed to have similar spectrum of resistance to that of gene Pc-62. To test whether these two genes were the same, race CR 107, virulent on gene Pc-62 was used on families heterozygous for gene A. Gene A was shown to confer resistance to the race tested (Table VII), thus it is considered to be distinct from gene Pc-62.

B. CAV 4656

In the CAV 4656 x Sun II^2 cross (Table IX), 62 F_2 backcross families segregated alike for resistance to races CR 12, CR 13, CR 20 and CR 25, while 68 families were susceptible. The 1:1 ratio (P = 0.50 - 0.70) of segregating to susceptible families indicates that a single gene conditions resistance to these races. The rust reaction of plants within segregating families indicated that the gene is not completely dominant. A large

TABLE IX. Segregation for resistance to Puccinia coronata avenae in the F_2 backcross families of CAV 4656 x Sun II[2].

Crown rust race	Plant stage inoculated[a]	No. of families				No. of plants in the segregating families				
		Segregating	Susceptible	Ratio	P	Resistant	Moderately resistant	Susceptible	Ratio	P
CR 12	1st leaf	62	68	1:1	0.50 - 0.70	230	436	467	1:2:1	< 0.001
CR 13	1st leaf	62	68	1:1	0.50 - 0.70	279	234	306	1:2:1	< 0.001
CR 20	1st leaf	62	68	1:1	0.50 - 0.70	182	196	487	1:2:1	< 0.001
CR 25	2-3 leaf	62	68	1:1	0.50 - 0.70	216	180	423	1:2:1	< 0.001
CR 36	2-3 leaf		130					865		

[a]Races CR 13 and CR 25 were applied to the same planting.
Races CR 20 and CR 36 were applied to the same planting.

class of plants giving a moderately resistant reaction was obtained. Still, there was a poor fit to a 1:2:1 ratio with all rust tests as shown in Table IX.

All the F_2 backcross families were susceptible to race CR 36, as were the parents.

Results on adult plant tests conducted in the greenhouse and in the field with races CR 13 and CR 36 agreed with each other. All F_2 backcross families of CAV 4656 x Sun II^2 were susceptible to race CR 36. This is not surprising since CAV 4656 does not confer resistance to this race at the seedling stage. With race CR 13, F_2 backcross families which segregated for resistance at the seedling stage also segregated at the adult stage. However, it seems that resistance decreases with age of the plant. At the seedling stage, CAV 4656 conferred a $(;)(1)^+$ infection type to race CR 13. It is considered to be quite resistant to this race. But at the adult stage, CAV 4656 gave from a moderately resistant to moderately susceptible reaction.

In order to learn more about the inheritance of resistance in CAV 4656, five segregating and 11 susceptible F_2 backcross families were selected for further tests with races CR 11, CR 46, CR 56, CR 109, CR 116, CR 120, CR 123, CR 124 and CR 136. Results obtained indicate that the gene in CAV 4656 confers resistance to all races tested except race CR 109. Again, as in earlier extensive seedling rust tests, a large number of plants showing intermediate infection types and an excess of susceptible plants were present in segregating families. Susceptible families remained susceptible to all races used. Thus, these results further verify the fact that resistance in CAV 4656 is due to a single gene and that this gene is partially dominant.

Lines of Pendek carrying the single genes Pc-35, Pc-58, Pc-59, Pc-40, Pc-45, Pc-46, Pc-48 and Pc-56 were used as the male parents in crosses with CAV 4656. Results of seedling crown rust tests on the F_2 of these crosses are presented in Table X. Both genes Pc-35 and Pc-40 do not confer resistance to race CR 12, thus race CR 106 was used instead on crosses involving these two Pc genes. It was noted that plants with intermediate infection types again were present in all crosses except in the cross CAV 4656 x Pc-48. The number of these plants obtained varied with each cross. By combining these intermediate plants with the resistant plants, a good fit to a 15:1 ratio of resistant to susceptible plants was obtained in all crosses. This indicates that the resistance gene in CAV 4656 and the Pc-genes are independent of each other. This test also establishes the fact that the resistance in CAV 4656 is due to a single, partially dominant gene.

C. CAV 4904

Of the 109 F_2 families in the CAV 4904 x Sun II^2 cross (Table XI), 56 segregated for resistance to all five races tested, while 53 were susceptible. This is a good fit to a ratio of 1 segregating:1 susceptible ($P = 0.70 - 0.80$), indicating that a single gene confers resistance to these races. Within segregating families, the number of resistant and susceptible plants fit a 3:1 ratio, indicating that the single gene is dominant.

Results of adult plant tests conducted in the greenhouse and in the field with races CR 13 and CR 36 were similar to those of the seedling tests. Therefore, the resistance gene in CAV 4904 conditions resistance

TABLE X. Segregation of F_2 seedling population from intercrosses between CAV 4656 and lines of Pendek possessing Avena sterilis derived resistance (Pc) genes.

Cross	Crown rust race	No. of plants[a]			Ratio	P
		Res.	M.R.	Susc.		
CAV 4656 x Pc-35	CR 106	214	129	26	15:1	0.50 - 0.70
CAV 4656 x Pc-38	CR 12	282	22	20	15:1	> 0.95
CAV 4656 x Pc-39	CR 12	223	91	21	15:1	> 0.95
CAV 4656 x Pc-40	CR 106	136	21	11	15:1	0.80 - 0.90
CAV 4656 x Pc-45	CR 12	314	43	21	15:1	0.50 - 0.70
CAV 4656 x Pc-46	CR 12	263	27	23	15:1	0.30 - 0.50
CAV 4656 x Pc-48	CR 12	352	-	24	15:1	0.90 - 0.95
CAV 4656 x Pc-56	CR 12	230	64	24	15:1	0.30 - 0.50

[a]Res. = Resistant; M.R. = Moderately Resistant; Susc. = Susceptible

TABLE XI. Segregation for resistance to Puccinia coronata avenae in the F_2 backcross families of CAV 4904 x Sun II[2].

Crown rust race	Plant stage inoculated	No. of families[a]				No. of plants in the segregating families			
		Seg.	Susc.	Ratio	P	Resistant	Susceptible	Ratio	P
CR 12	1st leaf	56	53	1:1	0.70 - 0.80	793	236	3:1	0.10 - 0.20
CR 13	1st leaf	56	53	1:1	0.70 - 0.80	539	188	3:1	0.50 - 0.70
CR 20	1st leaf	56	53	1:1	0.70 - 0.80	497	154	3:1	0.30 - 0.50
CR 25	2-3 leaf	56	53	1:1	0.70 - 0.80	539	188	3:1	0.50 - 0.70
CR 36	2-3 leaf	56	53	1:1	0.70 - 0.80	497	154	3:1	0.30 - 0.50

[a]Seg. = Segregating; Susc. = Susceptible

throughout the life of the plant.

Five segregating and 11 susceptible backcross families were tested with nine more races. It was found that the families which had segregated previously to the five races also segregated for these races. The resistant plants within segregating families consistently produced either a (0)(;) or a faint (;) infection type to all races tested. Thus, it appears that the resistance gene in CAV 4904 conditions excellent resistance to many races.

Two of 11 susceptible families segregated for resistance to race CR 56. Since this resistance was observed to only one of the 14 races tested, the explanation for this resistance was not clear.

The results of seedling crown rust tests on the F_2 population of crosses between CAV 4904 and lines of Pendek possessing single Pc-genes are shown in Table XII. The progenies of the crosses involving Pc-35 and Pc-40 were tested with race CR 106. In the crosses involving genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-48 and Pc-56, the F_2 progeny segregated in a 15 resistant:1 susceptible ratio, indicating the presence of two independent dominant genes. With the cross CAV 4904 x Pc-46, no susceptible plants were obtained in a population of 668 F_2 plants. This suggests that gene Pc-46 and the gene CAV 4904 are either closely linked or allelic.

II. Inheritance of Floret Characters

In addition to the study of inheritance of crown rust resistance, the three backcrosses were studied for the inheritance of floret characters. Each F_1 plant of the three backcrosses was classified for awns, lemma

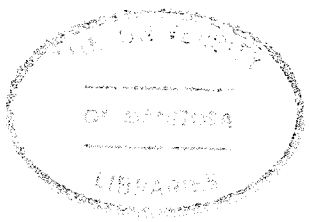


TABLE XII. Segregation of F_2 seedling population from intercrosses between CAV 4904 and lines of Pendek possessing *Avena sterilis* derived resistance (Pc) genes.

Cross	Crown rust race	No. of plants		Ratio	P
		Resistant	Susceptible		
CAV 4904 x Pc-35	CR 106	386	26	15:1	> 0.95
CAV 4904 x Pc-38	CR 12	409	25	15:1	0.50 - 0.70
CAV 4904 x Pc-39	CR 12	432	29	15:1	> 0.95
CAV 4904 x Pc-40	CR 106	428	26	15:1	0.50 - 0.70
CAV 4904 x Pc-45	CR 12	217	19	15:1	0.20 - 0.30
CAV 4904 x Pc-46	CR 12	668	0	15:1	< 0.001
CAV 4904 x Pc-48	CR 12	285	18	15:1	0.80 - 0.90
CAV 4904 x Pc-56	CR 12	332	25	15:1	0.50 - 0.70

color and lemma pubescence. The progeny of the Bc_1F_1 plants was classified as either segregating or non-segregating to each character. A summarized description of the parents is presented in Table I.

A. CAV 4248

In the CAV 4248 x Sun II^2 cross (Table XIII), 65 backcross families segregated for strong awns while 69 families were non-segregating. The 1:1 ratio (P = 0.70 - 0.80) of segregating to non-segregating families indicates that a single gene controls the development of awns in CAV 4248.

Of the 134 backcross families, 68 segregated for grey lemma color while 66 were non-segregating (1:1 ratio, P = 0.80 - 0.90), indicating the presence of a single gene governing grey lemma color. A monogenic ratio was also obtained for lemma pubescence.

B. CAV 4656

The CAV 4656 x Sun II^2 backcross F_2 families, as shown in Table XIII, gave an excellent fit to a 1:1 ratio for strong awns. It is evident that one gene governs this character. A good fit to a ratio of one F_2 backcross family segregating for lemma pubescence to one homozygous for glabrous lemma, indicates that lemma pubescence is also controlled by a single gene.

Of the 127 backcross families, 94 segregated for grey lemma color, while 33 were non-segregating. The 3:1 ratio (P = 0.70 - 0.80) of segregating to non-segregating families indicates that two genes govern grey lemma color.

TABLE XIII. Classification of floret characters in F_2 backcross families.

Cross	Awns				Lemma color				Lemma pubescence			
	No. of families[a]		Ratio	P	No. of families		Ratio	P	No. of families		Ratio	P
	Seg.	Non-seg.			Seg.	Non-seg.			Seg.	Non-seg.		
CAV 4248 x Sun II^2	65	69	1:1	0.70 - 0.80	68	66	1:1	0.80 - 0.90	69	65	1:1	0.70 - 0.80
CAV 4656 x Sun II^2	63	64	1:1	0.90 - 0.95	94	33	3:1	0.70 - 0.80	63	64	1:1	0.90 - 0.95
CAV 4904 x Sun II^2	53	48	1:1	0.50 - 0.70	54	47	1:1	0.30 - 0.50	54	47	1:1	0.30 - 0.40

[a]Seg. = Segregating; Non-seg. = Non-segregating

C. CAV 4904

In the CAV 4904 x Sun II^2 cross (Table XIII), 53 F_2 backcross families segregated for strong awns while 48 families were non-segregating. The 1:1 ratio (P = 0.50 - 0.70) of segregating to non-segregating families indicates that awn development is controlled by a single gene in CAV 4904.

A similar kind of segregation was obtained for lemma color and lemma pubescence. The P values of 0.30 - 0.50 for both characters indicated that segregation for brown lemma color and lemma pubescence were in agreement with the proposed 1:1 ratio.

III. Association Between Characters Studied

Tests of association were made between the various characters, using the Chi-square test for independence. As shown in Tables XIV and XV, no linkage relationships could be detected between the three floret characters and reaction to crown rust in any of the crosses studied.

Results of the X^2 test for independence between the three floret characters in all of the crosses showed that the gene for strong awns and the gene for grey lemma color were associated by a recombination value of 4.58 $\pm$ 1.86% in CAV 4248 (Table XVI). Moreover, the data from the F_2 families of CAV 4656 x Sun II^2 cross and CAV 4904 x Sun II^2 cross (Table XVII) showed that the gene for lemma color is linked with the gene for lemma pubescence. In the CAV 4656 x Sun II^2 cross, there are two genes governing grey lemma color, thus it is not known which of these two genes is associated with the gene for lemma pubescence by a recombination value of 28.30 $\pm$ 4.87%. For CAV 4904, no recombinant classes were obtained, thus the gene for brown lemma color and the gene for lemma pubescence appear to be allelic or tightly linked.

TABLE XIV. Data used for Chi-square test for independence between rust reaction and floret characters in F_2 backcross families of CAV 4248 x Sun II[2].

Crown rust race	Rust reaction	No. of families[a]					
		Awns		Lemma color		Lemma pubescence	
		Seg.	Non-seg.	Seg.	Non-seg.	Seg.	Non-seg.
CR 12	Segregating	31	30	30	31	33	28
	Susceptible	34	39	38	35	36	37
CR 13 or CR 25	Segregating	59	57	62	54	63	53
	Susceptible	6	12	6	12	7	11
CR 20	Segregating	52	43	53	42	54	41
	Susceptible	14	25	15	24	15	24
CR 36	Segregating	47	51	48	50	51	47
	Susceptible	18	18	20	16	18	18

[a]Seg. = Segregating; Non-seg. = Non-segregating

TABLE XV. Data used for estimating linkage between the gene for crown rust resistance and the genes for floret characters in F_2 backcross families.

Cross	Rust reaction	No. of families[a]					
		Awns		Lemma color		Lemma pubescence	
		Seg.	Non-seg.	Seg.	Non-seg.	Seg.	Non-seg.
CAV 4656 x Sun II[2]	Segregating	33	30	44	17	28	36
	Susceptible	28	36	50	16	32	31
CAV 4904 x Sun II[2]	Segregating	29	26	27	28	27	28
	Susceptible	24	22	27	19	27	19

[a]Seg. = Segregating; Non-seg. = Non-segregating

TABLE XVI. Data used for estimating linkage between the gene for awns and the genes for the other two floret characters in the three backcrosses.

Cross	Awns	No. of families[a]			
		Lemma color		Lemma pubescence	
		Seg.	Non-seg.	Seg.	Non-seg.
CAV 4248 x Sun II^2	Seg.	65	2	37	28
	Non-seg.	6	61	32	37
CAV 4656 x Sun II^2	Seg.	46	17	36	27
	Non-seg.	48	16	27	37
CAV 4904 x Sun II^2	Seg.	28	25	28	25
	Non-seg.	26	22	26	22

[a]Seg. = Segregating; Non-seg. = Non-segregating

TABLE XVII. Data used for estimating linkage between the gene(s) for lemma color and the gene for lemma pubescence in the three backcrosses.

Cross	Lemma color	No. of families	
		Lemma pubescence	
		Segregating	Non-segregating
CAV 4248 x Sun II^2	Segregating	38	30
	Non-segregating	31	35
CAV 4656 x Sun II^2	Segregating	56	38
	Non-segregating	7	26
CAV 4904 x Sun II^2	Segregating	54	0
	Non-segregating	0	47

In CAV 4248, lemma pubescence was inherited independently of awns and lemma color. Awns were inherited independently of lemma pubescence and lemma color in CAV 4656 and CAV 4904 (Tables XVI and XVII).

IV. Chromosome Pairing in Interspecific Hybrids

The chromosome number of the three A. sterilis accessions, Sun II and the F_1 hybrids was determined. All had 42 chromosomes. The behavior of the chromosomes was observed in microsporocytes at metaphase I (MI) and subsequent stages. The self-fertility of the parents, the F_1 plants and the BC_1F_1 plants was determined by scoring percent seed set, assuming a maximum of two florets per spikelet. For each plant, only the top 10 spikelets of the panicle of the main tiller were scored. Data from several plants were combined for analysis.

A. Meiosis in the Parents

The only meiotic irregularity observed in the parents was the occurrence of one or more univalents. These, and the products of their division, could be seen at MI and subsequent stages. The frequency of meiotic irregularities in the parents is shown in Table XVIII. It can be seen that about 5% of the pollen mother cells (P.M.C.'s) of Sun II had irregular meiosis at MI. The A. sterilis accessions had a higher frequency of irregular meiosis at MI. It was 15% and 14.2% for both CAV 4248 and CAV 4904, respectively. No data were obtained for CAV 4656. The seed set of the parents was calculated to be over 90%. Thus, it seems that fertility of the parents was not affected by the irregular meiosis at the observed frequencies.

TABLE XVIII. Frequencies of irregularities in pollen mother cells of parental species and F_1 plants.

Parental species or F_1 plants	Stage of meiosis					
	Metaphase I		Telophase I		Tetrads	
	No. cells obs.	% Cells with irregular meiosis	No. cells obs.	% Cells with irregular meiosis	No. cells obs.	% Cells with irregular meiosis
CAV 4248	20	15.0	33	9.1	112	16.1
CAV 4656	-	-	-	-	-	-
CAV 4904	120	14.2	47	6.4	52	3.8
Sun II	84	4.8	-	-	150	6.7
CAV 4248 x Sun II	565	55.0	204	50.0	-	-
CAV 4656 x Sun II	56	42.9	72	43.1	657	48.9
CAV 4904 x Sun II	290	51.4	207	47.3	117	94.0

B. Meiotic Behavior of F_1 Plants

A relatively high frequency of irregular meiosis was observed in all F_1 plants, as shown in Table XVIII. The frequency of irregular meiosis at MI was 55.0%, 42.9% and 51.4% for F_1 plants of CAV 4248 x Sun II, CAV 4656 x Sun II and CAV 4904 x Sun II, respectively. The mean frequency of univalents per P.M.C. observed at telophase I (TI) in all hybrids was similar to the mean frequency of univalents at MI. Based on the data obtained from F_1 plants of the cross CAV 4656 x Sun II, it seems that there was little difference in the frequency of irregular meiosis obtained at various meiotic stages.

The main meiotic abnormality observed in all hybrids was the appearance of univalents (mostly two or four univalents). The univalents observed showed characteristic movements at various stages of meiosis. At MI, while the bivalents move to the equatorial plate, the univalents usually lie off the plate (Plate III, Fig. A). At anaphase I (AI), most of the univalents move to the equatorial plate after the disjunction of the bivalents (Plate I, Fig. C; Plate III, Fig. B). The later behavior of the univalents is variable: (1) they may pass to the poles undivided, where they may or may not be included in the TI nucleus (Plate II, Fig. F) and then divide normally at the second division (Plate II, Fig. H; Plate III, Fig. G); (2) they may divide equationally with the sister chromatids moving to opposite poles (Plate II, Figs. C and D; Plate III, Fig. D) where they may or may not be included in the TI nuclei (Plate II, Fig. E; Plate III, Fig. E) or (3) they may misdivide.

Usually the univalents tend to divide equationally and sister chromatids pass to opposite poles. However, the sister chromatids resulting from either first division or second division may lag and form micro-

Plate I. Behavior of chromosomes at meiosis I in CAV 4248 x Sun II.

Fig. A. Metaphase I cell with an univalent and a trivalent (arrow).

Fig. B. Metaphase I cell with a quadrivalent (arrow).

Fig. C. Late anaphase I showing two lagging univalents and two separated sister chromatids.

Fig. D. Telophase I showing a bridge and a dividing univalent.

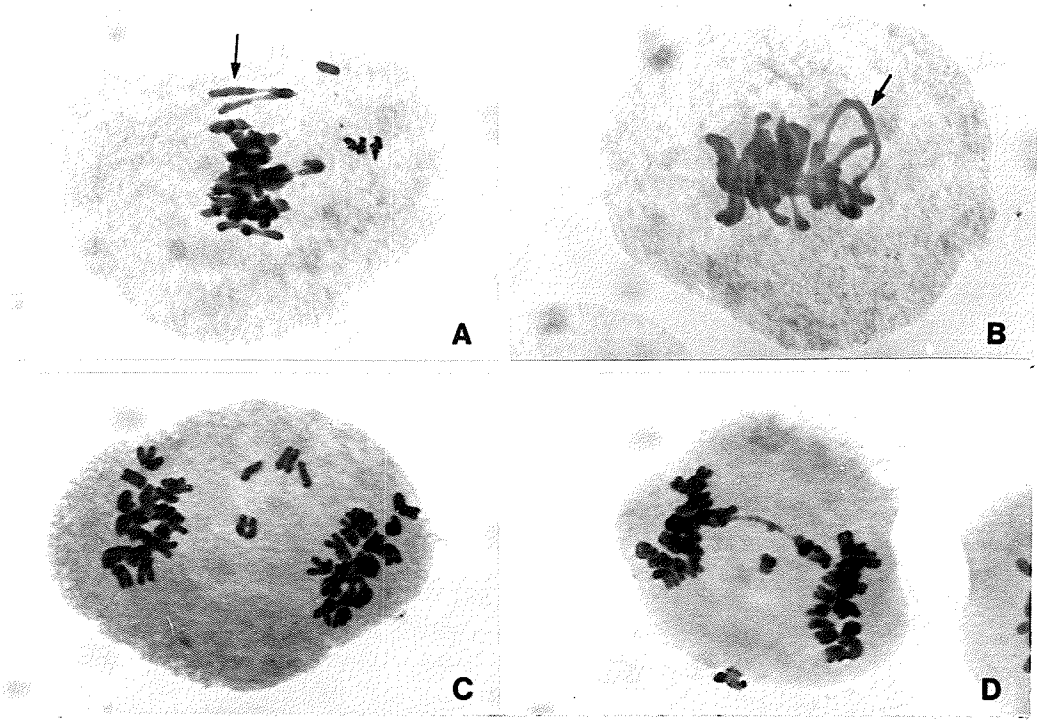

A
B
C
D

Plate II. Behavior of chromosomes at various meiotic stages in CAV 4656 x Sun II.

Fig. A. Metaphase I showing a ring of four.

Fig. B. Telophase I showing a bridge.

Fig. C. Telophase I showing sister chromatids at opposite poles.

Fig. D. Telophase I showing separated chromatids derived from two lagging univalents.

Fig. E. Late telophase I showing a micronucleus.

Fig. F. Late telophase I showing three undivided univalents.

Fig. G. Late anaphase II showing a bridge.

Fig. H. Late telophase II showing lagging chromatids.

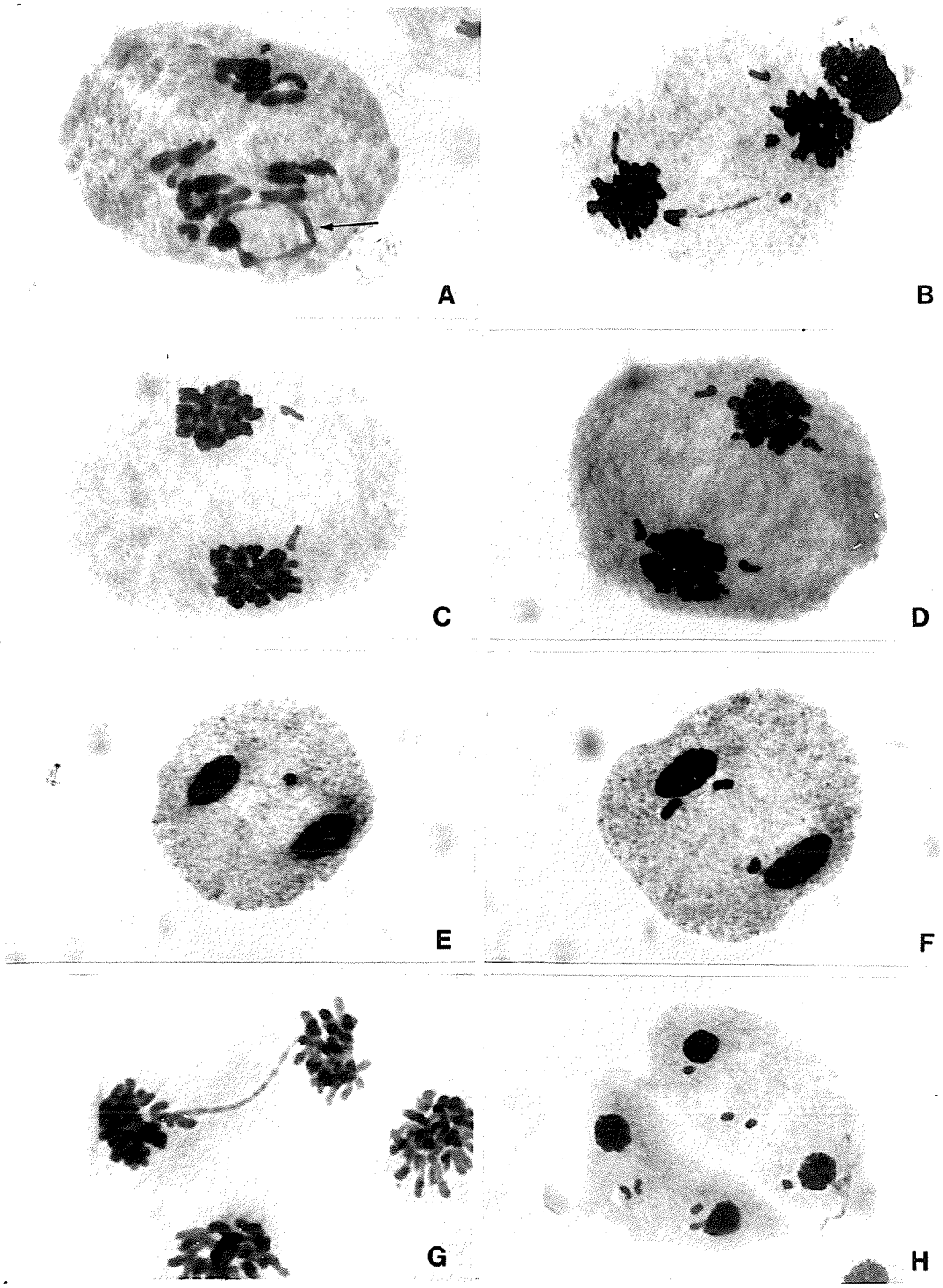

A
B
C
D
E
F
G
H

Plate III. Behavior of chromosomes at various meiotic stages in CAV 4904 x Sun II.

Fig. A. Metaphase I cell showing 4 univalents.

Fig. B. Anaphase I showing lagging univalents at equatorial plate.

Fig. C. Early telophase I showing two bridges.

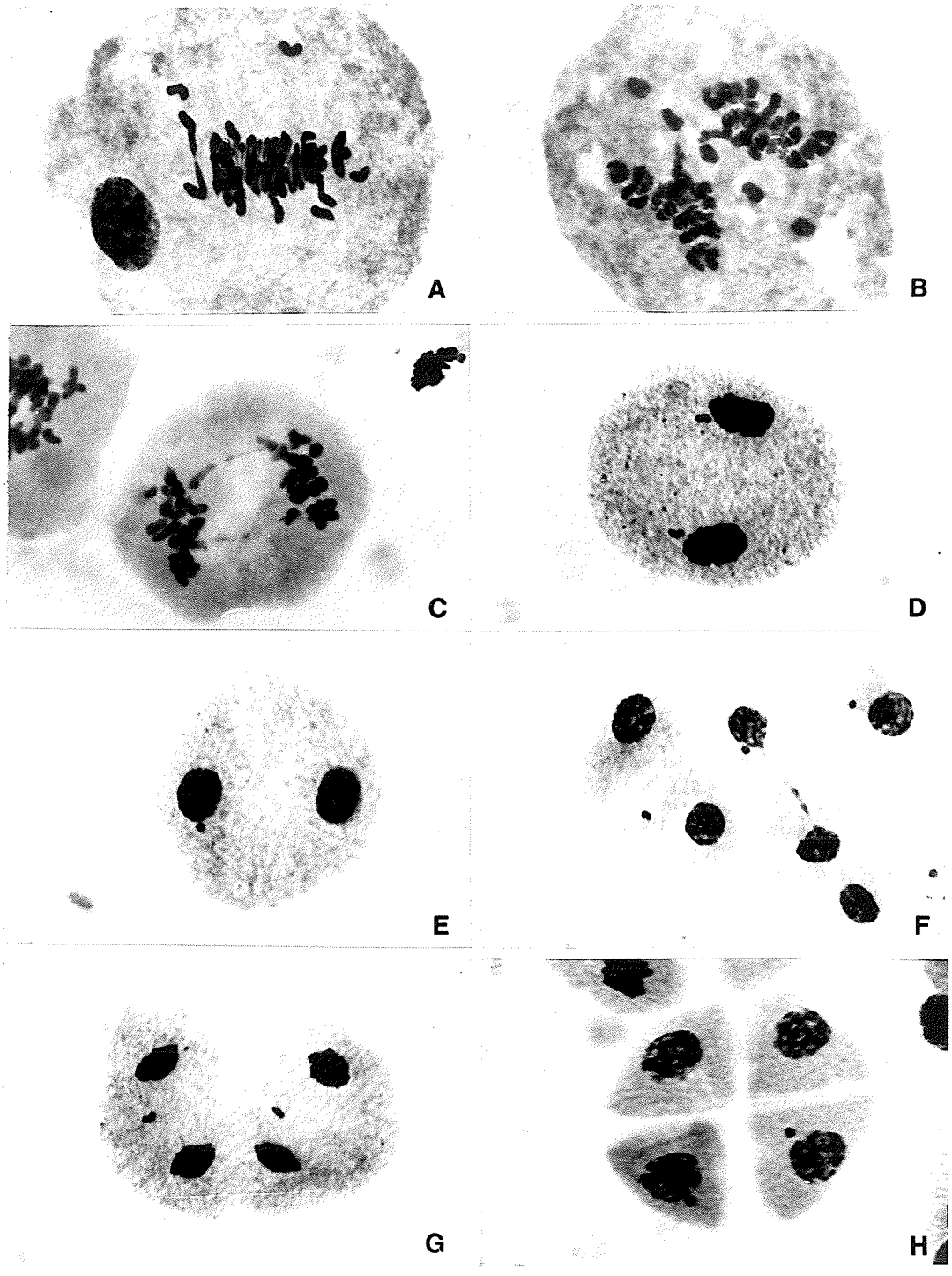
Fig. D. Telophase I showing separated chromatids at opposite poles.

Fig. E. Late telophase I showing a micronucleus.

Fig. F. Telophase II showing a bridge.

Fig. G. Late telophase II showing lagging chromatids in daughter cells.

Fig. H. A tetrad with two micronuclei.


A
B
C
D
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G
H

nuclei in the tetrad stage (Plate III, Fig. H). It is of interest to note that in the F_1 hybrids of the cross involving CAV 4904, the percentage of normal appearing cells was higher at TI than at telophase II (TII). This is reflected in the high population of tetrads having micronuclei, as shown in Table XVIII. The figure shown was obtained from one of the F_1 plants, thus it may not apply to other F_1 plants.

In addition to univalents, some pollen mother cells in the F_1 plants of the three crosses showed bridges. One or two bridges could be seen in either first division or second division (Plate I, Fig. D; Plate II, Figs. B and G; Plate III, Figs. C and F). For some hybrids, about 10% of the P.M.C.'s contained one or more bridges. Although it was not possible to ascertain the occurrence of fragments, the fact that the bridges did occur suggested the presence of a paracentric inversion.

Moreover, trivalents and quadrivalents were observed in the F_1 plants of CAV 4248 x Sun II (Plate I, Figs. A and B). Quadrivalents were also seen in the hybrids of CAV 4656 x Sun II (Plate II, Fig. A). The quadrivalents usually occurred in the form of a ring. Due to the stickiness of the chromosomes, the frequency of the occurrence of these multivalents could not be recorded. However, quadrivalents were observed to occur in a higher frequency in the hybrids of the cross involving CAV 4248. Thus, the presence of multivalents indicates the occurrence of interchanges in these hybrids.

All of these configurations strongly suggest that structural differences of the chromosomes are present. In this respect, these results indicate that Sun II differs from CAV 4904 by at least one pair of chromosomes and from CAV 4656 and CAV 4248 by two pairs of chromosomes. The relatively high frequency of univalents per P.M.C. observed at various

stages of meiosis in all hybrids also indicate that some structural differences exist between hexaploids.

Seed set of 18.9%, 87.1% and 42.4% was obtained for the hybrids of the crosses involving CAV 4248, CAV 4656 and CAV 4904, respectively. Apparently, the irregular meiosis observed in the F_1 plants of the cross involving CAV 4656 had little effect on the fertility. On the contrary, the relatively high frequency of P.M.C.'s showing univalents, bridges and multivalents in the hybrids of the cross involving CAV 4248 did affect the fertility of the F_1 hybrids to a great extent. In these two crosses, there is not much difference in the percentages of fertility among the F_1 plants within a cross.

In the cross, CAV 4904 x Sun II, fertility was greatly reduced in three of the four F_1 plants. For example, seed set of 12.2% was obtained for one of the F_1 plants in which 94% of tetrads had micronuclei. One of the F_1 plants had an unusually high fertility percentage of 99%. In this hybrid, the observed frequency of irregular meiosis was comparable to that of the other F_1 plants at MI. Unfortunately, the tetrad stage of this hybrid was not observed.

Seed set obtained in the Bc_1F_1 plants indicates that the percentage of fertility can be increased by backcrossing to Sun II. Seed set of 78.9%, 93.2% and 67% was obtained for the F_1 plants of the crosses involving CAV 4248, CAV 4656 and CAV 4904, respectively. The distribution of fertility percentage of Bc_1F_1 plants of the three crosses is shown in Table XIX. From these data, it can be seen that the Bc_1F_1 plants within crosses involving CAV 4248 and CAV 4656 had similar fertility percentage. That was not so with the cross involving CAV 4904. Plants derived from CAV 4904 x Sun II-2 had excellent fertility while plants

TABLE XIX. Distribution of fertility percentage of backcross F_1 plants.

F_1 plants	No. of Bc_1F_1 plants							
	% Fertility							
	≤ 30	31 - 40	41 - 50	51 - 60	61 - 70	71 - 80	81 - 90	91 - 100
CAV 4248 x Sun II - 1	1	0	1	1	1	4	9	6
2	1	4	2	2	6	7	9	8
3	2	0	3	4	5	4	7	11
4	1	1	0	3	4	5	9	8
5	0	1	2	1	1	3	6	8
CAV 4656 x Sun II - 1	0	0	0	0	1	6	5	34
2	0	0	0	0	2	3	12	36
3	0	0	0	0	1	3	6	22
CAV 4904 x Sun II - 1	5	7	6	3	4	0	1	1
2	0	0	1	0	2	2	11	29
3	5	2	5	2	5	2	3	11
4	9	9	5	2	1	3	2	1

derived from the other F_1 plants had relatively low fertility. It is not known what factors account for this significant difference in fertility level.

DISCUSSION

In crown rust inheritance studies, simple dominance of resistance is commonly observed as was the case in this study with CAV 4904. The resistance gene in CAV 4904 exhibited complete dominance in all rust tests. An equally common occurrence is resistance conferred by partially dominant genes. The resistance gene in CAV 4656 was found to be partially dominant. In CAV 4248, both genes A and C were partially dominant to the races that they conferred resistance to. As for gene B, the nature of dominance is not clear. It was partially dominant to race CR 20 and completely dominant to races CR 13 and CR 36. Apparently, the degree of dominance may vary with the rust race used or the conditions of the test. Simons (1970) found that the dominance of the Landhafer gene varied with different races of crown rust. Also, Fleischmann and McKenzie (1968) showed that gene Pc-39 reacted as a dominant against races 332, 295, 290 and 446, but manifested itself as an incompletely dominant against race 264.

Furthermore, in crosses involving CAV 4248 and CAV 4656, there was an excess of susceptible plants in the segregating backcross families where the resistance was conferred by partially dominant genes. This can in part be explained by the fact the expression of resistance of such genes can be modified by changes in the external environment. Frequently, plants heterozygous for the resistance gene are more sensitive to changes in the environment than are homozygotes. As demonstrated by

Luig and Rajaram (1972), the stem rust resistance gene, Sr 6, when homozygous in a Marquis background, was ineffective at constant temperatures of 24°C and above, whereas the heterozygous F_1 plants were susceptible at constant temperatures of 15°C and above.

Adult plant tests conducted in the greenhouse and in the field indicated that the resistance genes in the three backcrosses are operative throughout the life of the plant. However, it seems that the effectiveness of the gene in CAV 4656 decreases with age of the plant. When tested with race CR 13, CAV 4656 gave a highly resistant reaction at the seedling stage, whereas at the adult stage, it gave from a moderately resistant to a moderately susceptible reaction. Kiehn et al. (1976) also noted a decrease in effectiveness with the resistance gene Pc-55 in which the resistance afforded at the seedling stage became ineffective against race 305 as the plants matured. Although rust susceptibility is rarely associated with age of the plant, it has been noted in A. sterilis by Dinoor (1970). Similarly, Martens et al. (1968) showed that with the gene Pg-12, resistance to oat stem rust diminished as the plants developed.

Due to a very warm and dry summer in 1980, the incidence of crown rust in Manitoba was very low (Harder and Clark, 1981). Therefore, the field rust tests were not able to show the effectiveness of these resistance genes against the naturally occurring crown rust populations in Manitoba.

Lines of Pendek possessing the single genes Pc-35, Pc-38, Pc-39, Pc-40, Pc-45, Pc-46, Pc-48 and Pc-56 were used as the male parents in crosses with each of the A. sterilis accessions. Results of tests on the F_2 progenies indicate that the resistance gene in CAV 4656 is independent of these Pc-genes. Due to the nature of the rust tests, only one of the

three resistance genes in CAV 4248 was more or less fully tested with respect to its relationship with the Pc-genes. Gene A was found to be independent of the Pc-genes except gene Pc-40 for which the population size was too small to reach any conclusion concerning the interrelationship of genes A, B and Pc-40.

A 13:3 ratio was obtained in crosses involving genes Pc-48 and Pc-56. There are two possibilities that might explain this ratio. Either gene A or genes Pc-48 and Pc-56 must act as a recessive. Changes in dominance due to gene interaction or genetic background are known. Harder et al. (1980) reported that gene Pc-48 behaved as a dominant in the cross with gene Pc-63 but as a recessive in the cross with gene Pc-62. Thus, gene Pc-48 might behave as a recessive in the cross involving CAV 4248, resulting in a 13:3 ratio.

Both genes A and Pc-56 are partially dominant. Generally, plants heterozygous for the resistance gene are sensitive to environmental changes and stage of plant growth. Immature leaves are often more susceptible than older leaves. For instance, McKenzie et al. (1970) found that the fully matured leaves of plants heterozygous for the resistance gene Pg-13 were resistant to oat stem rust while the young leaves were not. Moreover, slight variations in temperature may cause plants heterozygous for the resistance gene to become more susceptible.(Luig and Rajaram, 1972). Thus, these factors might explain for the excess of susceptible plants, resulting in a poor fit to a 15:1 ratio.

In order to clarify the relationship between genes A, B, C and the Pc-genes where necessary, crosses with homozygous plants of desirable genotypes (AAbbcc, aaBBcc and aabbCC) and the Pc-genes will be required.

Nevertheless, genes A, B and C are distinct from known Pc-genes

previously isolated from A. sterilis, based on the infection types and the spectrum of their resistance to 15 different races.

The resistance gene in CAV 4904 appears to be allelic or closely linked to gene Pc-46 which is tightly linked or allelic with gene Pc-50 (Fleischmann et al., 1971). Gene Pc-46 produced resistant infection types ranging from a (;) to (2)N depending on the race used. Gene Pc-50 usually produced a (0)(;) or (;) infection type to the races that it conferred resistance to. The gene in CAV 4904 consistently produced a (0)(;) infection type to all races tested. It is known that gene Pc-46 does not confer resistance to a number of races including CR 13, CR 25, CR 107, CR 123 and CR 124. Gene Pc-50 confers resistance to these races but not to race CR 20 and a number of others. Since the resistance gene in CAV 4904 confers resistance to all these races while neither gene, Pc-46 or Pc-50 does, it is concluded that they are clearly different alleles if located at the same locus or closely linked genes. It is of interest that the stem rust resistance genes Pg-3 and Pg-9 also appear to be at or near this locus (Dr. R.I.H. McKenzie, personal communication). Furthermore, these Pg- genes are associated with gene Pc-44 in repulsion (Martens et al., 1968). Apparently, a cluster of genes conferring resistance to crown rust and stem rust are located at or near the same locus.

The close linkage, or possible allelic relationship, of the resistance gene in CAV 4904, genes Pc-46 and Pc-50 is of significance in the development of multigene cultivars. Assuming linkage, results obtained suggest that extremely large populations would have to be grown to recover recombinant types possessing the three resistance genes from repulsion-type crosses. If they are true alleles, then recombination will not be possible.

Similar events have been noted with other Pc- genes. Genes Pc-38, Pc-62 and Pc-63 appear to be tightly linked (Harder et al., 1980) as are genes Pc-39 and Pc-55 (Kiehn et al., 1976) and genes Pc-35 and Pc-54 (Martens et al., 1980). It could be of great interest to find out more about the complexity of these interrelationships.

On the basis of the rust races used in this study, the resistance gene in CAV 4904 appears to have the same spectrum of crown rust resistance as genes Pc-58 and Pc-61. Since races virulent on the latter are not available; these three genes can only be said to be distinct, based on the infection types. Both genes Pc-58 and Pc-61 usually produce characteristic (;) infection types to the races that they confer resistance to, while the resistance gene in CAV 4904 consistently produces a (0)(;) infection type.

Diallel crosses of the three A. sterilis accession were not made, thus it is not known if the resistance genes possessed by them are linked or allelic. However, these genes are clearly distinct as each has a different spectrum of resistance.

The inheritance of floret characters has been studied by a number of investigators including Fraser (1919), Florell (1931) and Philp (1933). Monogenic segregations are generally reported for awns and lemma pubescence. Lemma color is often reported to be either controlled by one or two genes. The results obtained from the three backcrosses agree with the earlier findings.

Results of the Chi-square test for independence between the three floret characters show that linkage exists between lemma color and awns in CAV 4248 x Sun II^2 and lemma color and lemma pubescence in crosses involving CAV 4656 and CAV 4904.

Kiehn et al. (1976) reported a gene for grey lemma color linked by 2.04 ± 2.00 recombination units to a gene for awns in the Pendek[2] x CAV 4963 cross. This is close to the crossover value of 4.58 ± 1.86% between the gene for grey lemma color and the gene for strong awns found in the CAV 4248 x Sun II[2] cross.

The gene for brown lemma color and the gene for lemma pubescence appear to be tightly linked in the CAV 4904 x Sun II[2] cross. No recombinant classes were obtained. In the CAV 4656 x Sun II[2] cross, one of the two genes governing grey lemma color is associated with the gene for lemma pubescence by a recombination value of 28.30 ± 4.87%. Similarly, Florell (1931) found that hairiness of lemma to be almost completely linked with brown color of lemma in the cross A. fatua x A. sterilis. Philp (1933) obtained no recombinants in the reciprocal F_2's of A. fatua x Banner and the F_2 of A. fatua x gigantica.

The study of linkage relations between disease reaction and morphological characters is of importance from a plant breeding point of view since it gives an indication of the possibility of combining desirable expressions of the latter with disease resistance by hybridization. No linkage was detected between the three floret characters and reaction to crown rust in any of the crosses studied. Furthermore, since linkage was noted only between floret characters derived from A. sterilis, there should be no difficulty in transferring the crown rust resistance genes.

The parental lines and their hybrids were examined cytologically. Univalents were the only meiotic irregularities observed in the parents. Quadrivalents have been reported to occur in relatively low frequencies in Sun II (Hacker and Riley, 1965; Lin, 1968). Hacker and Riley (1965) suggested that the incidence of quadrivalent formation may result from

translocation heterozygosity, or from the association of non-homologous chromosomes. Lin (1968) believed that at least part of the multivalent formation is due to the latter.

In this study, there was a high level of meiotic irregularity in all hybrids with univalents being the most common type although bridges were also observed. Multivalents were seen only in hybrids of CAV 4248 x Sun II and CAV 4656 x Sun II. Bridges and multivalents are evidence of paracentric inversions and interchanges, respectively. This cytological evidence strongly suggests segmental differences between the parental chromosomes. In this respect, Sun II and CAV 4904 differ by at least one pair of chromosomes while Sun II differs from CAV 4656 and CAV 4248 by two pairs of chromosomes. Lin (1968) also observed univalents and multivalents in hybrids of crosses involving Sun II which he concluded differed from Garry and Rodney by at least one reciprocal translocation and from Victoria by at least two reciprocal translocations.

The results obtained indicate that irregular meiosis in the hybrids of the hexaploid oat are apparently common. The occurrence of these meiotic irregularities could be the result of homoeologous pairing and structural differentiation (Nishiyama, 1929; Philp, 1933; Akerman and Hagberg, 1954; Marshall and Myers, 1961; Hacker and Riley, 1965). Ladizinsky (1970) believed that translocation between homoelogous chromosomes is most likely the major contribution to the variation observed.

All F_1 plants showed a lower seed set than the parents. This was probably caused by the rather high irregular meiosis. However, the fertility of the hybrids of CAV 4656 x Sun II was not as drastically reduced as that of the hybrids of the other crosses. This could be due to a more effective elimination of aberrant gametes and the buffering effect of

polyploidy. The improved fertility of the Bc_1F_1 plants of all crosses indicated that meiotic chromosome behavior is more stable in a more homozygous background. The hexaploid oat is an inbreeder and it is normal to show increased meiotic irregularities in a heterozygous state (Hafiz and Thomas, 1978).

The rich and heterogeneous source of resistance to crown rust in A. sterilis has an immediate practical value in the improvement of cultivated oat varieties. Since A. sterilis and A. sativa both are hexaploids, there should be no difficulty in transferring resistance genes. As demonstrated in this study, the resistance genes from the three A. sterilis accessions could be readily transferred into the susceptible variety Sun II, via the backcross method. Although the F_1 plants have a rather high proportion of P.M.C.'s with irregular meiosis, hybridization and gene-flow were effectively buffered by polyploidy as indicated by the homogeneous F_2 populations of the three backcrosses.

The crucial problem of classical breeding for resistance resides in the fact that new resistance genes in time become ineffective because of selections in favor of new corresponding virulence genes in the pathogen. To maximize the effectiveness of resistance genes, several strategies have been advocated. These include multigene varieties (McKenzie et al., 1972), multiline varieties and deployment of resistance genes (Browning and Frey, 1969; Frey et al., 1977). However, any of these systems require the use of a number of resistance genes.

To determine the usefulness of the resistance genes identified in this study, further investigations are needed to ascertain the relative spectrum of resistance afforded by each gene. Of all the resistance genes identified, the resistance gene in CAV 4904 and gene A in CAV 4248

were shown to have a wide spectrum of resistance. Therefore, these two genes would provide effective resistance when combined. The resistance gene in CAV 4656 and genes B and C in CAV 4248 could be useful for the breeding of multiline cultivars. These three genes are effective only against some of the prevailing virulent races. This would fit in the "dirty crop approach" advocated by Browning et al. (1969).

Thus, these five resistance genes may be very useful in prolonging the life of the cultivars in which they will be released.

SUMMARY

The inheritance of crown rust resistance and floret characters in three A. sterilis accessions was studied using Bc_1F_2 families. In CAV 4248, the crown rust resistance was conferred by three independent, partially dominant genes. These were designated A, B and C. Gene A conferred resistance to all but one of the races tested; gene B conferred resistance to nine of the 15 races tested and gene C to six of them. CAV 4656 had one partially dominant gene which conditioned resistance to 13 of the races tested. The resistance gene in CAV 4904 was dominant, conferring resistance to all races tested.

All the resistance genes conferred resistance throughout the life of the plant.

In CAV 4248, gene A was independent of genes Pc-35, Pc-38, Pc-39, Pc-45, Pc-46, Pc-48 and Pc-56. Gene B was independent of genes Pc-35 and Pc-38. The population size of the cross, CAV 4248 x Sun II, was too small to indicate the relationship between genes A, B and gene Pc-40. The interrelationship of genes B, C and the other Pc- genes were not tested. The resistance gene in CAV 4656 and the eight Pc- genes were inherited independently. The resistance gene in CAV 4904 was allelic or closely linked with gene Pc-46. It was independent of the other Pc- genes.

Awns and lemma pubescence were inherited monogenically in the three crosses, while grey lemma color was controlled by one gene in the cross

involving CAV 4248 and by two genes in the cross involving CAV 4656. In the CAV 4904 x Sun II^2 cross, the brown lemma color was controlled by one gene which appeared to be completely linked with the gene for lemma pubescence. In the CAV 4656 x Sun II^2 cross, one of the two genes governing grey lemma was associated with the gene for lemma pubescence by a recombination value of 28.30 $\pm$ 4.87%. In the CAV 4248 x Sun II^2 cross, the gene for grey lemma and the gene for strong awns were linked with a crossover value of 4.58 $\pm$ 1.86%.

No significant association was found between crown rust reaction and the three floret characters studied.

There was considerable meiotic instability in all hybrids. Chromosome pairing suggested that Sun II differs structurally from CAV 4904 by at least one pair of chromosomes and from CAV 4656 and CAV 4248 by two pairs of chromosomes.

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