

THE INHERITANCE OF RESISTANCE  
IN RYE TO PUCCINIA RECONDITA  
F. SP. TRITICI AND SECALIS

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the University of Manitoba in partial fulfillment of the requirements  
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## FOREWORD

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This thesis is written in the paper style, specified in the 1976 Plant Science Thesis Preparation Guide. It contains one manuscript entitled, 'The inheritance of resistance in rye to Puccinia recondita f. sp. tritici and secalis'. It is intended that the manuscript be submitted for publication to the Canadian Journal of Genetics and Cytology. This format has been approved by the Master's Thesis Examining Committee.

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## GENERAL ABSTRACT

MUSA, GABRIEL LEONTELIE CHANDA

M.Sc., The University of Manitoba, February, 1982

THE INHERITANCE OF RESISTANCE IN RYE  
TO PUCCINIA RECONDITA F. SP. TRITICI AND SECALIS

ADVISOR: D.J. SAMBORSKI

The genetics of seedling resistance in rye (Secale cereale L.) to rye leaf rust (Puccinia recondita secalis) and wheat leaf rust (P. recondita tritici) was studied in the F<sub>2</sub> and F<sub>3</sub> generations. The genetic relationships between the six resistant parents were studied in the F<sub>2</sub>. Genetic studies were carried out using isolate RLR 213/78 of rye leaf rust and race 30 of wheat leaf rust. The spectrum of resistance present in seven inbred ryes and some selected lines were further tested with races 5, 9, 15, 76 and 126a of wheat leaf rust. The parents were also tested for seedling reaction to rye stem rust isolates RSR 59/79, RSR 101/80, RSR447/78 and wheat stem rust races C17(56), C53(15 Bil) and C61 (38). Furthermore, the parents were also tested for field resistance in a rust nursery.

Resistance to RLR 213/78 was conditioned by single genes in UM8003, UM8071 and UM8301, two genes in UM8336 and UM8340, and three genes in UM8295. UM8071 has a single recessive gene for resistance to race 30, UM8003 and UM8340 each have two genes for resistance to race 30, while UM8295, UM8301 and UM8336 each have three genes conditioning resistance to this race.

UM8295 and UM8301 were heterogeneous for their resistance genotypes. Resistance was recessive in UM8071, both recessive and dominant genes were present in UM8003 and UM8340, otherwise most parents had partially or completely dominant genes.

All the resistant parents appeared to have independent genes for resistance to RLR 213/78. At least some of the parents have identical or very closely linked genes for resistance to race 30. UM8340 has at least one gene that may condition resistance to both rust species. Gene LrGW1 in UM8301 appears to be readily influenced by modifying factors. UM8336 and UM8340 both appear to have a broad spectrum of resistance to both P. graminis and P. recondita. In field tests all six resistant parents and the susceptible parent UM8116 were resistant to both leaf rust and stem rust.

The genes identified in each resistant parent have been assigned the following temporary symbols; UM8003 - LrPk1 (RLR 213/78), LrPk2 and LrPk3 (race 30); UM8071 - LrPr1 (RLR 213/78), LrPr2 (race 30); UM8295 - LrGB1, LrGB2 and LrGB3 (RLR 213/78), LrGB4, LrGB5, and LrGB6 (race 30); UM8301 - LrGW1 (RLR 213/78), LrGW2, LrGW3 and LrGW4 (race 30); UM8336 - LrEm1 and LrEm2 (RLR 213/78) LrEm3, LrEm4 and LrEm5 (race 30); and UM8340 - LrHz1 and LrHz2 (RLR 213/78) LrHz3 and LrHz4 (race 30). The results obtained from this investigation indicate that in rye a reservoir of genes exist for leaf rust resistance that can be exploited in rye, wheat and triticale breeding programs.

SECTION I  
INTRODUCTION  
AND  
LITERATURE REVIEW

## 1. GENERAL INTRODUCTION

The leaf rust fungus (Puccinia recondita Rob. ex. Desm.) is one of the most specialized pathogenic fungi attacking cereals. It is divided into several varieties (formae speciales) according to the responses produced by the host. The leaf rust of rye (P. recondita Rob. ex. Desm. f. sp. secalis) is found on rye, while leaf rust of wheat (P. recondita Rob. ex. Desm. f. sp. tritici) occurs on wheat.

The terms, P. recondita tritici and secalis, will be used to describe wheat leaf rust and rye leaf rust, respectively. Both P. recondita tritici and secalis are co-extensive, for the two rusts are found practically in all parts of the world where their respective hosts are grown.

Epiphytotics of leaf rust can cause great losses in yield. However, the yield losses caused by leaf rust have not been fully appreciated. This is due to the comparisons with the more spectacular destruction caused by stem rust (Puccinia graminis tritici) (Anderson, 1961). Wheat yields have been markedly reduced by severe leaf rust infections (Samborski and Peturson, 1960; Johnston, 1973). However, the use of resistant cultivars has been a highly successful method for control of leaf rust and reduction of yield losses (Samborski and Peturson, 1960). Leaf rust has been reported to cause spectacular losses in the quality and or quantity of the wheat crop (Eversmeyer and Browder, 1974) and of rye (Starzycki, 1976) each year. Under severe infections, as much as 46 percent yield reduction has been

reported on susceptible cultivars (Srivastava et al., 1974). Zwatz (1977) reported a 20 per cent yield reduction after infection of wheat and rye by P. recondita. Losses in yield caused by wheat and rye leaf rust in the United States from 1918 to 1976 have been presented by Roelfs (1978).

Rye (Secale cereale L.) is a potential source of genes for disease resistance. Some individuals of rye resistant to rye leaf rust were discovered by Mains (1926), and Mains and Leighty (1923). Mains (1926) obtained plants from Abruzzes rye, which were highly resistant to leaf rust (P. recondita), stem rust (P. graminis) and powdery mildew (Erysiphe graminis secalis). Resistance was found to be dominant over susceptibility. Several genes for rust resistance have been incorporated into the wheat complement (Acosta, 1963; Driscoll and Jensen, 1963, 1964; Rao, 1977). It is now known that several European wheat cultivars derive their resistance to P. graminis, P. recondita and P. striiformis from rye chromosome IR, which was substituted for wheat chromosome IB or was translocated with chromosome IB (Zeller, 1973).

Recent genetic studies have revealed several genes for resistance to P. graminis tritici and secalis in inbred lines of rye (Tan et al. 1976, 1977). Resistance to P. graminis tritici was conditioned by a total of eight different genes, while six different genes conditioned resistance to P. graminis secalis.

Literature on the genetics of leaf rust resistance in

rye is rare. The heterozygous nature of rye complicates genetic studies thus making it difficult to breed for disease resistance. However, cultivars of rye resistant to leaf rust have been reported (Morey, 1956, 1970, 1973). The availability of inbred lines of rye has facilitated genetic studies. The present study attempts to create an understanding into the genetics of resistance in rye to both wheat leaf rust and rye leaf rust and to identify whether the genes conferring resistance to P. recondita tritici and secalis are the same or different. A knowledge of the number of genes conditioning resistance and the linkage relationships among the resistance genes will assist in the selection of a breeding procedure to be used in the development of resistant varieties.

This appears to be the first study to report on the inheritance of resistance in rye to P. recondita tritici and secalis.

## 2. LITERATURE REVIEW

### 2.1. Expression of Resistance

Resistance is any inherited characteristic of a host plant which lessens the effects of parasitism (Russell, 1978). Resistant plants are less damaged by parasites than are susceptible plants. Robinson (1969) defines resistance as the ability of the host to hinder a pathogen or disease causing agent.

Various degrees of resistance and susceptibility to rust have been found to occur within host species. The most susceptible hosts show an abundance of large, well developed uredia without any pronounced chlorosis of the host. Less susceptible hosts show fewer and smaller uredia occasionally with chlorosis. With increase in resistance, there is a decrease in the number and size of the uredia and an increase in the proportion of necrotic areas without uredia. In the most highly resistant varieties only faint flecks occur. The resistant phenotype of the host is the end result of the interaction of its genetic constitution with that of the pathogen and the environment.

## 2.2. Genetics of Resistance

Disease resistance in plants is often classified into two broad categories, race specific and race nonspecific resistance.

### 2.2.1. Specific Resistance

This form of resistance is presumed to be controlled by major genes each of which gives a large effect. Resistance of this type is effective against one or more races of a pathogen and ineffective against others. Effective resistance genes are those on which the pathogen race is avirulent, and ineffective resistance genes are those on which the pathogen race is virulent (Green, 1981).

Watson (1977) summarized specific resistance as one which is:

- (1) Controlled by single genes throughout the life of the plant.
- (2) Controlled by single genes in the adult plant stage only.
- (3) Controlled by a combination of specific resistance genes each of which operates throughout the life of the plant.
- (4) Combination of genes giving seedling resistance with those giving adult plant resistance.

More often specific resistance is dominant over susceptibility. The ability of a pathogen to overcome genes for specific resistance is usually a recessive trait. (Samborski and Dyck, 1974; Nelson, 1975). The genes conditioning specific resistance can be differentiated on the reaction to a particular race(s). Seedling plant reactions are used for the identification of rust races through the use of "single - gene differentials" (Green, 1981). Although specific resistance is often overcome by a



pathogen that has acquired virulent genes it is the most popular method of controlling disease because it is relatively easy to handle. Knott (1972) has reviewed the use of race-specific resistance in managing the evolution of plant pathogens.

#### 2.2.2. Nonspecific Resistance

This type of resistance is considered to be determined by many genes, each of which gives a small effect. This effect is not restricted to particular races of a pathogen and the minor genes are considered to be effective against all individuals of the pathogen species. This kind of resistance is called horizontal resistance, a controversial term coined by Van der Plank (1968). Nelson (1972) states that this type of resistance reduces the amount of disease that develops and the rate of disease increase. However, Watson (1977) indicates that this type of resistance is still poorly defined in the case of cereal rusts. Where defined studies are made, nonspecific resistance may be shown to be simply inherited (Ellingboe, 1975).

Recently, Ellingboe (1981) presented some studies on the development of mildew (Erysiphe graminis) on Genesee wheat, a slow mildewing cultivar. He showed that with experiments in the greenhouse, where the environment is somewhat variable, the results suggested that the slow mildewing is controlled by a large number of genes (quantitatively inherited trait). Under controlled environments the experiments suggested that the slow mildewing trait was controlled by a single gene. Ellingboe (1981) concluded that careful studies seem to support the fact that non-

specific (horizontal) resistance, is resistance that has not yet been shown to be race specific (vertical). When the experiment is of a cursory nature, resistance is frequently considered to be nonspecific (horizontal) in nature. But when experiments are more precise and analytical, resistance seems to be of a specific (vertical) nature. Therefore, nonspecific (horizontal) resistance, is resistance where the gene-for-gene relationship between host and pathogen has not been precisely determined.

### 2.3. Genetics of Rust Resistance

In 1905, Biffen reported that resistance to yellow rust of wheat is inherited in a Mendelian manner. In general, resistance to wheat leaf rust is inherited in a Mendelian fashion when hybrids from lines are tested for reaction to pure rust races. The literature on inheritance of resistance to physiologic rust races in wheat and corn is voluminous. The examples presented in this review only show its diversity. Chester (1946) reviewed early studies of inheritance of leaf rust in common wheat and found that leaf rust resistance was inherited in a simple Mendelian fashion.

Most studies on physiologic specialization have involved specific resistance. This resistance is usually expressed by seedlings but may also be seen in older plants (Dyck et al. 1966; Dyck and Samborski, 1979). Segregation for specific resistance usually fits simple genetic ratios.

Rust resistance can be conditioned by a single gene, two or several genes acting independently. Genes may be linked, show gene interaction or transgressive segregation.

#### 2.3.1. Single Gene Inheritance

Resistance that is due to a single completely dominant gene is the commonest and simplest mode of inheritance. Single partially dominant genes conferring resistance to leaf rust are less common. However, some partially dominant genes have been reported by Ausemus (1943), Dyck (1977) and Dyck and Kerber (1977).

Single recessive genes have been known in several hosts to rust fungi (Rajaram et al. 1971). Rashid et al. (1979) found that leaf rust resistance in three durum wheats was conditioned by a recessive gene. Segregation ratios indicated that one recessive gene conditioned resistance in D561 and D6733. Recessive genes for resistance to corn leaf rust have also been reported by Hooker (1967), and Malm and Hooker (1962). Tan et al. (1976) found a recessive gene that conditions a 2+ infection type to Puccinia graminis secalis in the rye variety 'Elbon x Gator'. Single recessive genes governing adult plant resistance have also been identified in wheat (Dyck and Samborski, 1979).

#### 2.3.2. Two or more genes conditioning resistance in a cultivar

Resistance of a cultivar can be conditioned by several genes. Genetic studies often reveal two, three or more genes for resistance to the same pathogen in one host (Sanghi and Luig, 1971; Dyck and Samborski, 1981).

The genes may be dominant, recessive or a combination of both or show a form of gene interaction (Fitzerald et al. 1957; Dyck and Samborski, 1981). Resistance may also be due to two independent recessive genes or a combination of dominant and recessive genes (Dyck and Samborski, 1968). Anderson (1961) found that two genes conditioned resistance to races 1a and 15a in Exchange and Selkirk. Each of the two genes in Selkirk behave in a dominant manner with the gene responsible for the (;1=) type of reaction being epistatic to that giving the (2) type

reaction. Statler (1972) found that Waldron wheat had one dominant and one recessive gene conditioning resistance to culture 70 - 1 of wheat leaf rust.

Wu and Ausemus (1953), studied leaf rust reaction in a spring wheat cross and reported that Lee and Mida wheat are differentiated by two gene pairs which act additively. Resistance to race 9 and 37 was dominant, while resistance to race 37 and 57 was recessive. Duplicate recessive genes have been reported in wheat by Statler (1973). Fitzgerald et al. (1957) found that resistance to race 65 is controlled by duplicate recessive genes designated as Lr7 and Lr8.

The inheritance of resistance to rust can be complex. Some studies have revealed more than two genes conferring resistance to one physiologic race. Sanghi and Luig (1971) found four genes conditioning resistance to P. graminis tritici and secalis in Mentana wheat. As many as three genes conditioning resistance to strain 21 - 0 of P. graminis tritici have been found in rye (Tan et al. 1977). The observed resistant infection types corresponding to the three postulated genes were ;, ;1 and 2<sup>-</sup>.

Complex resistance to leaf rust has been reported in wheat (Dyck and Samborski, 1981). They showed that Terenzio wheat had four genes (Lr3, Lr30, LrT1 and LrT2) for seedling resistance to leaf rust races used in their study. The crosses involving Terenzio segregated for four genes when tested with race 1, three genes (Lr30, LrT1 and LrT2) when tested with race 126a and two genes interacted to give resistance to race 76.

### 2.3.3. Linkage

Genes can separate independently if they occupy sites on different chromosomes or are located fifty or more cross over units apart on the same chromosome (Hooker, 1967). When two genes are so closely associated that they always segregate together upon coming from the same parent, linkage between them is considered as complete or tight. Complete linkage between genes on the same chromosome is a rarity in most sexually reproducing species (Strickberger, 1968). If the linkage is not complete, the gene pairs in most linkage groups assort at least partially independent of each other. This linkage is regarded as incomplete or loose. Loose linkage of rust resistance genes has been commonly noted (Wu and Ansemus, 1953; McIntosh and Dyck, 1975) but tight linkage has also been observed between genes for rust resistance (Fitzerald et al. 1957; Dyck and Samborski, 1970). Fitzgerald et al. (1957) observed a tight linkage between genes Lr5 and Lr6 with a crossing over percentage of 5.5. Dyck and Samborski (1970) found that two genes, one from Selkirk and the other from Maria Escobar, each giving an X reaction to different races of leaf rust, were alleles or very closely linked. Results from the progeny test of a plant resistant to cultures R - 64 x 4 and R - 67 x 4 indicated that the genes were segregating in coupling phase with an estimated recombination value of  $0.16 \pm 0.16$  per cent. The two genes were considered as alleles and the symbol Lr14a was assigned to the allele in Spica and Selkirk. The allele in Maria Escobar was designated as Lr14b.

In some instances resistance to one rust species has been found to be closely linked or associated with resistance to another rust species (McIntosh et al. 1970; McIntosh and Luig, 1973). The wheat stem rust resistance gene Sr23 is completely linked with Lr16 for reaction to P. recondita (McIntosh and Luig, 1973; McIntosh et al. 1974). In 1976, McIntosh et al. also reported that the wheat cultivars Agent and Agatha each possess closely linked genes for resistance to P. graminis tritici and P. recondita derived from Agropyron elongatum. The genes in Agent located in chromosome 3D, were designated Sr24 and Lr24. The genes in Agatha for resistance to P. graminis tritici was designated Sr25 and is linked with Lr19 in chromosome 7D (McIntosh et al. 1976).

#### 2.3.4. Gene Interaction

Genes interact in a manner so that together they condition a higher level of resistance than each conditions singly. Hooker (1967) states that genes for resistance appear to act as autonomous units, with interaction occurring between alleles of each gene but not between genes which occupy other loci. However, gene products interact and this is reflected in genetic analyses by the appearance of complementation, modification, and epistasis (Hooker and Saxena, 1971).

Complementary gene action describes the interdependence of two or more genes, all of which are essential for the ultimate expression of a character. Two genes conferring a low level of

resistance can interact to give a higher level of resistance. This has been shown by Dyck and Samborski (1981) who found that the two complementary genes in Terenzio, Lr T1 and Lr T2 which confer an intermediate level of resistance, interact to give a high resistant expression in both seedling and adult tests.

Modifier genes bring about a relatively small change in the effect of another locus. In the case of rust reaction the resistance may be either enhanced or reduced. Major genes for rust reaction sometimes modify the action of other genes (Hooker and Saxena, 1971; Nelson, 1972). The effect of a modifier gene can be influenced by the genetic background of the susceptible parent (Dyck and Samborski, 1968). Modifier genes that affect rust reaction have been reported by several investigators (Heyne and Johnson, 1954; Dyck et al. 1966; McIntosh et al. 1967).

The effect of genetic background has been noted with rust resistance genes. Dyck et al. (1966) found that adult plant resistance in Frontana was conditioned by gene Lrl3 which conditions a 2+ reaction to race 5 and is partially dominant. However, in Manitou, which has adult plant resistance transferred from Frontana, this gene is recessive. They also reported, that Lrl2 in Exchange and Lrl3 both require one or more modifiers to produce fleck reactions. Both genes give resistance to a wide range of races of leaf rust. Gene Lrl2 in Exchange conditions a type 2 reaction to race 5. The resistance conferred by Lrl2 can be increased from a type 2 to a fleck reaction in the



presence of modifiers. The genes and their modifiers are very sensitive to environmental change. This was shown by McIntosh and Dyck (1972) who reported that a gene carried by Thatcher inhibited the expression of Lr23 under Canadian test conditions, but acts as a partial inhibitor under Australian test conditions. Differences in temperature or light or both were thought to be involved.

Epistasis results when a gene at one locus superimposes its effect on a gene at another locus or inhibits its expression. It has been reported that genes that condition a higher level of rust resistance are commonly epistatic to those conditioning a lesser reaction (Anderson, 1961; Hooker, 1967; Morrison, 1977). Anderson (1961) found two dominant genes that condition resistance to races 1a and 15a in Selkirk. The gene designated as LrL responsible for the ;1= type of reaction was epistatic to that giving a type 2 reaction. Choudhuri (1958) designated the gene conditioning the ;1= type in Selkirk as Lr10. Morrison (1977) found that the partially dominant genes conditioning a fleck infection type to Cl7. and C33 of P. graminis tritici in the Triticale cultivar 6A 406 were epistatic to those conditioning a type 2 reaction.

Reversal of dominance of resistance genes is not uncommon. In some instances it has been reported that a gene may be expressed as dominant to some biotypes of the fungus and as recessive to others (Hooker, 1967; Dyck and Samborski, 1968). Exchange and Selkirk both carry a dominant gene giving

moderate resistance to races 1a and 15a of leaf rust. But the same gene acts as a recessive to races 5a, 11, and 126a (Anderson, 1968). Dyck and Samborski (1968) observed that the gene for resistance to race 15 in Loros exhibits reversal of dominance. In the cross Thatcher X Loros, the gene was recessive. On the other hand, in the cross with Red Bobs the gene from Loros was dominant. Gene Lr 23 has been shown to exhibit reversal of dominance (McIntosh and Dyck, 1975). Reversal of dominance has also been reported in resistance to stem rust (Bartos et al. 1970).

#### 2.3.5. Transgressive Segregation

Transgressive segregation for rust reaction refers to the appearance of plants in the F<sub>2</sub> or later generations that are either more resistant or more susceptible to rust than either of the two original parents (Hooker, 1967).

In corn, transgressive segregation for adult plant resistance to Puccinia sorghi is not unusual. Lines more resistant and lines more susceptible to rust are both obtainable in the F<sub>3</sub> generation of crosses between resistant and susceptible inbreds (Hooker, 1967). Sharp (1972) reported that genes for stripe rust resistance were found to occur in many winter cultivars which combined through transgressive segregation to condition high levels of resistance in the progeny. These genes were additive and no epistasis was involved.

#### 2.4. Nature of the Pathogen, Leaf Rust (Puccinia recondita)

Puccinia recondita Rob. ex. Desm. the fungal pathogen that causes leaf rust, attacks wheat, rye, and some grasses.

Heavy infections destroy much photosynthetic tissue and draw heavily on the plants supply of food material in the development of the rust, especially for its large spore production. It also increases evaporation through the rupturing of the epidermis of the leaves (Mains and Leighty, 1923; Johnson, 1973). In rye, this disease causes premature drying up of the leaves which adversely affects the quality and feeding value of the straw (Starzycki, 1976).

P. recondita is a complex species that is divided into formae speciales according to host specialization. Wilson and Henderson (1966) include 13 formae speciales of P. recondita. Thus, the pathogen which causes leaf rust of wheat is known as P. recondita tritici (P. triticina Erikss.) while that on rye is known as P. recondita secalis (P. dispersa Erikss.) (Starzycki, 1976; Anikster and Wahl, 1979). Other formae speciales occur on Agrostis, Agropyron, Bromus and other grasses.

P. recondita tritici and secalis, exist on their respective hosts as numerous morphologically similar, but pathogenically distinct, races. Variation in pathogenicity may derive from mutation, hybridization, heterokaryosis or parasexualism (Johnson, 1953; Day, 1960).

Both P. recondita tritici and secalis are heteroecious rusts with a full developmental cycle. The uredia and telial stages of P. recondita tritici and secalis occur on wheat and rye, respectively.

The pycnial and aecial stages of P. recondita tritici occur on species of Thalictrum (meadow rue) and Isopyrum sp., while those of P. recondita secalis occur on Anchusa officinalis and Lycopsis arvensis. In North America, these alternate hosts are probably of little importance in propagation and survival of the organism or in the origin of new physiologic races (Arthur, 1929; Johnston, 1973; Starzycki, 1976). In Portugal, P. recondita tritici commonly infects its alternate host (D'Oliveira and Samborski, 1966) while natural infection of Thalictrum spp. by the wheat leaf rust fungus in North America is rare (Young and Prescott, 1977).

The uredial stage of P. recondita secalis has been observed to overwinter in the rye plant itself (Morey, 1973). Other cereals and wild grasses play no part in the overwintering and spread of this disease because it has been found that this rust is closely restricted to rye in as much as P. recondita tritici is restricted to wheat. Thus, most wheats are resistant to P. recondita secalis and most ryes are resistant to P. recondita tritici.

Unlike the stem rust fungi (P. graminis tritici and secalis), which can be hybridized fairly easily (Watson and Luig, 1959; Green, 1971), and both can attack cultivated and wild barley (Hordeum vulgare L., and H. jubatum L., respectively), the leaf rust fungi (P. recondita tritici and secalis) are cross-incompatible (Anikster and Wahl, 1979). Both P. recondita tritici and secalis are thus highly specialized pathogens with a narrow host range.

#### 2.4.1. Wheat Leaf Rust ( P. recondita tritici)

The leaf rust of wheat (P. recondita tritici) is present in varying degrees of severity in all regions where wheat is grown. Wheat leaf rust occurs every year in most wheat growing areas in Canada (Samborski, 1980). Because of its wide distribution the importance of leaf rust in the wheat industry is second only to stem rust (P. graminis). The loss in yield is due to a reduction in the number and size of the kernels. Numerous sources of resistance exist among the species of Triticum. According to Chester (1946) a high degree of susceptibility is characteristic of species with the haploid number of 21 chromosome pairs. The 7 - chromosome wheat, T. monococcum has a very high degree of resistance to leaf rust. The tetraploids (14 chromosome wheats), are characterized by moderate to high resistance to leaf rust.

The severity of leaf rust on wheat has been minimized through the use of resistant varieties. However, resistance is often overcome by new physiologic races.

In North America the persistence of leaf rust from year to year is due to the overwintering of the uredial stage in the southern United States and Mexico (McDonald, 1967). Much of the information in this area has been reviewed by Quinones (1972).

#### 2.4.2. Rye Leaf Rust ( P. recondita secalis)

Leaf rust of rye (P. recondita secalis) is generally prevalent on rye. It is widely distributed on this host and many wild species of the genus Secale (Dickson, 1956).

In economic importance this rust is quite similar to wheat leaf rust (P. recondita tritici) especially when the relative value of the two hosts is considered. If heavy infection occurs early leaf rust can cause a reduction in tillering and grain yields (Dickson, 1956; Leonard and Martin, 1963). Losses occur in greater abundance in the southern range of rye culture where the fungus overwinters in greater abundance (Dickson, 1956). Morey (1973) states that leaf rust of rye is the most serious disease of rye in Georgia especially in the Coastal Plain area.

Leaf rust of rye is not very destructive in Western Canada, because winter rye, which is widely grown, matures before the rust has had time to produce much infection (McDonald, 1967). However, under conditions favourable to infection, the rust fungus can cause considerable damage, especially to spring rye. Severe infections with rye leaf rust occur in Western Europe and the Soviet Union where large acreages of rye are grown.

Resistant individuals have been found in a number of varieties (Mains, 1923; Morey, 1956, 1973; Martin and Leonard, 1967). A study of the inheritance of resistance in crosses involving resistant individuals indicated that resistance was probably dominant (Mains and Leighty, 1923).

Gator and Explorer ryes in the southern United States carry leaf rust resistance (Martin and Leonard, 1967). Morey (1970, 1973) indicates that Weser rye is resistant to rye leaf rust while Gator rye has satisfactory resistance to leaf rust,

stem rust, and powdery mildew. Certain varieties, Prolific, Rosen and Tetra Petkus rye (a tetraploid version of diploid Petkus rye) are very susceptible to rye leaf rust (Quinones, 1972; Morey, 1973).

The existence of physiologic races in rye leaf rust was demonstrated by Mains (1926) and Gassner and Kirchoff (1934). Mains (1926) found that an inbred line of Abruzzes rye was highly resistant to one physiologic form but susceptible to another.

#### 2.5. Resistance of Wheat - Rye Hybrids to Leaf Rust

Leaf rust has been reported on wheat-rye hybrids (Chester, 1946; Mains and Leighty, 1923; Zillinsky, 1974). Chester (1946) pointed out that numerous wheat-rye hybrids partake of the wheat parents reactions; susceptibility to wheat leaf rust and resistance to rye leaf rust.

Jensen and Kent (1952) reported rust resistance from Rosen rye in a winter wheat selection. Driscoll and Jensen (1964) studied this leaf rust resistance. They reported that "all plants with either a single or double dose of a gene for resistance exhibited the mesothetic (x) reaction at the first leaf stage, but later stabilized at the "1" reaction type at the six leaf stage". Similar results were reported later by Mukade et al. (1970) and Mukade (1978) who transferred leaf rust resistance from rye to wheat. Their results indicated that the added rye chromosome had a dosage effect. Both monosomic and disomic additions were found to be highly resistant under field conditions.

Leaf rust has been reported on triticales (Larter et al. 1969). However, although leaf rust is more of a problem in triticales than stem rust adequate resistance is available (Larter, 1975). The resistance of triticales to leaf rust has been reported by several workers (Stuchilikova and Martos, 1979; Gospodinova and K'rzhin, 1980; Korodkova, 1980). Stuchilikova and Martos tested a set of 187 triticales to three isolates of P. recondita secalis and P. graminis secalis. All the triticales were resistant to P. recondita secalis and most to P. graminis secalis although fluctuating reactions and mixtures of resistant and susceptible plants were observed.

The inheritance of resistance to leaf rust in hexaploid triticales has been studied by Quinones (1972). Quinones tested six hexaploid triticales and found that resistance to leaf rust was controlled by a single dominant gene in each resistant parent. He also concluded that the resistance carried by the rye parent was not expressed in the F<sub>1</sub> triticales hybrids. However, Quinones (Pers. Comm.) contends that this may only be true in certain cases. Resistance to leaf rust in triticales can come from either wheat or rye (Samborski, Pers. Comm.). Morrison (1977) indicated that all the three ryes which Quinones had used in synthesizing the amphiploid triticales were susceptible to rye leaf rust and resistant to wheat leaf rust.

If ryes resistant to both rusts had been used different results could have been obtained. This view is supported by the



fact that certain European wheat cultivars derive their resistance to P. graminis, P. recondita and P. striiformis from rye chromosome IR which was either substituted for or translocated with wheat chromosome IB (Zeller, 1973).

SECTION II  
THE INHERITANCE OF RESISTANCE  
IN RYE TO PUCCINIA RECONDITA  
f. SP. TRITICI AND SECALIS

## 1. ABSTRACT

THE INHERITANCE OF RESISTANCE IN RYE  
TO PUCCINIA RECONDITA F. SP. TRITICI AND SECALIS.

G.L.C. MUSA

The genetics of seedling resistance to isolate RLR 213/78 of rye leaf rust (Puccinia recondita f. sp. secalis Rob. ex Desm.) and race 30 of wheat leaf rust (P. recondita f. sp. tritici Rob. ex Desm.) was investigated in six inbred lines of rye (Secale cereale L.) The inbred line UM8116 used as the susceptible parent in the crosses was susceptible to both rusts. The following temporary symbols have been assigned to the genes identified in each resistant parent that condition resistance to RLR 213/78 and race 30; UM8003 - LrPk1 (RLR 213/78), LrPk2 and LrPk3 (race 30); UM8071 - LrPr1 (RLR 213/78) LrPr2 (race 30); UM8295 - LrGB1, LrGB2 and LrGB3 (RLR 213/78), LrGB4, LrGB5 and LrGB6 (race 30); UM8301 - LrGW1 (RLR 213/78), LrGW2, LrGW3 and LrGW4 (race 30); UM8336 - LrEm1 and LrEm2 (RLR 213/78, LrEm3, LrEm4 and LrEm5 (race 30); UM8340 - LrHz1 and LrHz2 (RLR 213/78); LrHz3 and LrHz4 (race 30). One of the genes in UM8340 may condition resistance to both rusts. The genes for resistance to RLR 213/78 appear to be independently inherited while some of the genes conferring resistance to race 30 may be identical or very closely linked. The potential of rye as a source of genes for disease resistance in wheat and triticale improvement is discussed.

## 2. INTRODUCTION

Cultivars of cereal rye (Secale cereale L.) are in general resistant to wheat leaf rust (Puccinia recondita tritici) and some are resistant to rye leaf rust (P. recondita secalis). But, little if any information is available on the inheritance of resistance to these rusts, nor is there any report on whether there are genes conditioning resistance to both rusts. However, studies dealing with the genetic basis of resistance in wheat (Triticum aestivum L.) to both rye stem rust (Puccinia graminis f. sp. secalis Eriks. and Henn.) and wheat stem rust (P. graminis f. sp. tritici Eriks. and Henn.) have been reported by Sanghi and Luig (1971) and Sanghi and Baker (1972). Tan et al. (1976, 1977) have also reported on the inheritance of resistance in inbred rye to P. graminis tritici and secalis.

Rye has been used as a source of resistance to several wheat pathogens. Acosta (1963) developed several wheat translocation lines which derive their resistance from chromosome 3R of Imperial rye (Biellig and Driscoll, 1973). Certain European wheat cultivars derive their resistance to leaf rust, stem rust and stripe rust from rye chromosome IR which was substituted for or translocated with chromosome IB (Zeller, 1973). Driscoll and Anderson (1967) indicated that the wheat cultivar Transee derives its leaf rust resistance from rye chromosome 2R. Riley and Macer (1966) failed to associate stem rust and leaf rust resistance with rye addition lines derived from a Holdfast-King II amphi-

ploid and suggested that resistance in the donor rye parent (King II) was conditioned by chromosome interaction.

The resistance of rye can add to the genetic diversity in wheat and triticales breeding programs. The present investigation was made to determine the number and relationship of genes conditioning resistance to one culture each of P. *recondita* tritici and secalis in six resistant inbred lines of rye.

The inbred lines of rye, Secale cereale L. ( $2n = 14$ ) used as parents in this investigation, their UM Accession numbers, inbred generations and reactions to rye leaf rust isolate 213/78 and race 30 of wheat leaf rust are given in Table I. One hundred and ninety inbred lines of rye were tested to both rusts. Only lines which were resistant to both rusts and appeared to be homogeneous in pathological tests were selected. One inbred, UM 8116 was susceptible to both rusts and was used as a common susceptible parent. The six resistant parents were chosen because they differed in rust reaction and origin. The inbreds were originally developed by Dr. D. D. Morey of the University of Georgia, College of Agriculture, Coastal Plain Station, Tifton, Georgia, U.S.A. These lines were already inbred for several generations. (Table I).

The six resistant parents were crossed to the susceptible parent UM8116. To establish allelism or linkage relationships, the six resistant parents were intercrossed. All the crosses were made in the growth cabinet during the fall of 1979. The F1 plants of both susceptible x resistant and resistant x resistant crosses were grown in isolation in different growth cabinets or greenhouses. After seedling tests, the F2 plants of susceptible x resistant crosses were grown to maturity in the greenhouses. The heads on each plant were bagged in order to prevent outcrossing.

TABLE I

Parentage and Seedling Reaction of  
Inbred Lines of Rye to Isolate  
RLR 213/78 of Rye Leaf Rust and  
Race 30 of Wheat Leaf Rust

Accession Numbers	Parentage	Inbred Gen. *	Seedling reaction to leaf rust **	
			RLR 213/78	Race 30
8003	Petkus C.A.N. 1933	S7	1 <sup>+</sup>	0;1
8071	Self Fertile Prolific	S8	2-2 <sup>+</sup> c	2-2 <sup>+</sup> c
8116	Self Fertile Spring	S7	3-3 <sup>+</sup>	2 <sup>+</sup> -3
8295	Gator/Brazil	Sx + 2	0;1 <sup>-</sup>	;n
8301	Gator/Wrens	Sx + 1	0;1 <sup>+</sup> -1 <sup>+</sup>	0;
8336	Emory rye	Sx + 1	0;	0;
8340	Hazel rye	Sx + 1	0;	0;1n

\*Sx = Inbred for more than 10 generations; Sx + 2 = Inbred for two more generations.

\*\* 10 Seedlings of each inbred line were tested for rust reactions.

The F2 or F3 lines to be tested for reaction to leaf rust were grown in pots or flats in the greenhouse during the winter or spring months. At the 1 to 1½ leaf stage, the F2 seedlings from the susceptible x resistant crosses were inoculated with rye leaf rust RLR 213/78 by placing urediospores on the moistened index finger and using the thumb and index finger to streak spores on the surface of individual leaves. About 5 to 6 days later the second leaf was inoculated in a similar manner with wheat leaf rust race 30.

The F2 plants from resistant x resistant intercrosses and F3 lines from susceptible x resistant crosses were either inoculated by dusting with a mixture of talc and urediospores of one rust or by shaking the spores from rusted plants. The rust inoculum was increased on the susceptible cultivars, Little Club and Rosen rye, for wheat and rye leaf rust, respectively. Inoculated plants were incubated at approximately 100% relative humidity for 18 to 24 hours and classified for rust reaction 12 to 14 days later using the system described by Stakman et al. (1962) (Appendix 1). The chi-square test for goodness of fit was used to test segregating populations.

Where F2 data had indicated monogenic inheritance, 20 - 25 seedlings per F3 line were grown. However, where two genes were implicated 30-40 seedlings per F3 line were grown while 60 seedlings were grown where three genes appeared to be involved. Since the observed data did not fit the classical 3 gene ratio



of 37:26:1, a modified ratio of 42:21:1 or 40:23:1 was used. These 3 gene ratios are adjusted to account for the limited number of plants tested per F3 line. With the population of 30 to 40 plants for each F3 line a corrected ratio of 42:21:1 was used while the ratio of 40:23:1 was applied where the population per F3 line was 50 to 60 seedlings. The procedure for adjusting the ratio has been described by Wu and Ausemus (1953). The formula used in modifying the expected ratio is presented in Appendix V.

## 4. RESULTS

UM8003 (Petkus C.A.N. 1933):

UM8003 was developed from Petkus rye, an older cultivar selected many years ago in Germany. The seedling reactions of this resistant parent to RLR 213/78 and race 30 are shown in Table I. The population size in this cross UM8116 x UM8003 was reduced by poor germination and the presence of albinos.

The results from the F2 did not fit a 3 resistant:1 susceptible ratio or a 9 resistant:7 susceptible ratio (Table II) when tested with RLR 213/78. Trouble in classifying infection types may have caused this discrepancy. However, F3 data fit a single gene ratio (Table IV). Infection types on plants scored as resistant in segregating F3 lines ranged from 1<sup>+</sup> to 2<sup>+</sup>, indicating partial dominance. Occasionally, plants with 0;1 infection type were observed. The resistant gene conditioning infection type 1<sup>+</sup> to 2 to RLR 213/78 is temporarily designated LrPk1.

The F2 results with race 30, shown in Table III indicate the action of two genes for resistance to this race. This was confirmed by the F3 lines which segregated in a 7:8:1 ratio (Table V). F3 lines scored as homozygous resistant exhibited a 0;1 or 1<sup>+</sup> infection type. Segregation within the F3 lines indicated that the gene conferring the 0;1 infection type was partially dominant. This gene is assigned the temporary symbol LrPk2. The second gene conditioning infection type 1<sup>+</sup> to 2 segregated as a recessive and is temporarily designated LrPk3.

Gene LrPk1 is independent of genes LrPk2 and LrPk3  
( $\chi^2_4$  linkage = 3.1636, P = .70 - .50).

UM8071 (Self Fertile Prolific):

This inbred line is moderately resistant giving infection types 2 to 2<sup>+</sup>c to both RLR 213/78 and race 30. The mode of inheritance to both cultures were studied in the F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations.

All the F<sub>1</sub> plants were susceptible (3 to 3<sup>+</sup> infection type) to both RLR 213/78 and race 30, indicating that recessive genes condition resistance to the two rusts in UM8071. In the F<sub>2</sub>, segregation for reaction did not give a good fit to a one gene ratio (Table II). Resistant plants had infection type 1<sup>++</sup>. In this test, plants classified as resistant had small pustules with limited sporulation, however, since classification was difficult, some of the resistant plants may have been classified as susceptible infections. The data obtained from F<sub>3</sub> tests indicated a single gene inheritance by segregating in a 1:2:1 ratio (Table IV). The gene conditioning resistance to RLR 213/78 in UM8071 is assigned the temporary symbol LrPr1 (infection type 2 to 2<sup>+</sup>c).

The F<sub>2</sub> and F<sub>3</sub> results with race 30 are shown in Tables III and V. Segregation for reaction to race 30 suggested the presence of a single recessive gene for resistance to race 30 (Table III). The data from the F<sub>3</sub> confirmed the above hypothesis by giving a satisfactory fit to the expected single gene ratio (Table V). Homozygous resistant lines had infection type 2 to 2<sup>+</sup>c.

The gene conditioning this infection type to race 30 is temporarily designated LrPr2. The two genes LrPr1 and LrPr2 are independently inherited ( $X^2_4$  linkage = 7.0723, P = .20-.10).

UM8295 (Gator/Brazil):

During the course of the investigation it was found that UM8295 was heterogeneous for its rust genotype. Data from the F2 suggested that two genes are involved in conditioning resistance to RLR 213/78 (Table II). However, results obtained from the F3 indicated the activity of a third gene. The F3 data from the cross UM8116 x UM8295 are presented separately in Table VI. Segregation for resistance in four families gave a satisfactory fit to a 7:8:1 ratio (Table VI). The results from 2 families fitted a modified 42 resistant:21 segregating :1 susceptible ratio (Table VI). In the F3, some lines segregated for a fleck infection type, some only for a 0;1 infection type, some for a 1<sup>+</sup> infection type and others for all the types. Some lines were homozygous resistant for a fleck infection type, others 0;1 or 1<sup>+</sup>, indicating that there are three genes, one conditioning 0;, this gene is temporarily designated LrGB1 the second 0;1, and is given the temporary symbol LrGB2. The third gene confers a 1<sup>+</sup> infection type. This gene is temporarily designated LrGB3.

The F2 results for reaction to race 30 are shown in Table III. Segregation for resistance in the F2 did not give a good fit to a two gene ratio (Table III). However, three of the plants in the susceptible class had infection types 3<sup>-</sup> to 3<sup>-</sup>.

Assuming misclassification and combining these three plants with the moderately resistant group, the observed data of 108 resistant : 11 susceptible F2 plants would give a satisfactory fit to a 15 resistant : 1 susceptible ratio ( $P = .20 - .10$ ). The F3 data are shown separately in Table VI. Results obtained from two families fit a 7:8:1 ratio (Table VI) while those obtained from four families fitted a 42:21:1 ratio (Table VI). On the basis of infection types in F3 homozygous resistant lines, two duplicate dominant genes may be conditioning infection type ;n to ;ln. These two genes are temporarily designated as LrGB4 and LrGB5. Some lines were homozygous resistant or segregated for a  $1^+$  infection type. The rust reaction of plants within lines segregating for a  $1^+$  infection type suggests that this gene is partially dominant. It is tentatively designated LrGB6. Genes LrGB1, LrGB2 and LrGB3 are not associated with genes LrGB4, LrGB5 or LrGB6. ( $\chi^2_4$  linkage = 7.3276,  $P = .20 - .10$ ).

UM8301 (Gator/Wrens):

UM8301 gives infection type 0;  $1^+$  to  $1^+$  to RLR 213/78 and 0; to race 30. The F2 and F3 results with RLR 213/78 are presented in Tables II and IV. Segregation for resistance in the F2 fitted a single gene ratio (Table II). This was confirmed in the F3 which segregated in 1:2:1 ratio (Table IV). Lines scored as homozygous resistant exhibited infection type  $1^+$ . The gene conditioning infection type  $1^+$  is assigned the temporary symbol LrGW1. Within the segregating lines, 41 lines gave

dominance, 16 segregated for intermediate resistance, 6 segregated in a recessive manner and 9 deviated from any of these ratios. These results suggested that LrGW1 may be influenced by some modifying factors.

Segregation for reaction to race 30 in the F2 was variable with the resistant infection types varying from 0; to 2<sup>+</sup>. The F2 results as shown in Table III, fitted a two gene ratio. However, segregation in the F3 indicated a good fit to a 42:21:1 ratio (Table V). In the F3 generation, some lines segregated only for a 0; infection type, some for a 0;1 infection type, some for 1<sup>+</sup> infection type and some for all. Thus, three independent genes condition infection types 0;, 0;1 and 1<sup>+</sup> to race 30 in UM8301. These genes are assigned temporary symbols, LrGW2 (infection type 0;), LrGW3 (infection type 0;1) and LrGW4 (infection type 1<sup>+</sup>). Within lines segregating for the 1<sup>+</sup> gene, infection types varied from 1<sup>+</sup> to 2<sup>+</sup>, indicating that LrGW4 is partially dominant. Gene LrGW1 is independently inherited of genes LrGW2, LrGW3 and LrGW4 ( $\chi^2_4$  linkage = 7.1515, P = .20 - .10).

UM8336 (Emory rye):

Emory rye from which UM8336 was developed resulted from recurrent selection of lines from Explorer rye attempting to give it more leaf rust resistance than Explorer. UM8336 is highly resistant to RLR 213/78 and race 30, giving 0; infection type to both rusts (Table I). The F2 and F3 were tested

with RLR 213/78 and the results are presented in Tables II and IV. The F2 segregated in a 3 resistant:1 susceptible ratio (Table II), however, the F3 lines segregated in a 7:8:1 ratio (Table IV). In the F3, some lines were homozygous resistant for a 0; infection and others for a 0;1 infection type. Within the F3 lines segregating for resistance, some segregated for infection type 0; some only for infection type 0;1, and some for both. Thus, one dominant gene controls a 0; infection type, and this gene is tentatively designated LrEm1. The second dominant gene conditioning a 0;1 infection type is provisionally designated LrEm2.

The data obtained from F2 and F3 tests with race 30 are set out in Tables III and V. Segregation in the F2 population fitted a 63 resistant: 1 susceptible ratio (Table II), suggesting that three independent dominant genes condition resistance to race 30. Segregation of the F3 lines did not give a good fit to a modified 40:23:1 ratio (Table V) due to a deficiency of the segregating class. However, some F3 lines segregated for a 0; infection type, some only for a 0;1 infection type, and some for a  $1^+$  infection type. Similarly, there were some lines that were homozygous resistant for 0; others for 0;1 or  $1^+$ . These results suggested that three genes condition the corresponding infection type 0;, 0;1 and  $1^+$ , which have been assigned the temporary symbols LrEm3, LrEm4 and LrEm5 respectively. The two genes for resistance to RLR 213/78, LrEm1 and LrEm2 are independently inherited of genes LrEm3, LrEm4 and LrEm5 ( $X^2_4$  linkage = 9.8178, P = .30-.20).

UM8340 (Hazel rye):

The results of F2 and F3 seedling tests with RLR 213/78 are given in Tables II and IV. The F2 data fit a 15 resistant:1 susceptible ratio (Table II), indicating the presence of two independent dominant genes. Infection types of F2 resistant plants ranged from 0; to 0;2. The F3 lines confirmed this hypothesis by segregating in a 7:8:1 ratio (Table IV). Of the F3 lines segregating for resistance, some segregated for infection type 0;, some for 0;1 infection type and some for both. Segregation for each infection type conformed to a 3 resistant:1 susceptible ratio, and lines scored as homozygous resistant had infection type 0; or 0;1. These results suggest that one dominant gene confers the 0; infection type to RLR 213/78. This gene is temporarily designated LrHz1. The second gene conditioning infection type 0;1 is assigned the temporary symbol LrHz2.

F2 segregation for reaction to race 30 is shown in Table III. Segregation in the F2 fitted a 13 resistant :3 susceptible ratio (Table III). The infection type of F2 resistant plants ranged from 0;1 to 2<sup>+</sup>. The presence of two genes, one dominant and the other recessive was confirmed in the F3 which segregated in 7:8:1 ratio (Table V). Within the resistant F3 lines, infection types varied from 0;1n to 1<sup>+</sup>. This variation suggests that two genes are involved in conferring resistance, one giving a 0;1n infection type and the second a 1<sup>+</sup>. The expression of the 0;1n gene is characterized by necrosis and is provisionally designated LrHz3, while the second gene which is recessive, gives



infection type  $l^+$  and is given the temporary symbol LrHz4. There is a strong association for segregation to both rusts ( $\chi^2_4$  linkage = 28.6736,  $P = < .001$ ). If one of the genes conditions resistance to both rusts, the data should fit the expected ratio (19:8:1:8:22:2:1:2:1). A P value of .20-.10 was obtained and agreed with the hypothesis. However, the possibility of a more complex inheritance or gene linkage cannot be excluded.

TABLE II

Segregation for Reaction to Isolate  
RLR 213/78 of Rye Leaf Rust in F2  
Populations from Crosses Between  
Resistant and Susceptible Parents

Cross	Number of plants		Expected ratio	P-value
	Res.*	Susc.		
UM8116 x UM8003	42	50	3:1	<.001
			9:7	.05-.01
UM8116 x UM8071	15	92	1:3	.01-.001
UM8116 x UM8295	111	9	15:1	.70-.50
UM8116 x UM8301	73	31	3:1	.30-.20
UM8116 x UM8336	95	21	15:1	.001
			3:1	.10-.05
UM8116 x UM8340	106	12	15:1	0.10-.05

\*Res. = Resistant;   Susc. = Susceptible

TABLE III

Segregation for Reaction to Race 30  
of Wheat Leaf Rust in F<sub>2</sub> Populations  
from Crosses Between Resistant and  
Susceptible Parents.

Cross	Number of plants		Expected ratio	P-value
	Res.	Susc.		
UM8116 x UM8003	83	13	13:3	.20-.10
UM8116 x UM8071	34	73	1:3	.20-.10
UM8116 x UM8295	105	14	15:1	.05-.01
UM8116 x UM8301	95	6	15:1	.90-.80
			63:1	<.001
UM8116 x UM8336	114	2	63:1	.90-.80
UM8116 x UM8340	96	22	13:3	.99-.95

TABLE IV

Segregation for Reaction to Isolate  
RLR 213/78 of Rye Leaf Rust in F3  
Lines from Crosses Between Resistant  
and Susceptible Parents.

Cross	Number of lines			Expected ratio	P-value
	Res.	Seg.*	Susc.		
UM8116 x UM8003	13	47	28	1:2:1	.10-.05
UM8116 x UM8071	20	42	31	1:2:1	.20-.10
UM8116 x UM8301	39	73	45	1:2:1	.70-.50
UM8116 x UM8336	70	87	15	7:8:1	.50-.30
UM8116 x UM8340	41	36	9	7:8:1	.20-.10

\* Seg. - Segregating

TABLE V

Segregation for Reaction to Race 30 of  
Wheat Leaf Rust in F3 Lines from Crosses  
Between Resistant and Susceptible Parents.

Cross	Number of lines			Expected ratio	P-value
	R.	Seg.	Susc.		
UM8116 x UM8003	50	44	6	7:8:1	.50-.30
UM8116 x UM8071	25	54	18	1:2:1	.50-.30
UM8116 x UM8301	72	39	3	42:21:1	.70-.50
UM8116 x UM8336	125	46	3	40:23:1	.05-.02
UM8116 x UM8340	28	40	7	7:8:1	.50-.30

TABLE VI

Behaviour of F3 Lines of the  
Cross UM8116 x UM8295 Tested  
with Isolate RLR 213/78 and  
Race 30.

Rust Culture	No. of families	Number of lines			Expected ratio	P-value
		Res.	Seg.	Susc.		
RLR 213/78	4	57	56	12	7:8:1	.30-.20
	2	45	14	1	42:21:1	.50-.30
race 30	2	34	23	4	7:8:1	.20-.10
	4	69	38	3	42:21:1	.70-.50

Genetic relationships between the six resistant parents

The genetic relationships of the six parents resistant to rye leaf rust and wheat leaf rust were studied in the F<sub>2</sub> of resistant x resistant intercrosses. The results obtained from testing F<sub>2</sub> populations with RLR 213/78, as shown in Table VII, suggested that the six resistant parents have different genes for resistance to this isolate. The distorted ratios are due to an excess of susceptible segregates. The reasons for these distorted ratios will be discussed later.

F<sub>2</sub> populations from the resistant x resistant intercrosses were also tested with race 30 (Table VIII). The results of the cross UM8003 x UM8336 were difficult to interpret. In a preliminary testing of 189 F<sub>2</sub> plants derived from 6 F<sub>1</sub> plants, 6 susceptible segregates were observed from two families only. However, in a second testing of 692 F<sub>2</sub> plants derived from 8 F<sub>1</sub> plants which included the same 6 F<sub>1</sub>'s previously tested, no susceptible segregates were detected. The most susceptible plants in this test only had infection type 2. Thus, the six susceptible plants obtained from two families may have been misclassified.

It may be concluded that UM8003 and Um8336 might have identical or very closely linked genes for reaction to race 30.

No susceptible segregates were observed in the crosses UM8003 x UM8340, UM8295 x UM8301, UM8295 x UM8336, UM8295 x UM8340 and UM8340 x UM8336 (Table VIII). These results showed that some of the genes for seedling resistance in each of these

parents are identical or very closely linked.

UM8071 has gene LrPr2 for moderate resistance to race 30. The results, as shown in Table VIII, indicate that this gene is non-allelic with the genes present in UM8003, UM8295 and UM8340. However, in a cross between UM8071 and UM8336 only one susceptible plant was observed, and this is less than the expected number in a susceptible class. This susceptible plant could possibly be a contaminant or a misclassification.

UM8336 has gene LrEm5 that conditions an infection type 1<sup>+</sup>. The gene LrPr2 in UM8071 may be identical or tightly linked with LrEm5 in UM8336.

In summary, the genes for resistance to RLR 213/78 in the six resistant parents are inherited independently. However, some of the resistant parents have identical or very closely linked genes for resistance to race 30 of wheat leaf rust.



TABLE VII

Reaction of F2 Populations from  
Intercrosses Between the Inbreds  
UM8003, UM8071, UM8295, UM8301,  
UM8336, and UM8340 to Isolate  
RLR 213/78 of Rye Leaf Rust.

Cross	Number of plants		Expected ratio	P-value
	Res.	Susc.		
UM 8003 x UM8336	854	102	63:1	<.001
UM8003 x UM8340	1236	72	63:1	.20-.10
UM8071 x UM8003	885	156	13:3	.01-.001
UM8071 x UM8295	705	47	253:3	<.001
UM8071 x UM8336	802	85	61:3	<.001
UM8071 x UM8340	1106	231	61:3	<.001
UM8295 x UM8003	1125	51	255:1	<.001
UM8295 x UM8336	1356	23	1023:1	<.001
UM8295 x UM8340	1273	15	1023:1	<.001
UM8301 x UM8295	1254	41	255:1	<.001
UM8340 x UM8336	1267	53	255:1	<.001

TABLE VIII

Reaction of F2 Populations from Intercrosses Between the Inbreds UM8003, UM8295, UM8301, UM8336, and UM8340 to Race 30 of Wheat Leaf Rust.

Cross	Number of plants		Expected ratio	P-value
	Res.	Susc.		
UM8003 x UM8336	875	6	1021:3	.05-.02
UM8003 x UM8340	1192	-	255:1	
UM8071 x UM8003	1126	37	55:9	<.001
UM8071 x UM8295	1202	35	253:3	<.001
UM8071 x UM8336	1069	1	253:3	.01-.001
UM8071 x UM8340	1534	36	55:9	<.001
UM8295 x UM8003	1270	4	1021:3	.90-.80
UM8295 x UM8336	1353	-	4095:1	
UM8295 x UM8340	1307	-	1021:3	
UM8301 x UM8295	1354	-	4095:1	
UM8340 x UM8336	1243	-	1021:3	

## 5. DISCUSSION

The present genetic study indicated a Mendelian basis for resistance in rye to P. recondita secalis and P. recondita tritici. The results revealed that the inheritance of resistance in the six inbred ryegrasses was relatively simple, with one to three dominant genes providing resistance. Temporary gene symbols were assigned to the genes identified in each resistant parent. Since the same F<sub>2</sub> plants and F<sub>3</sub> lines were tested to both rye leaf rust and wheat leaf rust, an attempt was made to determine whether any of the genes give resistance to both RLR 213/78 and race 30.

The presence of chlorophyll mutants in the cross UM8116 x UM8003 complicated genetic analysis. Although a single gene, LrPkl was assumed to be conferring the 1<sup>+</sup> infection type to RLR 213/78, it is possible that there may be a second gene for resistance. In the F<sub>3</sub> lines there were several plants with fleck infection. These may have resulted from complementary gene action between the type 1<sup>+</sup> gene and possibly a second gene that may be conditioning the 2 infection type. Such type of complementary gene action has been reported in wheat (Dyck and Samborski, 1981). The gene conditioning the 2 infection type may be linked to the mutant gene for the albino character. Differential transmission of gametes, a phenomenon that has been reported in wheat by Luig (1960, 1964) may have contributed to deviations from the expected ratios. Several mechanisms of this phenomenon exist and these have been described (Luig, 1968).

The two recessive genes for resistance in UM8071, LrPr1 and LrPr2, that give infection type 2 to 2<sup>+</sup>c appear to be unstable and 'operate by delaying sporulation'. In a breeding program it is recommended that these two genes should not be used alone. However, the two could be valuable genes in combination with others, thus providing genetic diversity in a variety. The phenotype expressed by these two genes may be ascribed to the characteristic of partial resistance which has already been reported in barley (Parlevliet, 1975) and in rye (Parlevliet, 1977).

Tan et al (1976, 1977) reported that Wrens (5) and 'Elbon x Gator' were heterogeneous for resistance to P. graminis tritici and secalis. In this study, UM8295 and UM8301 were found to be heterogeneous for their rust genotypes. Since these two resistant inbreds had undergone more than 10 generations of inbreeding they were assumed to be genetically pure and suitable for this study. However, this heterogeneity may be due to the manner in which the plants were selfed.

Two genes condition resistance to RLR 213/78 in UM8336 (Table IV) while another three confer resistance to race 30 (Table V). UM8340 has four genes for resistance with two genes conditioning resistance to each rust. These two parents are highly resistant to both rye leaf rust and wheat leaf rust (Table I). They also appear to have a broad spectrum of resistance to P. recondita and should prove valuable in breeding for

disease resistance.

Different dominance relationships were observed in this investigation with each resistant parent having at least one partially dominant gene for resistance. Such genes should be isolated singly into one genotypic background to determine whether environmental influence, genetic background or specificity of the rust strains could have influenced the expression of these genes in heterozygotes. Knott (1981) reported that heterozygotes are more sensitive to the environment than homozygotes.

Modifiers affecting leaf rust resistance have been reported in several cases (Anderson, 1966; Dyck et al. 1966). The possible activity of modifying factor(s) was observed in gene LrGW1 present in UM8301. In some segregating F3 lines the gene behaved as a dominant while in others it behaved as a recessive. This gene should be isolated into other genetic backgrounds for further studies on its effectiveness.

On the basis of evidence from the present genetic study none of the resistant parents appear to have genes in common for resistance to RLR 213/78 (Table VIII). The absence of linkage indicates that the genes are independent. The distorted ratios which were observed are due to an excess of susceptible segregates. Since two tests were carried out at different times, environmental effects could have influenced the expression of rust reactions and the infection type 2<sup>+</sup> could have been misclassified as susceptible. Furthermore, rye is a naturally outcrossing crop and residual heterozygosity may express itself in later generations.

The reaction of the intercrosses to race 30 indicated that some resistant parents have identical or tightly linked genes (Table VIII). However, since no isogenic lines were used it was not possible to indicate specifically the genes that may be allelic or tightly linked. Use of isogenic lines would enable the study of gene interaction. Such a study is valuable in identifying resistance combinations when breeding for disease resistance.

The present study reveals the potential of cultivated rye (Secale cereale) as a reservoir of genes for leaf rust resistance. It also indicates that rye has specific genes for resistance to P. recondita tritici. Since most of the genes for rye leaf rust are independent of those for resistance to wheat leaf rust, there is a possibility that two different systems might be operating in rye. One system may operate against P. recondita tritici while the other may operate against P. recondita secalis. Sanghi and Luig (1971) reported a similar system for resistance in wheat to P. graminis tritici and secalis. The rye inbreds used in this study also have field resistance to leaf rust and stem rust, not investigated here.

Mains (1933) reported rye to be resistant to wheat leaf rust. Quinones (1972) indicated that the expression of the leaf rust resistance of rye was inhibited by the AABB genomes in the F1 hybrids of hexaploid triticale. On the other hand, Mukade (1978) found that the leaf rust resistance of Petkus rye was expressed in octaploid triticale and that the added

Petkus rye chromosome had a dosage effect for the leaf rust resistance.

The potential of rye as a source of disease resistance has already been reported in a number of cases. Several European wheat cultivars derive their resistance to stem rust and leaf rust from rye chromosome 1R. Transeg wheat carries a single gene for leaf rust resistance derived from rye chromosome 2R (Driscoll and Anderson, 1967).

A weakness in the present study is that only one isolate or race of each rust was used and that none of the genes identified were isolated due to the extreme variability in infection types in some homozygous resistant lines. It is suggested that inbred ryes with a higher percentage of genetic purity be used in further studies.

The need to develop isogenic lines cannot be overemphasized. Such isogenic lines have more resolving power (Person, 1967) and may be used in differentiating between strains of P. recondita secalis. The genes identified have the potential of adding to the genetic diversity in rye, wheat and triticales breeding programs.

SECTION III  
GENERAL OBSERVATIONS  
GENERAL DISCUSSION  
SUMMARY AND CONCLUSIONS



## 1. General Observations

### 1.1. Testing for Spectrum of Resistance with other Races

The inbred lines used in the present study and selected lines from different crosses were tested to several races of leaf rust. The infection types produced by the seedlings are presented in Appendix II.

UM8116 was found to be variable in its reaction to the different races to which it was tested. It was moderately resistant to race 5 but susceptible to races 9, 30, 76, 126a and RLR 213/78. However, its reaction to race 15 was heterogeneous with certain plants giving moderate resistant infection type 2<sup>+</sup> and others infection type 3<sup>+</sup> (Appendix II). UM8003 was resistant to races 5, 9, 30, 126a and RLR 213/78 but was susceptible to races 15 and 76 while UM8071 gave moderate resistant infection types to all the races to which it was tested. The parental inbreds UM8295, UM8301, UM8336 and UM8340 gave highly resistant infection types to all the races to which they were tested. These results suggest that these resistant inbreds may have a broad spectrum of resistance to leaf rust (P. recondita Rob. ex Desm). The reaction of F4 lines selected from different crosses are also presented in Appendix II. These lines possibly carry one or more genes for resistance to leaf rust.

### 1.2. Reaction to Stem Rust

Three races of wheat stem rust (P. graminis tritici) and three isolates of rye stem rust (P. graminis secalis) were used in this study. The seedling reactions produced on each inbred line are shown in Appendix III.

All the inbreds including UM8116 which is susceptible to leaf rust in the seedling stage were found to be highly resistant to wheat stem rust races C17(56), C53(15 Bil) and C61(38) as shown in Appendix III.

Reaction to rye stem rust was variable with certain of the rye stem rust isolates attacking some of the ryes. UM8071 was susceptible to all the stem rust isolates while the other inbreds were resistant to at least one of the isolates. UM8336 and UM8340 have excellent resistance to both wheat stem rust and rye stem rust. Only fleck reactions were observed after testing the two parents to these rust races or isolates (Appendix III).

The results of seedling reactions to the two formae speciales indicate a high degree of physiological specialization on rye in rye stem rust but no evidence was obtained for specialization in wheat stem rust.

### 1.3. Field Testing of the Parental Inbreds

The field reaction of the seven inbreds were obtained at the Rust Nursery, Glenlea Research Station during the summer of 1980. The adult plant reactions are presented in Appendix IV. The rust in this nursery consisted largely of P. recondita tritici and P. graminis tritici.

All the inbreds were found to be resistant under field conditions. Reactions to leaf rust varied from 0 to 50M (Appendix IV). The reaction to stem rust was similar. All the

inbreds were resistant to stem rust with only UM8336 giving trace (TR) to moderate susceptible (5MS) reaction. The results of this study indicate that the resistant inbreds used in this investigation have both seedling and field (adult plant) resistance. UM8116 which was used as the susceptible parent was resistant under field conditions. This indicates that this inbred line has adult plant resistance.

## 2. GENERAL DISCUSSION

The purpose of this investigation was to study the genetics of seedling resistance in rye to isolate RLR 213/78 of rye leaf rust (*Puccinia recondita secalis*) and race 30 of wheat leaf rust (*P. recondita tritici*). The genetic relationship between the six resistant parents and the genes conferring resistance to the two rusts was also studied. This may be the first report on the inheritance of seedling resistance in inbred rye to leaf rust (*P. recondita*).

Some difficulty was experienced in classifying plants for disease reaction especially where partially dominant genes were involved. Most of the partially dominant genes conditioned intermediate reaction types. Such genes are most frequently subject to environmental influence and modifying factors or genetic background of the host and parasite (Samborski and Dyck, 1976; Dyck and Samborski, 1981). UM8071 has two recessive genes, vis; LrPr1 and LrPr2 that confer resistance to RLR 213/78 and race 30, respectively. These genes appear to be unstable and are probably influenced by the environment. Syamananad and Dickson (1959) showed that rust reaction was greatly influenced by temperature, particularly in inbreds in which resistance is recessive.

The level of resistance in the F3 generation of some crosses varied, probably indicating the presence of modifiers. Haggag and Dyck (1973) reported that Prelude wheat has a single gene that modifies the expression of Lr3 to certain wheat leaf rust

cultures. UM8301 has a single gene that confers resistance to RLR 213/78. This gene appears to be under the influence of some modifying factors.

It is common to find heterogeneity in rye. This was evident in inbreds UM8295 and UM8301. Even after 10 or more generations of inbreeding (selfing), a line or cultivar may still be heterogeneous. UM8295 and UM8301 had been inbred for more than 10 generations. Since rye is a naturally outcrossing crop, many plant types may exist within one line or cultivar. Tan et al. (1976) proposed that single plant selections should be made, so that the results obtained using progeny of the same plant are repeatable and comparable. Since individual plants in a collection may react differently due to other sources of genetic impurity, proper selection of parental material and their hybrids is necessary in a genetic study of disease reaction. Chlorophyll mutants (albinos) were observed in the cross UM8116 x UM8003. These chlorophyll mutants complicated genetic analysis in this cross due to reduced population sizes.

The relationship of the resistance genes was not established. In view of the evidence for 3 genes conditioning rust reaction in some inbreds and possible interactions between different loci, these relationships could not be studied adequately in crosses between the six resistant parents. Thus, host lines each of which carries a single gene for resistance in a homozygous state, should be utilized for this purpose. A study of segregation in crosses between lines carrying isolated genes

for resistance in an appropriate background is needed to establish genetic relationships in such instances. Anderson (1961) listed the possible uses of isogenic lines, and Person (1967) indicated that such lines have in theory more resolving power in differentiating different strains of pathogens. Tan et al. (1975) have used self-fertile lines of Secale cereale possessing single genes (Sr) for resistance to differentiate between Australian cultures of P. graminis secalis and of putative P. graminis tritici x secalis hybrids. Similar isogenic lines carrying Lr genes in rye can also be used to distinguish between cultures of P. recondita secalis.

The results obtained from this study indicated that all the resistant parents, except UM8340, have independent genes for resistance to both rusts. UM8340 has at least one gene which may be conditioning resistance to both RLR 213/78 and race 30. The failure to detect linkage in other parents may have been due to the small population (30-40 seedlings per F3 line). This was not expected because the same F3 lines were tested to both rusts. It is suggested that larger populations be used in subsequent studies. Furthermore, results from resistant x resistant intercrossees indicated that the six resistant parents have independent genes for resistance to RLR 213/78. However, some of the parents have identical or very closely linked genes for resistance to race 30. The F2 segregations in the resistant x resistant intercrossees used in this study do not provide as critical evidence on complicated gene interactions as may be

obtained by analysis of F3 progenies. Further studies should aim at advancing the segregating material to the F3 generation.

The method of study used in this investigation is similar to that used by Berg et al. (1963) and Gough and Williams (1963). However, Knott and Anderson (1956) indicated that the backcross was the best method for genetic analysis of rust resistance. In the backcross, the ratios are simpler and it is easier to separate genes for resistance and to study their effects singly. Furthermore, ratios involving backcross families are more dependable than observations on individual plants (Oggema, 1972). The only disadvantage of the backcross lines may be the reduction of the level of resistance obtained in some cases (Haggag, 1970).

The genes identified in this study should prove valuable in rye, wheat and triticale breeding programs. Since single genes for resistance are easily overcome by new virulent races of a pathogen, plant breeders should aim at combining several of these genes in desirable cultivars. Using multiple genes would provide a longer lasting resistance because a physiologic race would have to acquire several genetic abilities to overcome resistance conditioned by several genes. The genes from inbreds UM8336 and UM8340 should prove valuable in this respect. These parents are highly resistant to both P. graminis and P. recondita (Appendix II and III).

This study has revealed that wheat leaf rust (P. recondita) tritici) can attack some ryes, and that rye has specific genes for resistance to this formae speciales. It is also possible

that there may be some genes conditioning resistance to rye leaf rust (P. recondita secalis) that may or may not confer resistance to wheat leaf rust. Subsequent studies should concentrate on identifying such genes, so that they may be used in specific breeding programs.

According to the gene-for-gene relationship of host-parasite interaction as postulated by Flor (1946), a host resistance gene is evident only when the parasite culture possesses a corresponding gene for avirulence. Therefore, more resistance genes would be differentiated on the average in a cross between resistant and susceptible hosts by a widely avirulent culture than with a widely virulent one (Berg et al. 1963; Sanghi and Baker, 1972). Thus more genes can be identified from rye if several avirulent cultures of leaf rust (P. recondita) are used. The cultures used in the present study were randomly chosen since little was known about genes for resistance in rye to leaf rust.



Apart from the suggestions for further study already mentioned in the text, the following should also be taken into consideration.

- 1) ryes with a higher percentage of genetic purity should be carefully selected and used in these kinds<sup>s</sup> of genetic studies
- 2) isolate the genes conferring specific infection types from F3 lines homozygous resistant for one infection type, from F3 lines segregating in a 3 resistant: 1 susceptible ratio, or by backcrossing them into one genotypic background,
- 3) intercross the isogenic lines with specific infection types in order to identify suitable combinations for breeding programs and in studying linkage relationships,
- 4) test the single gene lines to many cultures of leaf rust and determine the spectrum of resistance,
- 5) study the partially dominant genes at different temperatures and/or in different genetic backgrounds in order to study the influence of these factors as well as rust specificity,
- 6) conduct correlated studies between seedling and adult plant resistance and identify specific genes that may have adult plant resistance for use in breeding programs.

### 3. SUMMARY AND CONCLUSIONS

The mode of inheritance to rye leaf rust and wheat leaf rust was studied in six inbred lines of rye (Secale cereale L.). The inbred line UM8116 used as the susceptible parent in these crosses was susceptible to both isolate RLR 213/78 of rye leaf rust and race 30 of wheat leaf rust. Since the six resistant inbred lines were resistant to both rust species, progeny of the crosses could be tested with both rye leaf rust and wheat leaf rust. The genetic relationship between the six resistant inbreds was also studied. Furthermore, several races of leaf rust and stem rust were used in determining the spectrum of resistance. The inbreds used in this study were also grown in a rust nursery in order to detect field resistance to both leaf rust and stem rust.

Resistance in the inbred lines was conditioned by recessive, partially dominant and completely dominant genes. The inheritance of resistance was relatively simple being conditioned by one to three genes. During the period of these studies, it was found that the inbreds UM8295 and UM8301 were heterogeneous for resistance. This may be due to the manner in which the plants were selfed. The gene conditioning resistance to RLR 213/78, LrGW1 in UM8301 may be under the influence of some modifying factors.

The genes for resistance to RLR 213/78 appear to be independently inherited since no linkage was detected in resistant x resistant intercrosses. However, linkage relationships were detected in reaction to race 30 indicating that some

of the resistant inbreds have identical or very closely linked genes for resistance to this race.

On the basis of information obtained from this investigation it may be concluded that a number of genes for rust resistance are present in cultivated rye. Two systems may be operating in rye, one system involving genes for resistance to rye leaf rust and the second involves genes for resistance to wheat leaf rust. Cultivated rye should be exploited in broadening the genetic variability in rye, wheat and triticale improvement programs, especially with respect to disease resistance.

SECTION IV  
LITERATURE CITED  
APPENDIX

## REFERENCES

- Acosta, A.C. 1963. The transfer of stem rust from rye to wheat. Diss. Abstr. 23: 34-35.
- Anderson, R.G. 1961. The inheritance of leaf rust resistance in seven varieties of common wheat. Can. J. Plant Sci. 41: 342-359.
- Anderson, R.G. 1966. Studies on the inheritance of resistance to leaf rust of wheat. Proc. 2nd Int. Wheat Genet. Symp. Lund, 1963. Hereditas Suppl. 2: 144-155.
- Anikster, Y., and Wahl, I. 1979. Coevolution of the rust fungi on gramineae and Liliaceae and their hosts. Ann. Rev. Phytopath. 17: 367-403.
- Arthur, J.C. 1929. The plant rusts (Uredinales). John Wiley and Sons. Inc., New York. 446p.
- Ausemus, E.R. 1943. Breeding for disease resistance in wheat, oats, barley and flax. Bot. Rev. 9: 207-260.
- Bartos, P., Green, G.J., and Dyck, P.L. 1970. Reactions to stem rust and genetics of stem rust resistance in European wheat varieties. Can. J. Bot. 48: 1439-1443.
- Berg, L.A., Gough, F.J., and Williams, N.D. 1963. Inheritance of stem rust resistance in two wheat varieties Marquis and Kota. Phytopathology. 53: 904-908.
- Biffen, R.H. 1905. Mendel's laws of inheritance and wheat breeding. J. Agric. Sci. 1: 1-48.
- Chester, K.S. 1946. The nature and prevention of cereal rusts as exemplified in the leaf rust of wheat. Chronica Botanica Co., Watham, Mass. 269p.
- Choudhuri, H.C. 1958. The inheritance of stem and leaf rust resistance in common wheat. Indian J. Genet. Plant Breed. 18: 90-115. Cited by Anderson (1961).
- Day, P.R. 1960. Variation in phytopathogenic fungi. Ann. Rev. Microbiol. 14: 1-16.
- Dickson, J.G. 1956. Diseases of field crops. Second edition, McGraw - Hill Book Co., Inc. York, PA. 517p.

- D'Oliveira, B., and Samborski, D.J. 1966. Aerial stage of Puccinia recondita on Ranunculaceae and Boraginaceae in Portugal. Pages 133-150 in R.C.F. Macer and M.S. Wolfe, eds. Cereal Rust Conference 1964. Proc. Plant Breeding Inst. Cambridge, England.
- Driscoll, C.J., and Anderson, L.M. 1967. Cytogenetic studies of Transec a wheat - rye translocation line. Can. J. Genet. Cytol. 9: 375-380.
- Driscoll, C.J., and Jensen, N.F. 1963. A genetic method for detecting induced intergeneric translocations. Genetics 48: 459-468.
- Driscoll, C.J., and Jensen, N.F. 1964. Characteristics of leaf rust resistance transferred from rye to wheat. Crop Sci. 4: 372-374.
- Driscoll, C.J., and Jensen, N.F. 1965. Release of a wheat - rye translocation stock involving leaf rust and powdery mildew resistances. Crop Sci. 5: 279-280.
- Dyck, P.L. 1977. Genetics of leaf rust resistance in three introductions of common wheat. Can. J. Genet. Cytol. 19: 711-716.
- Dyck, P.L., and Kerber, E.R. 1977. Inheritance of leaf rust resistance in wheat cultivars Rafaela and EAP 26127 and chromosome location of gene Lr 27. Can. J. Genet. Cytol. 19: 355-358.
- Dyck, P.L., and Samborski, D.J. 1968. Genetics of resistance to leaf rust in common wheat varieties Webster, Loros, Brevit, Carina, Malakof and Centenario. Can. J. Genet. Cytol. 10: 7-17.
- Dyck, P.L., and Samborski, D.J. 1970. The genetics of alleles for leaf rust resistance at the Lrl4 locus in wheat. Can. J. Genet. Cytol. 12: 689-694.
- Dyck, P.L., and Samborski, D.J. 1979. Adult plant leaf rust resistance in Pl 250413, an introduction of common wheat. Can. J. Plant Sci. 59: 329-332.
- Dyck, P.L., and Samborski, D.J. 1981. The inheritance of resistance to Puccinia recondita in a group of common wheat cultivars. Can. J. Genet. Cytol. (In Press).

- Dyck, P.L., Samborski, D.J., and Anderson, R.G. 1966. Inheritance of adult - plant leaf rust resistance derived from the common wheat varieties Exchange and Frontana. *Can. J. Genet. Cytol.* 8: 665-671.
- Ellingboe, A.H. 1975. Horizontal resistance: an artifact of experimental procedure. *Australian Plant Path. Newsletter.* 4: 44-46. Cited by Watson (1977).
- Ellingboe, A.H. 1981. Changing concepts in host - pathogen genetics. *Ann. Rev. Phytopath.* 19: 125-143.
- Eversmeyer, M.G., and Browder, L.E. 1974. Effect of leaf and stem rust on 1973 Kansas wheat yields. *Plant Dis. Repr.* 58: 469-471.
- Fitzerald, P.J., Caldwell, R.M., and Nelson, O.E. 1957. Inheritance of resistance to certain races of leaf rust of wheat. *Agron. J.* 49: 539-543.
- Flor, H.H. 1946. Genetics of pathogenicity in Melampsora lini. *J. Agric. Res.* 73: 335-357.
- Gassner, G., and Kirchhoff, H. 1934. Einige Versuche zum Nachweis biologischer Rassen innerhalb des Ragenbraunrostes, Puccinia dispersa Erikss. and Henn. *Phytopath. Zeitschr.* 7: 479-486. Cited by Dickson (1956).
- Gospodinova, E., and K'rzhin, Kh. 1980. Research on the reaction of triticales specimen to the causal agents of wheat brown and stem rust. *Rev. Plant Pathol.* 59: 560 (Abstr.).
- Gough, F.J., and Williams, N.D. 1963. Inheritance of stem rust reaction in two durum varieties Acme and Mindum. *Phytopathology* 53: 295-299.
- Green, G.J. 1971. Hybridization between Puccinia graminis tritici and Puccinia graminis secalis and its evolutionary implications. *Can. J. Bot.* 49: 2089-2095.
- Green, G.J. 1981. Identification of physiologic races of Puccinia graminis f. sp. tritici in Canada. *Can. J. Plant Pathol.* 3: 33-39.
- Haggag, M.E.A. 1970. A study of host - parasite interactions involving four different alleles of the Lr3 locus for leaf rust resistance in common wheat. Ph. D. Thesis, University of Manitoba, Winnipeg, Man.

- Haggag, M.E.A., and Dyck, P.L. 1973. The inheritance of resistance in four common wheat varieties with genes at or near the Lr3 locus. *Can. J. Genet. Cytol.* 15: 127-134.
- Heyne, E.G., and Johnson, C.O. 1954. Inheritance of leaf rust reaction in crosses among Timstein, Pawnee and Red Chief Wheats. *Agron. J.* 46: 81-85.
- Hooker, A.L., 1967. The genetics and expression of resistance in plants to rusts of the genus Puccinia. *Ann. Rev. Phytopath.* 11: 180-184.
- Hooker, A.L., and Saxena, K.M.S. 1971. Genetics of disease resistance in plants. *Ann. Rev. Genetics.* 5: 407-424.
- Jensen, N.F., and Kent, G.C. 1952. Disease resistance from a wheat x rye cross. *J. Hered.* 43: 252.
- Johnston, C.O. 1973. Leaf rust of wheat. p. 317-325. In Quisenberry, K.S. and Reitz, L.P. (eds.), Wheat and Wheat Improvement. Amer. Soc. Agron., Madison, Wisconsin.
- Johnson, T. 1953. Variation in the rusts of cereals. *Biol. Revs. Cambridge Phil. Soc.* 28: 105-157.
- Knott, D.R. 1966. The inheritance of rust resistance III. The inheritance of stem rust resistance in nine Kenya varieties of common wheat. *Can. J. Plant Sci.* 37: 366-384.
- Knott, D.R. 1972. Using race - specific resistance to manage the evolution of plant pathogens. *J. Environ. Qual.* 1: 227-231.
- Knott, D.R. 1981. The effects of genotypes and temperature on the resistance to Puccinia graminis tritici controlled by the gene Sr 6 in Triticum aestivum. *Can. J. Genet. Cytol.* 23: 183-190.
- Knott, D.R., and Anderson, R.G. 1956. The inheritance of rust resistance. 1. The inheritance of rust resistance in ten varieties of common wheat. *Can. J. Agric. Sci.* 36: 174-195.



- Koroc'kova, A.V. 1980. The use of wheat - rye hybrids in breeding. *Rev. Plant Pathol.* 59: 179 (Abstr.).
- Larter, E.R. 1975. A review of the historical development of triticale. p. 35-52. In Chao, C. Tsen (ed.). *Cereal Chemists, Man - Made Cereal.* Am. Assoc. Cereal Chemists, St. Paul, Minnesota.
- Larter, E.R., Tsuchiya, T., and Evans, L.E. 1969. Breeding and cytology of triticale. *Proc. 3rd. Int. Wheat Genet. Symp., Canberra*, p. 213-221.
- Leonard, W.H., and Martin, J.H. 1963. *Cereal crops.* The McMillan Co., London. 824p.
- Luig, N.H. 1960. Differential transmission of gametes in wheat. *Nature.* 185: 636-637.
- Luig, N.H. 1964. Heterogeneity in segregation from wheat crosses. *Nature.* 204: 260-261.
- Luig, N.H. 1968. Mechanisms of transmission of gametes in wheat. *Proc. 3rd Int. Wheat Genet. Symp.* Canberra, Australia, p. 322-323.
- Luig, N.H., and Rajaram, S. 1972. The effect of temperature and genetic background on host gene expression and interaction to *Puccinia graminis tritici*. *Phytopathology* 62: 1171-1174.
- Mains, E.B. 1926. Rye resistant to leaf rust, stem rust and powdery mildew. *J. Agr. Res.* 32: 201-221.
- Mains, E.B. 1933. Host specialization in the leaf rust of grasses, *Puccinia rubigo - vera*. *Michigan Acad. Sci.* 17: 289-394. Cited by Quinones (1972).
- Mains, E.B., and Leighty, C.E. 1923. Resistance in rye to leaf rust, *Puccinia dispersa* Erikss. *J. Agr. Res.* 25: 243-252.
- Malm, N.R., and Hooker, A.L. 1962. Resistance to rust, *Puccinia sorghi* Schw., conditioned by recessive genes in two corn inbred lines. *Crop Sci.* 2: 145-147.
- Martin, J.H., and Leonard, W.H. 1967. *Principles of field crop production.* Second Edition. The McMillan Co., New York. 1044p.

- McDonald, W.C. 1967. Diseases of Field Crops in the Prairie Provinces. Canada Department of Agriculture. Publication 1008. 100p.
- McIntosh, R.A., and Dyck, P.L. 1975. Cytogenetical studies in wheat. VII. Gene Lr23 for reaction to Puccinia recondita in Gabo and related cultivars. Aust. J. Biol. Sci. 25: 765-773.
- McIntosh, R.A., Dyck, P.L., and Green, G.J. 1974. Inheritance of reaction to stem rust and leaf rust in the wheat cultivar Etoile de Choisy. Can. J. Genet. Cytol. 16: 571-577.
- McIntosh, R.A., Dyck, P.L., and Green, G.L. 1976. Inheritance of leaf rust and stem rust resistances in wheat cultivars Agent and Agatha. Aust. J. Agric. Res. 28: 37-45.
- McIntosh, R.A., and Luig, N.H. 1973. Linkage of genes for reaction to Puccinia graminis f.sp. tritici and Puccinia recondita in Selkirk wheat and related cultivars. Aust. J. Biol. Sci. 26: 1115-1152.
- McIntosh, R.A., Luig, N.H., and Baker, E.P. 1967. Genetic and Cytogenetic studies of stem rust, leaf rust and powdery mildew resistance in Hope and related wheat cultivars. Aust. J. Biol. 20: 1181-1192.
- Morey, D.D. 1956. Reaction of rye varieties to leaf rust. Plant Dis. Repr. 43: 578-579.
- Morey, D.D. 1970. Registration of Weser rye. Crop Sci. 10: 209-210.
- Morey, D.D. 1973. Rye improvement and production in Georgia. Univ. of Georgia Expt. Sta. Res. Bull. 129. 38p.
- Morrison, R.J. 1977. The genetics of resistance to Puccinia graminis tritici in hexaploid triticale. Ph. D. Thesis, University of Manitoba, Winnipeg, Man.
- Mukade, K. 1978. Chromosome engineering and acceleration of generation advancement in breeding rust resistant wheat. Tropical Agric. Res. Series No. 11: 135-144.
- Mukade, K., Kamio, M., and Hosoda, K. 1970. The transfer of leaf rust resistance from rye to wheat by inter-generic addition and translocation. In Gamma Field Symp. No. 9: 69-87.

- Nelson, R.R. 1972. Stabilizing racial populations of plant pathogens by use of resistance genes. *J. Environ. Qual.* 1: 220-227.
- Nelson, R.R. 1975. Horizontal resistance in plants; concepts, controversies and application. In *Proceedings of the Seminar on Horizontal Resistance to Blast Disease of Rice*; ed. Galvez, G.E. pp. 1-20, Ser. C.E.-9. Cal, Colombia: CIAT.
- Oggema, M.W. 1972. The genetics of resistance to *Puccinia graminis tritici* in eight wheat varieties from Kenya. Ph. D. Thesis, University of Manitoba, Winnipeg, Man.
- Parlevliet, J.E. 1975. Partial resistance of barley to leaf rust, *Puccinia hordei*. I. Effect of cultivar and development stage on latent period. *Euphytica* 24: 21-27.
- Parlevliet, J.E. 1977. Variation for partial resistance in a cultivar of rye, *Secale cereale*, to brown rust, *Puccinia recondita* f. sp. *recondita*. *Cereal Rust Bull.* 5: 13-16.
- Person, C. 1967. Genetic aspects of parasitism. *Can. J. Bot.* 45: 1193-1204.
- Quinones, M.A. 1972. The inheritance of resistance to *Puccinia recondita* Rob. ex Desm. in hexaploid triticales. Ph.D. Thesis, University of Manitoba, Winnipeg, Man.
- Rajaram, S., Luig, N.H., and Watson, I.A. 1971. The inheritance of leaf rust resistance in four varieties of common wheat. *Euphytica* 20: 574-585.
- Rao, M.V.P. 1977. Transfer of genes for stem rust resistance from *Agropyron elongatum* and Imperial rye to durum wheat. In *Induced Mutations Against Plant Diseases. Proceedings of a Symposium.* p. 527-531.
- Rashid, G., Quick, J.S., and Statler, G.D. 1976. Inheritance of leaf rust resistance in three durum wheats. *Crop Sci.* 16: 294-296.
- Riley, R., and Macer, C.F. 1966. The chromosomal distribution of the genetic resistance of rye to wheat pathogens. *Can. J. Genet. Cytol.* 8: 640-653.

- Robinson, R.A. 1969. Disease resistance terminology. Rev. Appl. Mycol. 48: 593-606.
- Roelfs, A.P. 1978. Estimated losses caused by rust in small grain cereals in the United States. 1918-1976. U.S.D.A. Agr. Res. Serv. No. 1363. 85p.
- Russell, G.E. 1978. Plant breeding for pest and disease resistance. Butterworths, London. p
- Samborski, D.J. 1980. Occurrence and virulence of Puccinia recondita in Canada in 1979. Can. J. Plant Pathol. 2: 246-248.
- Samborski, D.J., and Dyck, P.L. 1976. Inheritance of virulence in Puccinia recondita on six backcross lines of wheat with single genes for resistance to leaf rust. Can. J. Bot. 54: 1666-1671.
- Samborski, D.J., and Peturson, B. 1960. Effect of leaf rust on the yield of resistant wheat. Can. J. Plant Sci. 40: 620-622.
- Sanghi, A.K., and Baker, E.P. 1972. Genetic basis for resistance in two common wheat cultivars to stem rust strains of unusual avirulence. Proc. Linn. Soc. N.S.W. 97: 56-71.
- Sanghi, A.K., and Luig, N.H. 1971. Resistance in wheat to formae speciales tritici and secalis of Puccinia graminis. Can. J. Genet. Cytol. 13: 119-127.
- Sharp, E.L. 1972. Additive genes for resistance to stripe rust. In Proc. European and Mediterranean Cereal Rusts Conf. Praha, Czechoslovakia, Vol. I. p267-629.
- Srivastava, K.D., Joshi, L.M., and Malhotra, R.K. 1974. Effect of brown rust on yield components of wheat variety Lal Bahadur, Indian Phytopathology. 27: 286-290.
- Stakman, E.C., Stewart, D.M., and Loegering, W.R. 1962. Identification of physiologic races of Puccinia graminis var. tritici. U.S. Dept. Agric. A.R.S. Bull. E617 (Revised).
- Starzycki, S. 1976. Diseases, pests and physiology of rye. In Rye: production, chemistry and technology. Bushuk, W. (ed.). Amer. Assoc. Cereal Chemists, Inc. St. Paul, Minnesota. p. 27-61.

- Statler, G.D. 1972. Inheritance of resistance to leaf rust in Waldron wheat. *Phytopathology* 63: 346-348.
- Statler, G.D. 1973. Inheritance of resistance in Leeds durum wheat. *Crop Sci.* 13: 116-117.
- Strickberger, M.W. 1968. *Genetics*. The McMillan Co. New York. 868p.
- Stuchilikova, A., and Martos, P. 1979. The resistance of triticale to Puccinia recondita secalis and P. graminis secalis. *Rev. Plant Pathol.* 58: 322. (Abstr.).
- Syamananada, R., and Dickson, I.G. 1959. The influence of temperature and light on rust reaction of inbred lines of corn inoculated with specific lines of Puccinia sorghi. *Phytopathology* 49: 102-106.
- Tan, B.H., Luig, N.H., and Watson, I.A. 1976. Genetic analysis of stem rust resistance in Secale cereale. I. Genes for resistance to Puccinia graminis f. sp. secalis. *Z. Pflanzenzuchtg* 76: 121-132.
- Tan, B.H., Luig, N.H., and Watson, I.A. 1977. Genetic analysis of stem rust resistance in Secale cereale. II. Genes for resistance to Puccinia graminis f. sp. tritici. *Z. Pflanzenzuchtg* 79: 299-309.
- Tan, B.H., Watson, I.A., and Luig, N.H. 1975. A study of physiologic specialization of rye stem rust in Australia. *Aust. J. Biol. Sci.* 28: 539-543.
- Van der Plank, J.E. 1968. *Disease resistance in plants*. Academic Press, Inc., New York. 206p.
- Watson, I.A. 1977. The national wheat rust control in Australia. Plant Breeding Institute, University of Sydney. 24p.
- Watson, I.A., and Luig, N.H. 1959. Somatic hybridization between Puccinia graminis var. tritici and P. graminis var. secalis. *Proc. Linn. Soc. N.S.W.* 84: 207-208. Cited by Morrison (1977).
- Wilson, M., and Henderson, D.M. 1966. *British rust fungi*. Cambridge University Press. pp. 278-279.
- Wu, C.S., and Ausemus, E.R. 1953. Inheritance of leaf rust reaction and other characters in a spring wheat cross. *Agron. J.* 45: 43-48.

- Young, H.C.R., and Prescott, J.M. 1977. A study of race populations to Puccinia recondita f.sp. tritici. Phytopathology 67: 528-532.
- Zeller, F.J. 1973. IB/IR wheat - rye chromosome substitutions translocations. Proc. 4th. Int. Wheat Genet. Symp., Columbia, Missouri, p. 209-221.
- Zillinsky, F.J. 1974. The triticales improvement program at CIMMYT. In Triticale. Proc. Int. Symp. El Batan, Mexico. eds. McIntyre, R., and Campbell, M. p. 81-85.
- Zwatz, B. 1977. Severe brown rust on wheat and rye. Rev. Plant Pathol. 57: 197 (Abstr.).

## APPENDIX I

Explanation of infection types, as described by Stakman et al. (1962).

<u>Infection type</u>	<u>Varietal Reaction and Reaction Classes</u>
	<u>Resistant</u>
0 Immune -	No uredia nor other indications of infection.
0; Nearly Immune -	No uredia, but hypersensitive flecks present.
1 Very Resistant -	Uredia minute; surrounded by distinct necrotic areas.
2 Moderately Resistant -	Uredia small to medium; usually in green islands surrounded by a decidedly chlorotic or necrotic area.
	<u>Susceptible</u>
3 Moderately Susceptible	Uredia medium in size; and usually separate; no necrosis but chlorosis may be present, especially under unfavourable conditions.
4 Very Susceptible -	Uredia large and usually coalesce to form large irregular pustules.

X      Heterogenous -      Mesothetic  
Uredia variable, sometimes including all infection types and intergradations between them on the same leaf.

The symbols -, =, +, ++ indicate variation within a given infection type.



APPENDIX II

Infection Types Produced on Parental Inbreds and Selected F4 Lines  
by Six Races of Wheat Leaf Rust and one Isolate of Rye Leaf Rust.

Parental inbred or line	Races						
	5	9	15#156 <sup>64</sup>	30	76	126a	RLR 213/78
UM8116	2 <sup>+</sup>	3 <sup>+</sup>	2 <sup>+</sup> 3 <sup>+</sup>	3	3 <sup>+</sup>	3 <sup>+</sup>	3-3 <sup>+</sup>
UM8003	2	0; 1-2	3 <sup>+</sup>	2	3-3 <sup>+</sup>	2 <sup>+</sup>	2 <sup>+</sup>
UM8071	2	2	2 <sup>+</sup>	2-2 <sup>+</sup> c <sub>-</sub>	1 <sup>+</sup> 2 <sup>+</sup>	2 <sup>+</sup>	2 <sup>+</sup> c
UM8295	0; 1	0;	0; 0; 1	in	0; 1	0;	0; 1 <sup>+</sup>
UM8301	0;	0;	0;	0;	0;	0;	1 <sup>+</sup>
UM8336	0;	0;	0;	0;	0;	0;	0;
UM8340	0; 1 <sup>-</sup> 1 <sup>+</sup>	0; 0; 1	0; 0; 1	0; 1n:	0; 1	0;	0;
UM8116 x UM8301	3	0;	0; 0; 1	0;	0;	0;	0;
6-1	0; -1	0;	0;	0;	0;	0;	3 <sup>+</sup>
9-1	0;	0;	0;	0;	0;	0;	1 <sup>+</sup>
UM8116 x UM8071	16	0;	0;	0;	0;	0;	1 <sup>+</sup>
17	3 <sup>+</sup>	3	2 <sup>+</sup> 3	1 <sup>+</sup> 2 <sup>+</sup>	2-2 <sup>+</sup>	3-3 <sup>+</sup>	3 <sup>+</sup>
18-1	2	2	1-1 <sup>+</sup>	1 <sup>+</sup> 2 <sup>+</sup>	2	2 <sup>+</sup> 3 <sup>+</sup>	3 <sup>+</sup>
UM8116 x UM8340	21-1	2	1 <sup>+</sup>	2-2 <sup>+</sup>	1 <sup>+</sup>	3 <sup>+</sup>	3 <sup>+</sup>
21-2	0; 1 <sup>-</sup>	0;	1 <sup>+</sup>	0; 1 <sup>-</sup>	1 <sup>+</sup>	0;	0;
24-1	-	-	0;	0; 1	-	0;	-*
UM8116 x UM8003	27	0;	0;	0;	0;	0;	0;
29	3 <sup>+</sup>	2-3	3 <sup>+</sup>	2 <sup>+</sup>	3 <sup>+</sup>	0;	0;
32	3 <sup>+</sup>	2-3	2 <sup>+</sup>	2 <sup>+</sup> 3	3 <sup>+</sup>	2 <sup>+</sup>	3 <sup>+</sup>
37-2	3 <sup>+</sup>	0; 1-3 <sup>+</sup>	3 <sup>+</sup>	2 <sup>+</sup> 3	3 <sup>+</sup>	1	2 <sup>+</sup>
UM8116 x UM8295	80-2	2	2	2	2 <sup>-</sup>	0	2
99-1	0; 1-1 <sup>+</sup>	2	0; 1 <sup>+</sup>	0; 1	2 <sup>+</sup>	0; 1 <sup>-</sup> 1 <sup>+</sup>	0; 1-1 <sup>+</sup>
UM8116 x UM8336	143	2	2	0; 1	2	1	-
	0;	0;	0;	0;	0;	0;	3

\* Dead or poor plant.

## APPENDIX III

Seedling Reaction of the Parental  
Inbred Lines to Different Races of  
Wheat Stem Rust and Isolates of  
Rye Stem Rust.

Inbred Line	Wheat Stem Rust Races			Rye Stem Rust Isolates		
	C17(56)	C53(15 Bil)	C61(38)	447/78	59/79	101/80
UM8003	;	;	;	3 <sup>+</sup>	-*	1
UM8071	;	;	1	4	3 <sup>+</sup>	4
UM8116	;	;	;	3 <sup>+</sup>	2	4
UM8295	;	;	-	-	-	1 <sup>+</sup>
UM8301	;	;1	;	4	4	1
UM8336	;	;	;	;	;	;
UM8340	;	;	;	;1	;	1 <sup>+</sup>

\* Dead or poor plant.

## APPENDIX IV

Adult Plant Field Reactions of the  
Resistant and Susceptible Inbreds  
at the Glenlea Rust Nursery in  
1980.

Inbred line	Field Reaction *	
	Leaf Rust	Stem Rust
UM8116	10 MR**	TR
UM8003	TR-50M	0
UM8071	TMR	10MR
UM8295	TR	10MR
UM8301	0	TMR
UM8336	0	TR-5MS
UM8340	TR	30M

\* 0 = No visible infection on plants.

TR = Trace reaction. Necrotic areas with or without minute uredia present.

MR = Moderately resistant. Small uredia present surrounded by necrotic areas.

M = Intermediate. Variable size uredia, some with necrosis and/or chlorosis.

MS = Moderate susceptible. Medium uredia with no necrosis but possibly some distinct chlorosis.

\*\* Estimate of the relative percentage of rust infection.

## APPENDIX V

Explanation of formula used in adjusting the expected ratio.

$$(p)^n \cdot R = Y$$

where

$p$  = probability of failing to detect a susceptible plant,

$n$  = average population per F3 line,

$R$  = Expected number of lines segregating for 3 genes.

$Y$  = proportion of undetected lines segregating for 3 genes which would be included in the homozygous resistant class.

Seedling Infection Types Exhibited by Six  
Resistant Inbreds and their Respective Genes  
for Resistance.

Gene	Source	Rust reaction	
		RLR 213/78	Race 30
LrPkl	UM8003	1 <sup>+</sup> to 2	-*
" 2	"	-	0;l <sub>+</sub>
" 3	"	- <sup>+</sup>	1
	Parent	1 <sup>+</sup>	0;l
LrPr1	UM8071	2 to 2 <sup>+</sup> c	-
" 2	"	-	2 to 2 <sup>+</sup> c
	Parent	2 to 2 <sup>+</sup> c	2 to 2 <sup>+</sup> c
LrGB1	UM8295	0;	-
" 2	"	0;l	-
" 3	"	1 <sup>+</sup> to 2	-
" 4	"	-	;n to ;ln
" 5	"	-	;n to ;ln
" 6	"	-	1
	Parent	0;l <sup>-</sup>	;n
LrGW1	UM8301	1 <sup>+</sup>	-
" 2	"	-	0;
" 3	"	-	0;l
" 4	"	-	1 <sup>+</sup> to 2
	Parent	0;l <sup>+</sup> to 1 <sup>+</sup>	0;
LrEm1	UM8336	0;	-
" 2	"	0;l	-
" 3	"	-	0;
" 4	"	-	0;l <sub>+</sub>
" 5	"	-	1
	Parent	0;	0;
LrHz1	UM8340**	0;	-
" 2	"	0;l	-
" 3	"	-	0;ln
" 4	"	-	1 <sup>+</sup> to 2
	Parent	0;	0;ln

\* - Ineffective

\*\* At least one gene conditions resistance to both RLR 213/78 and Race 30.

## APPENDIX VII

Virulence Combinations of Puccinia recondita  
 Races and Isolate Used in Studying the Spectrum  
 of Resistance.

Race or Isolate	Avirulence/virulence formula
5	2a, 2b, 2c, B, 3ka, 9, 11, 16, 17, 18, 21, 23, 24/1, 3, 10, 14a, 15
9	B, 3, 3ka, 9, 11, 14a, 16, 18, 21, 23, 24/1, 2a, 2b, 2c, 10, 15, 17
5#156 <sup>64</sup>	1, 2a, 2b, 2c, 3ka, 9, 11, 17, 18, 21, 23, 24/B, 3, 10, 14a, 15, 16
30	B, 3ka, 9, 11, 16, 18, 21, 24/1, 2a, 2b, 2c, 3, 10, 14a, 15, 17, 23
76	1, 2a, 2b, 9, 11, 14a, 16, 17, 21, 23, 24/2c, B, 3, 3ka, 10, 15, 18
126a	2a, 3ka, 9, 11, 16, 18, 21, 24/1, 2b, 2c, B, 3, 10, 14a, 15, 17, 23
LR 213/78	-