AN INVESTIGATION OF A SOURCE OF RESISTANCE TO WHEAT LEAF RUST PUCCINIA RECONDITA F. SP. TRITICI IN A CROSS OF "KR/TM//?/3/5*CMN" AND OF CHANGES FOR INCREASED VIRULENCE IN RACE "6B"

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CHAPTER I

INTRODUCTION

Wheat is the single most important crop in the world today, and more people eat wheat as a staple food than any other cereal grain (17). Its consumption is not limited to human food; it also serves as food for livestock either as grain or forage pasture.

By reason of a high average human population growth rate and an increasing life expectancy with the resultant food deficit due to population explosion, food production losses can no longer be tolerated for any reason. Food losses due to disease, for example, can range from an unmeasurable quantity to a disaster depending on the combination of host genotype, pathogen genotype and environment (40).

Leaf rust is the most destructive disease of wheat on the major part of the four hundred million acres used to produce that crop (3). The disease is coextensive with wheat cultivation, and perhaps most prevalent in the major wheat growing areas of the world including the United States and Canada, Western Europe, Eastern Russia, Siberia, China, Argentina, and Brazil. It is also severe at times in Mexico, Peru, Chile, Uruguay, Kenya, India, Egypt, Japan, Australia, Poland, England, and the Scandinavian countries (35).

The amount of loss due to leaf rust of wheat often can be alleviated by the means of certain control measures, perhaps in consequence of simplicity of the use by the farmers and the low cost, the use of

inherited host resistance is the commonly preferred control method (24, 25). Effective leaf rust resistance prevents yield loss by inhibiting reproduction and subsequent spread of the pathogen and within areas planted with resistant varieties the spore population is kept at a low level (36).

Puccinia recondita Rob. ex. Desm. f. sp. tritici Johnston the causal agent of the leaf rust disease of wheat, is an obligate parasitic fungus. The population of this fungus consists of morphologically similar but parasitically distinct genetic biotypes. Various mechanisms are involved in the production of such biotypes. They have been shown to originate through hybridization, heterocaryosis, parasexualism and mutation (21, 31, 34, 49, 51). Mutation is the only mechanism by which new virulence genes can occur; naturally occurring mutation to greater virulence in the cereal rusts has been reported to occur in the laboratory as well as in nature (47, 55).

The study of parasite populations, changes in pathogenic potential of parasite populations and the detection of new or unusual genes for virulence is as important in the use of resistance for control as it is to identify potentially useful genes in available host material. Using the genetic information of both host and parasite can give opportunity to bring useful genes for resistance into commercially grown cultivars or genetic source material.

The object of this study was to evaluate the changes in virulence of a race called "6B" that has been observed to parasitize the line KR/TM//?/3/5*CMN (52) which is being used in breeding because of its resistance to the known cultures of the leaf rust fungus in Oklahoma and to attempt to identify the gene for low reaction in this line.

CHAPTER II

LITERATURE REVIEW

Leaf rust is the most important single disease of wheat on a world-wide basis and the most common, prevalent and damaging disease in most of the major wheat producing areas. It is important on both winter and spring types of wheat, especially in the warmer, humid and semi-humid regions (10). Leaf rust rarely causes crop losses more than 50 percent, but it is regularly present over broad areas very often causing considerably higher accumulative losses than those caused by stem and stripe rust (6). In some years, rather severe epidemics occur in part or in the entire central plains wheat region of the United States. In 1938, a leaf rust epidemic from Texas to Canada caused a loss estimated to be more than 30 percent (26). Annual losses from all diseases for the period 1951-60 were 14 percent. During that same period leaf rust is estimated to have resulted in losses 2.5 percent by itself (1).

Leaf rust is a leaf and leaf sheath disease which retards photosynthesis, interferes with leaf functions and increases transpiration causing plants to ripen prematurely. If wheat plants are infected in the early growth stage, the yield of a susceptible cultivar can be reduced as much as 94 percent (26, 26). Approximately 75 percent of the grain loss caused by leaf rust resulted from a reduction in the number of kernels per head and the remainder from a reduction in weight per kernel. The percentage of protein in the grain of susceptible cultivars of both

hard and soft winter wheat was very significantly reduced by severe leaf rust infection. Because of reduced number and size of kernels the total quantity of starch laid down per kernel and head was distinctly reduced by leaf rust (9). Mains (29) showed that grain yield of wheat could be reduced by 37 percent when 100 percent leaf rust infection developed by the time of flowering. Yield was reduced largely by a decrease in the number of kernels per spike. Samborski and Peturson (37), indicated that a heavy infection of leaf rust initiated at an early stage of plant development materially reduced the yield, kernel weight and bushel weight of one susceptible and even of three resistant cultivars.

The effect of heavy infection is reflected not only in reduction of grain yield, but also in straw yield and in a deterioration of the root system (18, 49). Johnston and Miller (19) showed that heavy infection resulted in rapid deterioration of the roots as indicated by root discoloration, a decrease in fibrous roots, and a marked increase of root rotting.

Although leaf rust can be suppressed by fungicide application, such as dusting with sulfur (30), chemical control never has been totally successful because of high cost and short control period. Many chemicals are hazardous to use or accumulate in the grain. For this reason, disease resistance for control appears to be the most practical approach.

Specific resistance has long been used in wheat cultivar development to control the disease (10). Specific resistance is likely to be of greater value when combined with useful levels of non-specific resistance than when used alone (24). Incorporation of race specific

resistance with the highest possible level of non-specific resistance has been proposed by Young (52) and Browning et al. (9).

Knott (25) proposed the use of non-specific resistance as a useful alternative. Specific resistance has been shown to be effective against only certain clones or races of the pathogen, while against other clones or races such resistance is ineffective or less effective. Specific resistance to the leaf rust pathogen is identified with hypersensitive host response. By 1972, 20 different genes for resistance to leaf rust had been described (28). Many of these no longer have value as a source of resistance in the field. Knott pointed out that such resistant genes should never be used singly; those that have lost their present value may be removed from the present host population; and if the virulence of the leaf rust fungus is lost in time, these resistant genes could be used again, preferably two or more resistant genes in one cultivar. Roelfs (36) and Smith (41) suggested that cultivars with two or more genes for resistance can give longer term protection. This has been demonstrated in Kansas and Oklahoma. Virulence to resistance genes LR-1, LR-2 and LR-3 was present in the leaf rust population in Kansas. None of these genes by themselves show resistance in the field, but in combinations of any two there was a considerable reduction in amount of infection. When all three were present the amount of infection was much reduced (7). In the leaf rust population of Oklahoma virulence on the LR-24 and LR-9 host resistance genes is present. The LR-24 gene is susceptible to races designated as "2AAG" and "5AAG," and the LR-9 gene is susceptible to a race designated as "3TF." The lines containing both genes have been demonstrated to be resistant to all of the races that attacked either gene alone (40).

The ability of the pathogen to overcome single gene resistance has led pathologists to increase their effort to provide more stable resistance governed by many genes, and to better use of varieties incorporating monogenic resistance. Borlaug (4) proposed the use of monogenic resistance with multiline wheat varieties composed of a mechanical mixture of seed of a series of backcross derived lines each containing different genes for specific resistance but similar agronomically. In these instances, the resistance of individual plants is utilized to reduce the rate of epidemic development in the crop by a dilution process caused by the physical effect of the isolation that would exist between plants with genotypes with the same resistance gene (5, 23).

Experience has shown that in the pathological support of breeding programs it is necessary to provide host material carrying useful genes for resistance. In such a program it is necessary to isolate and identify as many host genes conditioning resistance to leaf rust as possible to obtain the most effective resistance possible. Obviously, genetic information about host and parasite relationships is necessary to determine which resistance gene or genes are needed to confer resistance in any given area.

The first detailed studies concerning the genetics of parasite and host relationships was done by Flor (13, 16) on the rust of flax. From these studies the gene-for-gene concept was established as a model for host-parasite interaction.

Loegering and Powers (27) presented a genetic model for the gene-for-gene system which in reality was an extension of Person's model (33). In the Loegering-Powers model, categories III and IV interactions were

of the interorganizmal type. Category III interactions are described as those between corresponding genes for pathogenicity in the parasite and for reaction in the host. Category IV interactions are those between sets of two or more corresponding gene pairs (27). By utilizing these models the genes for pathogenicity in the parasite and their corresponding genes for low reaction in the host can be detected. This system can be used to measure genetic ratios of the F_2 segregating generation of either host or parasite by the determination of infection types of the disease since the corresponding genes in two organisms interact to produce the disease infection type (52).

Browder (8) detected a gene for low reaction in the wheat cultivar "Bulgaria 88" by using a comparitive analysis of infection types of Puccinia recondita f. sp. tritici on the "Bulgaria 88" and eight host lines near iso-genic for certain specific "LR" host genes.

Experience has shown that a resistance gene may succumb to a new race or biotype even before it becomes a commercial cultivar. New races or biotypes can arise by the means of sexual and asexual reproduction; the mechanisms involved other than the sexual cycle, are heterocaryosis, parasexualism, and mutation. In 1955, Nelson, Wilcoxson and Christensen (31) demonstrated for the first time that new races and biotypes of stem rust of wheat could be obtained when seedlings of wheat were innoculated with mixture of two known races. Watson (46) and Ellingboe (12) have studied the production of new races of Puccinia graminis var. tritici by the means of nuclear reassortment as a result of hyphal fusion (anastomiosis of germtube) and nuclear exchange. In 1957 Vakili and Caldwell (44) isolated new races from the known mixtures of the leaf rust fungus of wheat. In the same year Flor (15) also

isolated new races in the flax rust fungus Melampsora lini as a result of hyphal fusion and exchange of intact nuclei between the two parental lines or races of that rust fungus.

However, undoubtedly the major cause of changes in pathogenicity in the leaf rust fungus in Oklahoma is mutation. It is not a rare phenomenon at all. Mutation was first reported to cause change in pathogenicity by D'oliveira (11) in Puccinia hordei in 1939. Johnson and Newton (22) reviewed mutation phenomenon in the cereal rusts up to 1946 and believed that mutations were the most significant source of variability in pathogenicity of those fungi. Watson (45) isolated 16 new races and biotypes that occurred by stepwise mutation in Puccinia triticina over a 16 year period in Australia. He (47) also reported changes in pathogenicity by mutation in P. graminis var. tritici. Flor (14) using Melampsora lini, and Zimmer and Schafer (54) and Zimmer, Schafer and Patterson (55) using Puccinia coronata studied spontaneous changes in those organisms attributed to mutation. In 1962, Samborski (38) observed a spontaneous mutation in a culture of P. recondita f. sp. tritici which produced an atypical infection type on cultivar 'Transfer.' In Oklahoma, while evaluating the stability of resistant cultivars to the natural population of the leaf rust fungus in trap plots, susceptible reactions were observed on the cultivars, Aniversario, Lucero, and a selection of the cross Wabash/American Banner//Aniversario. The cultures isolated from such infections produced high infection types on the same cultivars in greenhouse tests and were found to be variants of the race known as "UN6." Later, type "2" infection types (44) were observed on the varieties "Timpaw" and "Preska," which had previously exhibited only fleck (0;) infection types to cultures isolated from Oklahoma (39).

The occurrence of natural mutation for additional virulence during culture of the rust fungus in the greenhouse has been rare. Newton and Johnson (32) observed a variant what was thought to be a pure culture of the race "52" of *P. graminis* f. sp. *tritici* when it was removed from storage in a refrigerator at 8°C.

CHAPTER III

MATERIALS AND METHODS

A selection of the cross "KR/TM//?/3/5*CMN" (52) has been used in the wheat breeding program in Oklahoma because of its resistance to all known cultures of Puccinia recondita f. sp. tritici in Oklahoma. Neither KR (Kanred), TM (Tenmarg), nor the recurrent parent, CMN (Comanche) are known to carry any specific genes for resistance (52) to leaf rust. Therefore, it is assumed that an outcross with an unknown parent occurred and that the source of resistance in the selected line which exhibits a low infection type with the races "6B," "13A" and "Can C" came from that parent. Earlier studies had shown that the F_1 of the last backcross was resistant to race 6B, and the F_2 progeny segregated with the ratio of 13R:3S when tested to race 6B. Homozygous resistant selections from this backcross had exhibited an "0" infection type with race 6B until 1980. In 1980 a few plants of this line gave one or two "4" infection types when tested with race 6B. Isolations were made from 12 single pustules, and 12 isolates were obtained for further testing. Races 6B, 13A, and "Can C" were used for comparison with the isolates derived from the cross to help provide information concerning the gene or genes involved in the resistance (Table I).

The races 6B and 13A were isolated from collections made in wheat diseases observation nerseries or farmers' fields in Oklahoma. Race "Canada C" was obtained from Dr. D. J. Samborski, Canada Agriculture

Research Station, Winnipeg, Manitoba, Canada. All three races were identified and classified on the basis of differential cultivars suggested by Basile (2) and the additional cultivars Westar (CI 12110), Wesel (CI 13090), Agent (CI 13523), and Transfer (CI 13296) (Table II). The races "6B" and 13A" are found rarely in Oklahoma. The race "Can C" has been found only in Canada (52). The urediospores of these races used in this study were supplied by Dr. H. C. Young, Jr., and Dr. F. J. Gough, Department of Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

TABLE I

RACES USED FOR COMPARISON WITH THE ISOLATES

Local Name of Race	Avirulence/Virulence Formula
6B	LR2A, LR9, LR24/LR1, LR2C, LR3, LR10, Wesel
13A	LR9, LR24 Wesel/LR1, LR2A, LR2C, LR3, LR10
Can C	LR9, LR24 Wesel/LR1, LR2A, LR2C, LR3, LR10

In addition to the selection of the cross "KR/TM//?/3/5*CMN," selections from two other crosses were used for comparitive purposes. One was a locally designated line, T_1/4*CMN, which is "Wichita/4/(Wichita/3/Triticum species/A. elongatum/PM)/4*CMN" and possess LR24 gene and a line KR/H.F//?/3/5*CMN whose genes for resistance are unknown.

TABLE II

WHEAT VARIETIES USED TO DIFFERENTIATE
VIRULENCE IN PUCCINIA RECONDITA F. SP. TRITICI

Varieties	C.I. No.	Abbreviations	Gene for Low Reaction
Malakof	4898	Ma	LR1
Webster	3780	Wst	LR2A
Loros	3779	Ls	LR2C
Democrat	3384	Do	LR3
Westar	12110	Wtr	LR10
Wesel	13090	Wsl	LR10 + Unknown Gene
Agent	13523	Ag	LR24
Transfer	13483	Tf	LR9

Urediospores from the 12 single pustules were used to inoculate 12 day-old seedlings of the universal susceptible cultivar "Danne" (CI 13876) by the spatula-slide inoculation method (7). At the time of inoculation the temperature was between 22-24°C. Inoculated plants were kept overnight in moist chambers at a similar temperature. Subsequent increase of inoculum was made using the brush inoculation method, each isolate being maintained separately in isolation. When the final increase of spores was started, seeds of the lines and differential varieties to be tested were planted in three 10 cm pots by mechanical differential seeder. In this way a satisfactory amount of fresh inoculum for each isolate was ready to use when the test plants were at the desired stage for inoculation (8-10 days old).

This same procedure was used to obtain cultures of races 6B, 13A, and "Can C." The test plants of differential varieties were inoculated

with the unknown isolates and with the races using the brush method, kept overnight in separate moist chambers to avoid contamination, and removed to the separate growth chambers. Eight to ten days after inoculation notes were taken on infection types based on the classical system of Stakman, et al. (42).

Assured that selection of each race and isolates were pure, seed of the cross of "KR/TM//?/3/5*CMN" from which the 12 isolates were obtained and of the other two lines from the crosses "T_1/4*CMN" and KR/HF//?/3/5*CMN" were planted in wooden flats 30x50x10 cm by ten rows to each flat. On the tenth day these plants were inoculated with each of three races and a mixture of the 12 isolates by the brush technique. They were kept overnight in separate moist chambers and removed to a greenhouse into separate cloth cages. The temperature of the greenhouse was maintained between 23-27^{o}C.

CHAPTER IV

RESULTS

All the isolates obtained from the 12 single pustules attacked the selection of the cross KR/TM//?/3/5*CMN and gave the same infection type ("4") regardless of their pathogenicity on the other differential varieties used.

All of the isolates were avirulent to near isogenic lines containing the single host genes LR1, LR9 and LR24, but all were virulent to the lines containing LR2A, LR2C, LR3, LR10 and the differential variety Wesel (Table III). The response of the differential cultivars to 6B, 13A and Can C also is given in Table III.

TABLE III

THE RESPONSE OF DIFFERENTIAL CULTIVARS INOCULATED WITH CERTAIN ISOLATES AND RACES OF *PUCCINIA RECONDITA* F. SP. *TRITICI*

Isolates or Races	Response of Near Isogenic Lines Containing Leaf Rust Resistance Genes: LR1	LR2A	LR2C	LR3	LR10	LR24	LR9	Differential Variety Wesel
Isolates [1]	R	S	S	S	S	R	R	S
6B	S	R	S	S	S	R	R	S
13A	S	S	S	S	S	R	R	R
Can C	S	S	S	S	S	R	R	R

[1] All 12 isolates obtained from a selection of the cross KR/TM//?/3/5*CMN gave the same response on each of the differentials.

Neither the mixed urediospores from the 12 isolates nor any of the races used attacked the line "T_1/4*CMN" which possesses the host gene LR24. However, the selection from the cross KR/HF//?/3/5*CMN was attacked by the mixture of isolates and by the races 13A and Can C. It was not attacked, however, by race 6B (Table IV).

TABLE IV

THE RESPONSE OF SELECTIONS OF THE CROSSES KR/TM//?/3/5*CMN, T1/4*CMN, and KR/HF//?/3/5*CMN INOCULATED WITH A MIXTURE OF ISOLATES WITH UNKNOWN VIRULENCE AND WITH CERTAIN KNOWN RACES OF P. RECONDITA F. SP. TRITICI

Isolates or Races	Host Response KR/TM//?/3/5*CMN	T1/4*CMN	KR/HF//?/3/5*CMN
Mixture of Isolates [1]	S	R	S
6B	R	R	R
13A	S	R	S
Can C	S	R	S

[1] A mixture of 12 isolates obtained initially from a selection of the cross KR/TM//?/3/5*CMN.

CHAPTER V

DISCUSSION

In previous work (52) the reaction of F_2 generation from the last backcross "KR/TM//?/3/5*CMN" to race 6B of Puccinia recondita f. sp. tritici indicated that resistance was conditioned by more than a single dominant gene. Phenotypic ratio of F_2 was a good fit to 13R:3S. Thus, we may accept that two genes are involved in the expression of resistance to that race.

Epistasis in the host, a category II interaction, would be the logical explanation for such a ratio.

The determination of unknown genes by comparitive analysis here indicated that the selection of the cross being studied possesses the gene LR2A for low reaction. Such a conclusion is justified because all the isolates attacked LR2A, but not LR1, LR9 or LR24 while race "6B" attacked LR1 but did not attack LR2A, LR9 or LR24. The difference between isolates and races 13A and "Can C" was that the races attacked LR1, but the isolates did not. Also, the isolates attacked Wesel while these races did not.

The cross was not attacked by race 6B since it possessed LR2A. However, the cross selection was attacked by both races "13A" and "Can C," neither of which would attack LR24 or LR9 but did attack LR2A. It is obvious, then, that the second resistance gene in the cross selection was neither LR9 nor LR24. Another gene not revealed by these

studies must be the second gene for resistance in this selection.

It is possible that pathogen race "6B" already possessed virulence to that gene, and a mutation at the LR2A locus caused the cross to succumb. Production of a pathogenic variant in the culture of race "6B" could have resulted from heterocaryosis, parasexualism, or most likely spontaneous mutation.

Genetic reassortment as a result of hyphal anastomosis and nuclear exchange could be the case, and variation would result from exchange of intact nuclei as Ellingboe (12) has reported. A pure culture would be less likely to have this potential. As a matter of fact, more evidence is needed to show whether this phenomenon has been responsible for production of new races or biotypes with leaf rust. Some exhaustive studies yielded no evidence of this (52).

The only other mechanism that could give rise to a variant in the absence of the sexual cycle is mutation which in this case is a quite plausible explanation. One of the concepts derived from the gene-for-gene hypothesis is that mutation to virulence is perpetuated by the selection pressure of host resistance. If this is so, mutation to virulence on LR2A may have occurred in race "6B" since cultures of it were used on the cross repeatedly for many generations. However, mutation to virulence would be detected only if the culture was heterozygous at that locus or if stepwise mutations occurred at the same locus in the same variant.

Avirulence is generally conditioned by dominant genes, and a single mutation in a heterozygous population or simultaneous mutations in a homozygous population would result in a change from avirulence to virulence if the corresponding gene in the host were the only resistance

gene present. Obviously, however, two genes are present in the selection of the cross studied here. Stepwise mutation in Puccinia triticina as suggested by Watson is possible. However, the occurrence of natural mutation for new virulence during culture in the greenhouse has been very rarely observed. Shank (39) reported that a new race was obtained from the culture which had been stored for several months as did Newton and Johnson (32) when they found that a culture of a race of P. granimis var. tritici thought to be pure had changed in virulence during storage. According to Young (52) and Watson (46) rust can seldom be cultured without the possibility of the contamination even when special precautions are taken. Therefore, it is possible that contamination occurred in this study. However, the new race or biotype which emerged is different in its pattern of virulence and avirulence than any culture or race yet observed here.

CHAPTER VI

SUMMARY

1. A selection of the cross "KR/TM//?/3/5*CMN" has been used as a resistance source to existing cultures of Puccinia recondita f. sp. tritici in Oklahoma. Its resistance is governed by an unknown gene or genes that must have come from an unknown parent in an outcross. Previous studies of the F_2 generation from the last backcross to the susceptible cultivar Comanche indicated a good fit to 13:3 ratio - a two gene epistatic, category II interaction.

2. Twelve isolates were made from pustules which appeared on this line following inoculation with race "6B."

3. Subsequent inoculation studies showed all isolates were virulent on the line.

4. Races "6B," "13A" and "Canada C" were compared with the isolates on a series of differential varieties and the line. The isolates differed from race "6B" on LR1 and LR2A, but were unlike any other race or culture identified before at this location.

5. Comparitive analysis of the reaction of the new isolates and the known races on the line from the cross "KR/TM//?/3/5*CMN" indicated the line contained the resistance gene LR2A and one or more unknown resistance gene(s).

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