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Wheat Leaf Rust

D. J. Samborski

*Agriculture Canada, Research Station,
Winnipeg, Manitoba, Canada*

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I. Introduction

Wheat leaf rust, *Puccinia recondita* Rob. ex Desm. f. sp. *tritici*, usually does not cause spectacular damage, but on a worldwide basis it probably causes more damage than the other wheat rusts. The devastating losses previously caused by wheat stem rust in North America

obscured the economic significance of leaf rust in this region for many years. In Eastern Europe, leaf rust has long been recognized as the major rust on wheat.

The early history of research on leaf rust of wheat was described by Chester (1946), who also noted the extensive research conducted in the Soviet Union. This research continues but is not well recognized outside of Eastern Europe. The Soviet journal *Genetica* is available in English translation and contains valuable contributions on genetical aspects of the wheat leaf rust system. In addition, contributions by Soviet and eastern European leaf rust workers to the European and Mediterranean Cereal Rust Conferences are usually in English. These conferences attract many rust workers from outside of Europe and the Mediterranean area and are the primary international forum. The North American Wheat Leaf Rust Research Workers Committee consists of workers from Canada, the United States, and Mexico. In the past, the committee has largely dealt with the mechanics of race identification and nomenclature.

It is not possible to list all the workers who have contributed to our present understanding of leaf rust of wheat. However, important contributions were made by Mains, Caldwell, Johnston, and Chester (United States), Newton, Johnson, and Brown (Canada), Vallega (Argentina), da Silva (Brazil), Waterhouse and Watson (Australia), d'Oliveira (Portugal), Sabilia (Italy), Hassebrauk (Germany), and a number of workers in the Soviet Union whose contributions were described by Chester (1946).

Physiologic specialization in leaf rust of wheat was investigated extensively by the early workers, but there was no consideration of the involvement of specific genes in the parasite, although genes for resistance to leaf rust were recognized. Consideration of specific gene interactions had to wait for general acceptance of the gene-for-gene theory proposed by Flor (1956) for flax and flax rust, which was later elaborated by Person (1959) into a general concept of host-parasite interactions. In the last 20 years there has been considerable progress in the genetic aspects of host-parasite interactions, but there has been little progress in elucidating the chemical products of the genes involved in gene-for-gene interactions. The leaf rust organism can be grown in axenic culture, although growth is limited (Katsuya *et al.*, 1978). Therefore, although availability of nutrients in the host probably influences the rate and amount of rust development, specific nutrients are not likely to be responsible for the specificity shown in gene-for-gene interactions.

II. Distribution and Importance of Wheat Leaf Rust

Wheat leaf rust occurs wherever wheat is grown, and it is the commonest, most widely distributed of all cereal rusts (Chester, 1946). Although the parasite has no doubt occurred on wheat through the course of its development, it is probably more damaging now that large areas tend to be sown to single, genetically homogeneous cultivars or to closely related cultivars.

In the eastern prairies of Canada, leaf rust normally reduces yields by 5–15% when widely grown cultivars are susceptible. However, higher losses can occur if the disease becomes severe before flowering (Samborski and Peturson, 1960). In the United States, epidemics of leaf rust have occurred more frequently on winter wheats in the southern half of the country than in areas further north (Roelfs, 1978). Yield losses in winter wheat can be severe. For example, losses attributable to leaf rust in Oklahoma and Kansas from 1973–1975 have been estimated at 4,110,000 tonnes (Roelfs, 1978).

Leaf rust is now the most important wheat disease in Mexico [International Maize and Wheat Improvement Center (CIMMYT), 1977]. An epidemic of leaf rust affected commercial fields of the cultivar Jupateco 73 in Northwest Mexico during 1976–1977. Severe infections on young plants caused yield reductions up to 40% (Dubin and Torres, 1981).

Leaf rust is endemic in the southern cone countries of South America, and its importance to wheat production has long been recognized. Consequently, wheat breeders in Argentina and Brazil have produced highly resistant cultivars; some of these cultivars have been used extensively as sources of resistance to leaf rust by breeders in other countries. The cultivar Frontana, produced by Beckman in Brazil in 1945 (da Silva, 1966), has been used extensively in North America. An Argentine spring wheat, Klein 33, was the leaf-rust-resistant parent in crosses that produced the cultivars Besostaya 1 and Besostaya 4 at Krasnodar in the U.S.S.R. (Prutskova and Ukhanova, 1972).

Leaf rust is not considered to be a serious problem in Western Europe, but is the most damaging wheat disease in Eastern Europe (Dwuzrazna *et al.*, 1980; Berlyand-Kozhevnikov *et al.*, 1973; Chumakov, 1963), causing an average yield reduction of 3–5%. It is endemic in the dry delta of Egypt, where irrigation provides moisture conditions suitable for rust infection (Saari and Wilcoxson, 1974). The disease is also severe in most years in Ethiopia (Dmitriev and Gorshkov, 1980). In

India, average losses of 3% have been estimated, although higher losses occur in certain areas if the cultivars are susceptible to leaf rust (Saari and Wilcoxson, 1974). It is now the most important disease of wheat in Pakistan, and a severe epidemic in 1978 resulted in an average national loss of 10% or 830,000 tonnes of wheat (Hussain *et al.*, 1980). The importance of leaf rust in Australia has been well documented (Waterhouse, 1952).

III. Taxonomy

Wheat leaf rust was recognized as a species distinct from the other rusts in 1815 by de Candolle, who described it as *Uredo rubigo-vera* (Chester, 1946). Eriksson and Henning in 1894 described *Puccinia dispersa*, which included leaf rusts of wheat and rye (Chester, 1946). In 1899, Eriksson described wheat leaf rust as *Puccinia triticina* (Chester, 1946). In 1932, Mains subdivided *P. rubigo-vera* into 56 *formae speciales*, one of which, f. sp. *tritici*, corresponded to Eriksson's *P. triticina* (Mains, 1932). In 1956, Cummins and Caldwell suggested that *Puccinia recondita* was the valid name for the leaf rusts of grasses (Cummins and Caldwell, 1956). The term *P. recondita* f. sp. *tritici* is now used by most, although not all, leaf rust workers.

The leaf rusts of grasses are mainly distinguishable by reference to haplont or diplont host relations, and it is not always clear whether they should be considered as *formae speciales* or whether some should be classified as separate species. However, the leaf rusts exhibit parasitic specialization on the hosts for both haplont and diplont phases of the fungus, suggesting that it is more realistic to classify them as *formae speciales* (d'Oliveira and Samborski, 1966; Anikster and Wahl, 1979; Wilson and Henderson, 1966).

IV. Physiologic Specialization

A. DIFFERENTIAL HOSTS

Wheat leaf rust, *P. recondita* Rob. ex Desm. f. sp. *tritici*, can be further subdivided by the reactions of genetically different strains of wheat to pure isolates of the parasite. Such physiologic specialization in wheat leaf rust was first reported by Mains and Jackson (1921).

Mains and Jackson by 1926 could distinguish 12 physiologic races on 11 differential cultivars (Mains and Jackson, 1926). Three of these differentials were subsequently dropped (Johnston and Mains, 1932), but the remaining eight differentials became accepted internationally.

Since the differentials were used widely and the results were compared, it was important to have cultivars in which the rust reactions were not affected by differences in environment. Three of the eight standard differentials were considered labile with respect to environment, and Basile (1957) proposed new race keys based on the remaining five differentials. This change resulted in more consistent rust reactions but also in the loss of genes *Lr2b*, *LrB*, and *Lr11* from the original series. This was of considerable importance, since only seven genes for resistance to leaf rust were present in the original eight differentials. In practice, therefore, most workers used all the differentials and presented their results according to both keys.

Although physiologic race surveys can be very useful in determining the spread of races from one area to another, their main purpose is to determine the range of variability in the parasite. They are indispensable when deciding which cultivars to use as resistant parents in breeding programs, and in monitoring changes in virulence that affect commercial cultivars and breeding programs. Shortly after resistant cultivars were first released in Canada, it was noted that they were attacked by strains or biotypes of leaf rust that could not be differentiated from avirulent strains on the standard differentials (Johnson and Newton, 1946). Therefore, supplementary differentials were introduced and Hope or its derivatives were the first such differentials used in Canada. Cultures virulent on Hope resistance were designated by the letter "a" after the race number. A number of other supplementary differentials were later introduced to meet the changing needs related to disease control.

The genes for resistance that are present in resistant commercial cultivars or in cultivars that are being used as resistant parents should also be represented in the differential host series. This became obvious after Flor published his studies on flax and flax rust and proposed the gene-for-gene theory (Flor, 1956). Subsequently, backcross lines containing single genes for resistance to leaf rust were developed and were soon adopted as differential hosts in race surveys. These single-gene lines provided an effective means of characterizing the parasite populations in terms of specific gene interactions. A list of the named genes conditioning resistance to leaf rust has been published by Browder (1980).

The single-gene lines developed at Winnipeg with the cultivar

Thatcher as the backcross parent are now used throughout the world. In 1979, 19 single-gene lines were used in Canada, and new lines are added when they become available (Samborski, 1980). North American isolates of leaf rust can apparently detect only genes *Lr1*, *Lr2a*, *Lr2b*, *Lr2c*, *LrB*, *Lr3*, and *Lr11* in the old standard differentials. If single-gene lines, each with one of these seven genes, are included in race surveys, the results of present and earlier surveys can be compared. Older data, in terms of reactions of the standard differentials, can be interpreted in terms of specific gene interactions. Although single-gene lines are now the most important differentials, cultivars of known or unknown genotype are often included. All of the differentials used in Canada are important for epidemiological purposes or in relation to the breeding program.

B. NOMENCLATURE OF RACES

Race nomenclature was simple as long as the early standard differentials were used and a key was provided for the identification of physiologic races (Johnston, 1961). The introduction of supplementary hosts required further designations. This resulted in several systems of nomenclature, none of which was completely satisfactory (Young and Browder, 1965). At present, the North American leaf rust workers use a formula system like that introduced by Green for wheat stem rust (Green, 1981). However, the leaf rust workers do not designate strains of leaf rust characterized by a particular virulence formula with a formal race designation. Cultures of leaf rust used in further studies and those that appear in publications are identified by their survey number (Samborski, 1981). In North America, the leaf rust workers consider that race designations based on a set of differential hosts are cumbersome since differentials may be dropped or added. This lack of race designations makes it difficult to follow trends involving gene combinations, particularly since most differentials are retained for a considerable period. Race designations are given in Australia, but their system is unique (Watson and Luig, 1961).

V. Evolutionary Trends in Leaf Rust Races

The determination of evolutionary trends in leaf rust races must be based on race surveys, since trends can only be determined from con-

tinuous observations carried out for many years. Before dealing with trends that have been revealed, the mechanisms that most likely contribute to the evolution of leaf rust races will be considered.

A. SOURCES OF VARIABILITY

1. *Alternate Hosts*

Jackson and Mains (1921) demonstrated that *Thalictrum* spp. could function as the alternate host of leaf rust of wheat. Several other alternate hosts have been reported to function in restricted areas. These include *Isopyrum fumarioides* L. in Siberia (Chester, 1946), *Anchusa* spp. in Portugal (d'Oliveira and Samborski, 1966), and *Clematis* spp. in Italy (Sibilia, 1960) and in the Soviet Far East (Azbukina, 1980). It is not clear how important the aecial hosts are in the evolution of new races, but they must play a role by reassortment of variability during sexual recombination. Yamada *et al.* (1973) found infected plants of *Thalictrum thunbergii* DC near wheat fields in Japan. They concluded that this species is not important as a source of inoculum of leaf rust of wheat in Japan but is significant in producing new races. In general, where alternate hosts grow in close proximity to wheat fields, they would have a definite effect on the evolution of leaf rust races. This does not appear to operate in North America. Although some infection can be obtained experimentally (Saari *et al.*, 1968), natural infection of *Thalictrum* spp. native to North America occurs rarely, and thus the alternate host does not play an important role in the origin of new races of leaf rust on this continent.

2. *Asexual Recombination*

Anastomosis of germ tubes and hyphae occurs readily in rust fungi, and it is reasonable to expect mitotic recombination to occur. In fact, new strains have been isolated from hosts inoculated with mixtures of urediospores of two races of various rusts (Webster, 1974). Other workers obtained negative results when races were mixed (Barr *et al.*, 1964; Bartoš *et al.*, 1969b). At the present time, it is not possible to assess the importance of asexual recombination of nuclei in the evolution of leaf rust races.

3. *Mutation*

Mutations provide the basic variation that occurs in the rusts. When one considers the tremendous number of spores that are produced by

the leaf rust parasite in any one year, it is obvious that mutations can account for most or all of the changes in virulence that are observed. The dikaryotic nature of the parasite when on wheat provides for considerable conservation of the variation caused by mutation. A number of leaf rust isolates have been selfed, and these cultures have been found to be heterozygous at many loci (Samborski and Dyck, 1968, 1976; Statler, 1977, 1979; Statler and Jones, 1981). Since the parasite reproduces asexually on its main host, deleterious mutations are also conserved; these include spore color mutants. Segregants with orange-colored urediospores are often obtained when pure cultures of leaf rust are selfed, but there is only one report of a color mutant collected from natural populations of leaf rust (Johnston, 1930). In many cases, orange-spored isolates obtained from the aecial host do not grow well on wheat, and could not compete in nature with the normal brown-spored members of the population.

Avirulence in leaf rust is usually dominant; a recessive mutation to virulence at one allele of any locus can therefore only be detected by selfing cultures on the aecial host. Thus, when part of a rust population is heterozygous for virulence at a particular locus, a mutation occurring at the other allele would result in a virulent strain in the rust population. In some cases they will be so infrequent that they cannot be detected by normal survey procedures, but if there is widespread cultivation of a cultivar with the corresponding gene for resistance, such strains have a selective advantage and they increase in the population to the point where they are readily detected.

A few loci conditioning avirulence show incomplete dominance, and in such cases, a mutation at one of the alleles can be detected by the higher infection type that is produced (Samborski, 1963).

B. LONG-TERM CHANGES IN LEAF RUST RACES IN NORTH AMERICA

Annual surveys of leaf rust populations have been carried on for many years in North America, and a considerable body of information is available for analyses of evolutionary trends (Johnston *et al.*, 1968; Johnson, 1956). Since standard differentials were used for many years and the genes for resistance in these cultivars are known, the data can be analyzed in terms of specific gene interactions.

As mentioned, the aecial host is of no epidemiological importance in North America and there do not appear to be any susceptible wild-grass hosts. Leaf rust overwinters largely on winter wheat in Texas and

Oklahoma, although it can and does survive on living wheat leaves farther north. Winds carry the inoculum north in the spring and it reaches Manitoba, Canada, in mid June on average. It is generally agreed that urediospores are blown south in the fall to reinfest winter wheat in the overwintering area. This is an oversimplification of the situation, but the epidemiology will be expanded by Roelfs in Chapter 13, this volume.

1. *Influence of Resistance Genes in Overwintering Areas*

It is obvious that genes for resistance in cultivars grown in the area where leaf rust overwinters must have a marked effect on the rust population of the whole area the following summer. When the cultivar Agent (resistance gene *Lr24*) was released in Oklahoma and Texas, virulence on *Lr24* had not been detected in North America. In 1971, Agent occupied 13,350 hectares in Oklahoma and virulent strains of leaf rust occurred on it in trace amounts, but cultures virulent on gene *Lr24* were not detected in Canada. In 1972, when Agent occupied 50,600 hectares (about 2.2% of the wheat area) in Oklahoma and leaf rust occurred at 1% severity, these cultures were isolated in Canada (Samborski, 1972).

2. *Influence of Resistance Genes in Cultivars Grown in the Rust Area of Western Canada*

The cultivar Renown, with resistance to leaf rust from Hope (*Lr14a*), was the first resistant cultivar to be widely grown in western Canada. Renown was released in 1937 but became severely affected by leaf rust in 1943. The cultivar Lee (gene *Lr10*) was licensed in 1950, but virulent strains of leaf rust were soon detected. In 1954, Selkirk (genes *Lr10*, *Lr16*) was released. Since gene *Lr10* was present in Lee, part of the rust population was virulent on this gene when Selkirk was released. Gene *Lr16* does not appear to have been in any other cultivar at this time, and all cultures tested were avirulent on cultivars with *Lr16*. Selkirk rapidly occupied most of the rust area in Canada and the adjoining states. Virulence on hosts with *Lr10* increased rapidly in the rust population, since *Lr10* conditions a high level of resistance and *Lr16* a moderate level that permits considerable sporulation. Virulence on cultivars with *Lr10* thus had a distinct advantage where Selkirk was grown. Virulence on hosts with *Lr16* was not detected until 1961 and increased gradually until 1966, when 56% of the isolates in the leaf rust race survey were virulent on *Lr16* (Samborski, 1967). The release

of the cultivar Manitou (gene *Lr13*) and subsequently Neepawa (gene *Lr13*) led to a decline of the area sown to Selkirk after 1966, which was followed by a decline of the proportion of strains in the leaf rust population virulent on cultivars with *Lr16* (Fig. 1). Selkirk has occupied about 10% of the wheat area in Manitoba since 1972; however, no cultures virulent on host plants with *Lr16* have been isolated since 1976.

These results show that gene recycling as proposed by Person (1966) would be effective with gene *Lr16*. It should be emphasized that Selkirk was replaced by other cultivars while only about half of the rust population was virulent on *Lr16*. Virulence on *Lr13* appeared a few years after Manitou was released, but it occurred in that portion of the rust population that was avirulent on cultivars with *Lr16*. The cultivars grown in the rust area of Western Canada since 1966 do not have the Hope or H-44 resistance to leaf rust that was present in Renown, but all cultures isolated in this region during the annual race surveys are still virulent on Hope and H-44 resistance.

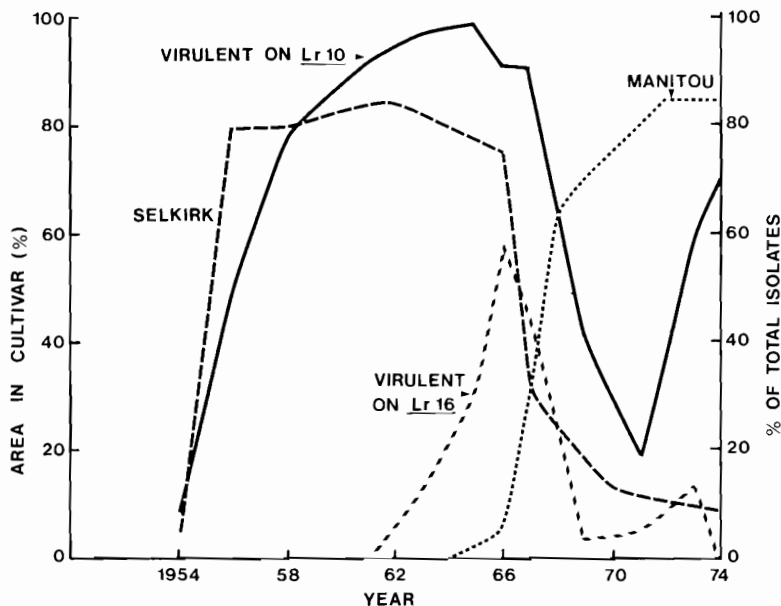


Fig. 1. Percentage of wheat area planted to the wheat cultivars Selkirk and Manitou and the percentage of leaf rust isolates virulent on genes *Lr10* and *Lr16* in Selkirk during the period 1954–1974. Manitou has gene *Lr13* conditioning adult plant resistance. From D. J. Samborski (unpublished results).

3. Changes in Leaf Rust Races That Are Not Related to Resistance Genes in Commercial Cultivars

Pawnee, released in 1943–1944, was the first winter wheat cultivar grown in the United States to have a marked influence on leaf rust races (C. O. Johnston, personal communication). Since Pawnee was resistant to race 9, which had been dominant for many years, it was soon replaced by race 5 and race 15. Resistance to race 9 was probably due to the presence of *Lr3*, on which race 9 is avirulent, while races 5, 15, and 126 are virulent. Other cultivars grown in the United States and Canada did not have any resistance corresponding to the genes in the standard differentials, so that changes in prevalence of races 5, 15, and 126 cannot be explained by the action of genes for resistance in the host; the changes in these races are shown in Fig. 2.

The most interesting long-term changes in race prevalence are shown by race 5 and race 15. Race 5 differs from race 15 on the standard differentials only on the cultivar Malakof (gene *Lr1*): race 5 is virulent and race 15 is avirulent on cultivars with gene *Lr1*. Both races appeared to be equally well adapted races, and there is no ready explanation for the dominance of race 15 since the mid 1950s. These changes cannot

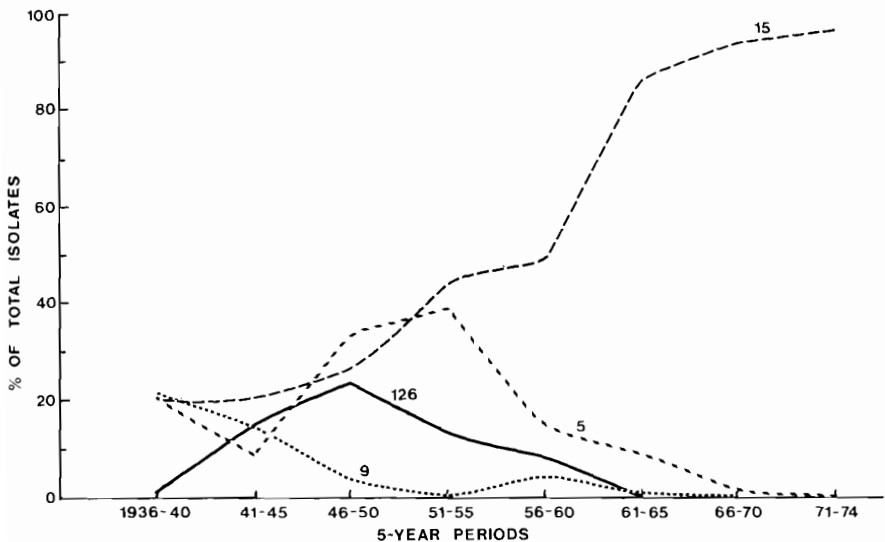


Fig. 2. Changes in prevalence of wheat leaf rust races 5, 9, 15, and 126 during the period 1936–1974. From D. J. Samborski (unpublished results).

be projected further, since cultivars with *Lr1* and *Lr2a* are now widely grown and have influenced subsequent changes in the rust population.

VI. Host-Parasite Genetics in the Wheat Leaf Rust System

Studies on the inheritance of virulence in wheat leaf rust were preceded by studies on the inheritance of resistance in wheat and by the development of backcross lines containing single genes for resistance. The availability of single-gene lines enabled analyses of avirulence to be carried out with small populations of segregating cultures. The same populations could then be used to study cultivars of unknown genotype, and segregation on these hosts could be compared to that on the single-gene lines. Although it is difficult to produce a large number of cultures on the aecial host, the segregating population equivalent to an F_1 or F_2 can be maintained indefinitely and used repeatedly with new groups of wheats.

A. TELIOSPORE PRODUCTION

Wheat leaf rust does not produce teliospores readily under greenhouse or growth-chamber conditions. Teliospores do form on seedling wheat plants (Jackson and Young, 1967; Takahashi *et al.*, 1965; Freitas, 1972), but this is often very erratic. Teliospores can be most readily obtained by injecting urediospores into the culms of moderately resistant wheat plants in the boot stage. Severe infections are desirable, and teliospores form on the leaf sheath.

B. TELIOSPORE GERMINATION

It is sometimes assumed that teliospores of wheat rusts require a cold treatment in order to germinate. However, with wheat leaf rust a cold treatment is not necessary, and in areas such as Portugal, teliospores germinate in nature during the fall rains after a hot, dry summer. For genetic studies, teliospores will usually germinate if subjected to alternate wet-dry periods without a cold treatment. Teliospores of some cultures germinate readily, while others require a lengthy period of such cycles. Teliospores usually germinate best if they are collected while the plants are still green. Infection of the alternate host is readily

carried out by suspending the teliospores over young plants of a susceptible species of *Thalictrum*. At Winnipeg, *Thalictrum speciosissimum* Loefl. is used routinely. Self-fertilization or crosses between rust cultures are carried out by transfer of pycnial nectar in a variety of ways (Samborski and Dyck, 1968; Dyck and Samborski, 1974).

C. GENE-FOR-GENE RELATIONSHIPS IN THE WHEAT-LEAF RUST SYSTEM

Studies on the inheritance of virulence on a number of genes in wheat conditioning resistance to leaf rust have been carried out, and in most cases, classical gene-for-gene interactions were demonstrated (Samborski and Dyck, 1968, 1976; Dyck and Samborski, 1970; Statler, 1977, 1979). However, interactions at two loci, *Lr2* and *Lr3*, each with several alleles, are unusual in that the action of a recessive gene for virulence appears to be modified or inhibited by a second gene (Samborski and Dyck, 1968; Dyck and Samborski, 1974; Haggag *et al.*, 1973). Interactions at the *Lr2* locus are particularly interesting since individual cultures are always least virulent on hosts with *Lr2a*, most virulent on hosts with *Lr2c*, and intermediate on plants with *Lr2b*.

Three types of cultures showing physiologic specialization at the *Lr2* locus are found in the North American leaf rust population. Cultures virulent on plants with *Lr2a* are virulent on the other alleles and are homozygous for gene *p2*. Cultures avirulent on all three alleles are either heterozygous or homozygous for a single gene *P2*, and segregation is identical on the three alleles. Cultures that produce an intermediate infection type on plants with *Lr2a* and that are virulent on plants with *Lr2c* are heterozygous for *P2* and presumably for another gene that affects the expression of *P2*.

D. ANALYSES OF CULTIVARS OF UNKNOWN GENOTYPE

A comparison of the patterns of infection types on backcross lines containing single genes for resistance with the patterns of infection types on cultivars of unknown genotype can often be used to identify genes for resistance in those cultivars (Bartoš *et al.*, 1969a; Browder, 1973; Dyck and Samborski, 1982). Unfortunately, rust cultures with critical combinations of genes for virulence are often not available. For example, culture 10-77 isolated in Manitoba is virulent on seedlings of the cultivar Tobari 66. This seedling resistance appears to be present in many cultivars (Dyck and Samborski, 1982), but culture 10-77 is avi-

virulent on gene *Lr10*, which is present in many Mexican wheats that may also have the type of seedling resistance present in Tobar 66.

A further complication results from the ghost effect reported by Samborski and Dyck (1982). The cultivar Columbus has gene *Lr16* conditioning seedling resistance and gene *Lr13*, which conditions adult plant resistance to wheat leaf rust. Cultures of leaf rust that are virulent on wheat lines containing gene *Lr16* alone are not virulent on seedlings of Columbus. An interaction between genes *Lr16* and *Lr13* results in an incompatible reaction, when compatibility would be expected. In a screening test, it would be concluded that the seedling gene for resistance in Columbus was not gene *Lr16*. It has also been found that genes that singly condition moderate levels of seedling resistance to leaf rust can interact to give much higher levels of resistance (Dyck and Samborski, 1982; Samborski and Dyck, 1982). Therefore, characteristic infection types produced on lines with single genes for resistance cannot always be relied on when interpreting infection types obtained on multigenic cultivars.

Assessment and designation of genotypes becomes difficult when a large number of host cultivars and rust cultures are involved. Computer analysis and machine sorting of data are useful in such cases (Loegering and Burton, 1974; Browder and Eversmeyer, 1976). In many cases, the method proposed by Person (1959) for analyzing host cultivars can be very useful.

VII. Control

A. RESISTANT CULTIVARS

Selection of resistant parents is usually done on the basis of their reactions in small plots or rows in experimental fields. When tested in this manner, a cultivar may be highly resistant for many years since selection pressure is negligible under these conditions. However, if a cultivar with this type of resistance is widely grown, selection pressure is severe and races in the population with corresponding virulence may increase rapidly.

It is generally accepted that virulent strains of leaf rust will evolve rapidly on cultivars with single genes for resistance, while cultivars with multigenic resistance may remain resistant much longer. In both cases, the appearance of virulent strains is accelerated if large areas are planted to a single cultivar. Durum wheat (*Triticum durum* Desf.)

cultivars grown in western Canada are, and have always been, resistant to wheat leaf rust. Durums in other parts of the world are not noted for their resistance to leaf rust (diCariello *et al.*, 1977; Dmitriev and Gorshkov, 1980), and the long-lived resistance of durum cultivars in Canada is probably due to the fact that they are grown on a much smaller area than the bread wheats, *Triticum aestivum* L.

The importance of multigenic resistance can be illustrated by the cultivars Manitou and Chris. Both cultivars derived their resistance to leaf rust from Frontana. Manitou and Chris were released at about the same time and were grown commercially in Canada and the United States, respectively. The data in Table I show that the parasite population quickly developed virulence on Manitou, which has gene *Lr13*, while Chris, which also has *Lr13*, was protected by at least one additional gene. Frontana has not been grown commercially in North America and is still highly resistant to leaf rust in this area, although it is now susceptible in Brazil.

The genes for resistance to leaf rust of wheat in Frontana interact to give a higher level of resistance than is conditioned by any gene alone (Dyck and Samborski, 1982). The data in Table I show that when this type of resistance is involved, selection for the highest level of resistance results in selection for the greatest number of genes for resistance.

Table I
Field Reactions of Three Cultivars of Wheat to Infection
with a Mixture of Races of *Puccinia recondita*^a

Year	Leaf rust reaction ^b		
	Frontana	Chris	Manitou
1967	0	0	2R
1968	0	TR	10M
1969	0	TMS	10M
1970	TR	5MS	20M
1971	TR	15MR	50MS
1972	TR	15MR	50MS
1973	TR	20MR	50MS

^aLeaf rust resistance in Chris and Manitou was derived from Frontana. Manitou has only gene *Lr13*. Chris has *Lr13* plus at least one additional gene, and Frontana has *Lr13* plus at least two additional genes for resistance to leaf rust.

^bR, resistant; TR, trace resistant; M, mesothetic; TMS, trace moderately susceptible; MS, moderately susceptible; MR, moderately resistant.

B. CHEMICAL CONTROL

Studies on chemical control of cereal rusts began in the last century, but it was soon concluded that chemical control was not economical with the available chemicals (Dickson, 1959). Organic compounds and mixtures of inorganic salts plus dithiocarbamate fungicides were later investigated and showed considerable promise (Rowell, 1968). The recent introduction of systemic fungicides has increased interest in chemical control of wheat leaf rust. Bayleton (Buchenauer, 1976) and Indar (von Meyer *et al.*, 1970) have proven particularly effective in controlling leaf rust of wheat (Rowell, 1972; Abdel Hak *et al.*, 1980; Line and Rakotondradona, 1980) and are of special interest since they can be applied as seed dressings. Indar is highly specific and controls only wheat leaf rust, while Bayleton also controls the other wheat rusts.

Although resistant cultivars will always be the best method of controlling leaf rust, an economical method of chemical control would be valuable for situations when new races of leaf rust develop and new resistant cultivars are not available. This occurred in northwest Mexico in 1976–1977, where a severe attack of leaf rust threatened the prevalent cultivar Jupateco 73. A large area was sprayed with Indar and Bayleton and major yield losses were prevented. New resistant cultivars were released before the next growing season, and there has been no further need for chemical control in this area (Dubin and Torres, 1981).

VIII. Conclusions

If we can learn any useful lessons from past experience, it must surely be clear that constant vigilance and diligent research are necessary if losses from leaf rust of wheat are to be kept to a minimum. It has been demonstrated time and again that cultivars with a single gene for resistance will not remain resistant very long. Yet new cultivars with single genes for resistance are continually being released for commercial use. In many cases, a wheat breeder does not know what genes for resistance are in his parental cultivars, although the information may be available. Close cooperation between breeders and pathologists is obviously essential.

It is probably too late to collect appreciable numbers of land race populations of wheat with the hope of extracting new genes for re-

sistance. The large number of entries in some existing wheat collections does not give much comfort for the future, since most of the entries are usually susceptible to leaf rust and many of the resistant entries have the same genes for resistance. However, genes for resistance to leaf rust of wheat can be transferred from hosts such as *Aegilops* spp. and *Agropyron* spp. and these hosts should be collected wherever possible.

Exotic genes for resistance are no better than any other genes if they are used alone. In North America, cultivars with *Lr9* from *Aegilops umbellulata* Zhuk. and *Lr24* [*Agropyron elongatum* (Host.) Beauv.] were released and virulent strains of leaf rust appeared quickly. In Europe, *Lr26* from *Secale cereale* L. was an important source of resistance, but virulent strains of leaf rust appeared soon after cultivars with this gene were released (Bartoš, 1973).

There is considerable promise for sustained control of leaf rust by gene management. For example, it is obviously good management to have different genes for resistance in spring wheat and winter wheat cultivars in North America. In addition, some genes can be usefully cycled if they are properly managed. However, for the foreseeable future, gene management with respect to wheat leaf rust is likely to be of only theoretical interest, at least in North America. It would entail the control of licensing and withdrawal of cultivars over an entire epidemiological area, as well as removing genes for resistance from particular lines in breeding programs. Although the economic benefits are obvious, the required degree of informal cooperation or governmental action is not likely to be forthcoming. However, gene management can be effectively carried out through the use of multilines and by the cultivation of a number of cultivars with different genes for resistance. If such multilines or cultivars have multigenic resistance, and cooperation between pathologists and breeders is maintained, wheat leaf rust should not be a major threat to wheat production.

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