RELATIONSHIP OR LINKAGE BETWEEN SOIL-BORNE WHEAT MOSAIC RESISTANCE AND CERTAIN LEAF RUST RESISTANCE GENES IN WHEAT

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CHAPTER I

INTRODUCTION

Soil-borne wheat mosaic (SBWM), caused by soil-borne wheat mosaic virus (SBWMV) and leaf rust of wheat, caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* Johnston are major and destructive diseases which occur in wheat-growing areas of Oklahoma and adjacent states in the southern Great Plains region of the United States (102). The destructive effect of these two diseases was demonstrated by yield losses in commercially-grown wheat cultivars of up to 50% and 27% resulting from a SBWMV-epiphytotic (96) and a leaf rust-epiphytotic (75) in Oklahoma in 1952 and 1938, respectively.

In the United States SBWMV and leaf rust have been effectively and economically controlled by the use of resistant varieties in many wheat-growing areas (41, 42, 46, 47). Nykaza et al. (69) reported more forage yield gained from populations of wheat resistant to SBWM than from susceptible ones. Similar results were shown to be true with leaf rust (99). Use of specific resistance has been most important in leaf rust control (12, 101) since the level of non-specific resistance has not proved to be adequate in the southern plains of the United States, particularly during the fall growing season (101).

Resistance to SBWMV became available soon after the disease was found (54). Although only few studies have been reported concerning the inheritance of the reaction to SBWMV and adequate techniques to manipulate resistance genes under-controlled conditions are not readily available, considerable number of resistant and tolerant wheat varieties to SBWMV have been developed by breeding and selection of plants from populations grown in infested soil (41, 53, 66, 84).

Since breeding for resistant varieties has been the most satisfactory approach for controlling wheat diseases, it is essential to consider all possible pathogens present in a particular wheat-growing area and to breed for multiple disease resistance. A successful cultivar for an area needs resistance to as many of the existing diseases as it is possible to obtain. Progress has been made in developing wheat varieties with combinations of resistance to diseases. Several wheat cultivars with combinations of genes for resistance to both SBWMV and some races of leaf rust have been developed (10, 102).

Basic knowledge of host-parasite relationships is still needed to facilitate the development of commercially acceptable varieties with desirable resistance combinations. Breeding for resistance to two or more diseases is often hampered when there is linkage between the genes conferring resistance to those diseases, making it difficult to incorporate them into a single, highly desirable cultivar, particularly if the genes concerned enter the cross in the repulsion phase. The experiment reported herein was conducted to determine whether an undesirable linkage pattern or independence existed between genes conferring resistance to these two wheat diseases.

CHAPTER II

LITERATURE REVIEW

Wheat is grown in more parts of the world and provides more basic diet for the world's people than any other food crop. Sufficient wheat production requires not only efficient application of crop-production techniques but also the effective means to reduce losses resulting from diseases. Fortunately, only a few diseases have been sufficiently widespread and serious enough to cause important over-all crop losses in wheat. However, SBWM and leaf rust are recognized to be among them.

Soil-borne virus disease of wheat was first observed in 1919 in Illinois and Indiana (34, 53). Two forms of the diseases, resetting and leaf mottling were described in 1923 (53) and the virus nature of the rosette form was recognized in 1925 (58). Strains of SBWMV were differentiated in 1931 (40, 55), as the mosaic-rosette strain (*Marmor tritici* var. *typicum* McK.), and the prairie wheat yellow-mosaic strain (*Marmor tritici* var. *fulvum* McK.) (56). SBWMVs have been reported in several states of the United States including Illinois, Indiana, Ohio, Michigan, North Carolina, South Carolina, Oklahoma, Kansas, Nebraska and Virginia (58), and more recently in Florida (42). The disease has also been reported in Canada (86) and Japan (64). Sill (82) compared the known characteristics of SBWMVs of the Great Plains and other areas of the United States in 1952. The evidence based on several known characteristics including symptoms, host range, methods of transmission, losses, control measures and other characteristics indicated that the various SBWMVs reported in the United States are possibly strains of the same virus. Two strains of SBWMV, as previously described, have predominated in the eastern states; Illinois, Indiana, North Carolina, South Carolina, and Virginia (57, 74). No evidence for strain differences has been found in Kansas, Oklahoma, and Nebraska, since the mosaic-rosette phase has never been detected in those areas (9,83,96). Even though both yellow and green symptoms occur, they have never been separated. Presumably, only the green-mosaic or leaf mottling strain of SBWMV exists in these areas (82). Sill (82) also compared the Japanese SBWMVs and those of the United States. He concluded that the Japanese SBWMVs were similar to the United States SBWMVs in some respects including mode of transmission, influence of temperature on symptom expression (33), and inheritance of disease resistance (64). There were two strains or possibly two viruses involved in SBWMVs reported in Japan: The green mosaic virus (67), and the yellow mosaic virus (68).

In 1972, Tsuchizaki et al. (95) compared three SBWMV isolates from Japan and three isolates from the United States for host range, particle lengths, shapes of inclusion bodies, and serological relationships. They reported that Japanese isolates were similar to United States isolates in physical properties and morphology but they were slightly different in host range and partially different in serological reactions. They also reported that serological tests indicated that isolates from the same countries were closely related. This evidence strongly indicated that various isolates of SBWMV from each country are strains of the same virus .

SBWMV is a serious disease of winter wheat in Florida (42), Kansas (21), Nebraska (71), and Oklahoma (98), where only the leaf mottling form occurs. The disease caused yield losses in these areas of from 42% to 52%. Since the first reported occurrence of SBWM in north-central Oklahoma winter wheat in 1952 (96), it has become a major disease of wheat throughout the state and presents the potential for serious losses.

Soon after SBWMV was discovered, the need for resistant varieties was reported (53), and since that time many resistant varieties and selections of winter wheat have been developed (53, 54). The need for resistant varieties was emphasized by several workers (42, 71, 74) and the use of resistant varieties for wheat production in SBWMV-infested areas has been extensively recommended (42,43,83). Resistant varieties appear to be the only satisfactory control measure for SBWM in the wheat-growing areas of the United States (7, 41, 66). The breeding procedure has consisted of screening varieties and selections in virus-infested field nurseries.

Considerable effort has been directed toward breeding and selecting wheat that is resistant or tolerant to SBWMV. Moseman et al. (66) studied the reactions of wheat varieties and selections to the SBWMV in the Southeastern United States. Observations were made over a period of years in North Carolina and Virginia and included cultivars known to be sources of resistance to leaf rust as well as those used in other breeding programs where SBWMV is known to be present. Sill et al. (84) reported that 56 wheats among 254 varieties, selections, and crosses of winter wheat were resistant in Kansas. But only Concho, Comanche, and Ottawa were recommended for production in Kansas. Both Concho and Comanche had been reported earlier as being highly resistant to SBWMV in Kansas (70). Nykaza et al. (69) recommended Centurk, a moderately resistant cultivar for prevention from severe losses to the disease and Concho and Newton, the highly resistant, symptomless cultivars for protection from the disease in Kansas.

A few inheritance studies of reaction to SBWMV have been reported in the United States (19, 24, 81). Caldwell and Compton (19) studied the inheritance of resistance to the rosette-mosaic disease in Indiana soil. The F_1, F_2, and

F_3 generations of crosses of the resistant wheat C.I. 11850 with the two susceptible wheats, Sel. 45-1634-1 and Sel. 45-1834-1, were studied by growing the plants in the field infested with the virus. Plants of backcrosses to each susceptible parent were also studied. Resistant to rosette-mosaic in these crosses was controlled by a single dominant gene. Shaalan et al. (81) reported that Ottawa carried two factors for resistance to the mosaic phase of SBWMV in Kansas. One factor appeared partially dominant for resistance and the other modified the effect of the first factor. Dubey et al. (24) studied the inheritance of the field reaction of winter wheats to the mosaic and mosaic-rosette phases of SBWMV in Illinois. Resistance to both phases was found to be controlled by a multiple allelic series consisting of three alleles. A single dominant gene conditioning resistance to both mosaic and mosaic-rosette was designated R^{mr}. Susceptibility to mosaic was conditioned by a gene designated r^m that was dominant over mosaic-rosette susceptibility. Susceptibility to mosaic-rosette was conditioned by the recessive gene r^{mr} which was recessive to both R^{mr} and r^m. The R^{mr} gene was carried by Monon and Crockett, the r^{mr} gene was carried by Bison.

In Japan, Miyaki (64) reported that the resistance to yellow and green mosaic strains of SBWMV resulted from a single dominant gene. Later (65), he reported two dominant genes, R_1 and R_2, conditioned resistance to the yellow mosaic strain. The R_1 gene was carried by Shinchucho (New

Mid-long) and Tochigiseki 1 (Tochigi Red 1), while the R_2 gene was carried by Norin 7. Nakagawa et al. (67, 68) reported three loci with multiple alleles were involved in conditioning susceptibility to the green and yellow strains in Japan. Two genes were responsible for susceptibility, designated H and M; one modifying gene, designated A, inhibited the H gene. Varieties containing H gene were most susceptible.

Leaf rust of wheat, caused by *P. recondita* f. sp. *tritici*, is widely distributed in all wheat-growing areas of the world. It is considered to be a major disease in the Central Plains spring wheat production area of North America (2) and in the southern Great Plains winter wheat production area of the United States (102). Although epiphytotics of leaf rust are less destructive than those of stem rust, yearly losses over wide areas and occasionally disastrous epiphytotics cause a greater aggregate loss than does stem rust (22). Loegering et al. (46) reported that yield reductions of approximately 40 million bushels per year has resulted from leaf rust in the spring wheat area of the United States and North America since 1960. Losses of 55 percent on susceptible cultivars in Kansas and Oklahoma in 1934 (37) and losses of 52% and 17% in Kansas and Oklahoma respectively in 1972 (17) were reported. Several workers have shown that heavy leaf rust infections cause reductions in the number of kernels and in kernel size and a reduction in protein content of grain (18). Reductions in plant height, straw production, and serious losses of fibrous roots, that resulted from heavy infections of leaf rust were indicated by Mains (51) and Johnston and Miller (37). More recently, Williams (99) reported that leaf rust-infected wheat reduced the forage production up to 50 percent. Breeding resistant varieties has been the most effective method used to control this cereal rust. Successful breeding of wheat for resistance to all rust fungi started from the demonstration of the inheritance of stripe rust resistance by Biffen in 1905 (6). Great advances have been achieved since the discovery of physiologic specialization and the development of adequate testing methods. Use of resistant varieties has proved to be the chief means of controlling leaf rust of wheat (12, 23). Specific resistance were and is of great value in the Great Plains wheat-growing area where some levels of specific resistance and tolerance exist in the current commercial wheat varieties (101). However, the effective life of a wheat variety containing a single gene for resistance is not long because resistance in the variety is overcome by the physiologic variation in the leaf rust organism (1). Variation in pathogenicity of leaf rust exists as demonstrated in 1921 by Mains and Jackson (49), and a total of 228 physiologic races was reported by Johnston and Browder (38) in 1966. The principles of the gene-for-gene hypothesis (30, 72) are found to be applicable in the relationships between *P. recondita* f. sp. *tritici* and the wheat plant (76).

To prolong the usefulness of specific resistance, several methods other than the use of single genes have been proposed (8, 14, 20, 80). Caldwell et al. (20) proposed the use of varietal diversification in a wheat-producing area to protect against losses by leaf rust. He reported that Dual (C. I. 13083), a winter wheat variety which was derived from intervarietal crosses involving four resistant parental varieties had a higher level of resistance to leaf rust in mature-plant stage than the resistant parental types. Borlaug (8) proposed the use of multiline cultivars to control stem rust and leaf rust in Mexico. Schafer et al. (80) suggested the use of combinations of resistance genes which yield a higher degree of resistance than that of either parental resistance gene to control leaf rust. This breeding method stemmed from the proposal made by Watson and Singh (98) in 1952, to incorporate as many genes for specific resistance as possible in a single variety to provide more protection against rust. Interaction of resistance genes to produce a lower infection types than that of the individual genes is useful to identify combinations of resistance (80). This type of resistance gene interaction to leaf rust was confirmed by Silpisornkosol (85) in 1981. Browder and Eversmeyer (14) proposed a system of identifying the most useful gene combinations for control of wheat leaf rust. They used virulence frequencies in the leaf rust population to identify single resistance gene lines useful in pairs. By this system, they determined the combination of LR1(TC) and LR2D(PL) genes to be the most desirable for leaf rust control in four out of eight geographic regions of the United States (14) at the time of their study. Those regions were the South Central, Central, North Central and North West.

The inheritance of leaf rust resistance of wheat has been studied by several workers. The earliest studies were done by Mains et al. (50) on resistance of different wheat varieties, both to a mixture of races in the mature plant stage and to specific races in the seedling stage. They reported that several genes were involved and the resistance of different sources to individual races was controlled by single genes inherited independently. In 1929, two types of resistance to leaf rust were recognized by Johnson and Melcher (35). Those were: 1) the adult plant resistance effective only during the adult stage of plant, and 2) the seedling resistance effective throughout the life of the plant. The inheritance of certain genes for adult plant resistance was reported in 1966 by Dyck et al. (25) and Dyck and Samborski (28). The early work on resistance to leaf rust was summarized by Ausemus et al. (3) in 1943, followed by Ausemus et al. (4) and Chester (22) in 1946. They noted that, in general, leaf rust resistance was inherited in a simple Mendelian fashion.

Investigations of the inheritance of leaf rust resistance in the wheat varieties used as differentials for race classifications have been conducted by Soliman et al. (91) in 1964 and by Dyck and Samborski (26) in 1968. Soliman et al. (91) reported that Webster, Loros, Carina, Brevit, Malakof and Hussar carried major dominant genes for resistance to race 15 of leaf rust, and Mediterranean and Democrat carried major dominant genes for resistance to race 9. Dyck and Samborski (26) confirmed the mode of inheritance of resistance in Webster, Loros and Malakof to race 15. They also found leaf rust resistance in Centenario was conditioned by a single dominant gene, but resistance in the differentials Brevit and Carina was controlled by two independently-inherited dominant genes.

The inheritance of leaf rust reaction also has been studied by many workers, and genes for resistance to certain races were identified (27, 31, 77, 93, 94, 100). More recently, Samborski and Dyck (77, 78), Dyck and Samborski (27) and Statler (93) conducted the inheritance studies of virulence in different leaf rust races on various isogenic wheat lines and cultivars with single genes for resistance. Statler (93) reported that the virulence of culture 73-47 on Lr 2C was conditioned by a single dominant gene inherited independently, but the virulence on Lr 24 was conditioned by a single recessive gene.

The gene symbol Lr for leaf rust resistance in wheat was suggested by Ausemus et al. (4). He assigned Lrl, Lr2 and Lr3 to resistance genes in Malakof, Webster, and Fulcaster respectively, based on the results of Mains et al. (50). Later, genes Lr4 through Lr8 were assigned by Fitzgerald et al. (29) to the breeding line 3369-61-1-1-10-8 (Waban, C.I. 12992). Since then, several Lr genes have been assigned to various wheat varieties. By 1972, twenty named Lr genes were documented from Lrl through Lr20 (23, 25, 26, 44, 48, 59, 60, 79, 90, 91). Recently, Browder (15) summarized detailed information of thirty-five named Lr genes including their origin, cultures, hosts, synonyms, chromosome locations, characteristic low infection types, and relative environmental sensitivity.

Designations of Lr2^3 and Lr^4 were made by Soliman et al. (90) in Brevit and Loros respectively. Dyck and Samborski (26) reported these genes to be alleles and designated them Lr2c and lr2d according to a change in the system of symbolization. Later, they were proved to be the same gene and it was designated Lr2C (61).

McKintosh et al. (63) assigned Lr24 to the gene on a small translocated chromosome segment from Agropyron elongatum (Host.) Beauv. in the wheat cultivar Agent (87). This gene was located on Chromosome 3D. Cultivars possessing Lr24 were widely grown in North America (16) and they were found to be resistant to leaf rust in many wheat-growing areas (32,89).

Linkage of resistance to leaf and stem rust of wheat has been studies extensively (39, 62, 63, 94). Swenson et al. (94) reported that there was no indication of linkage between leaf and stem rust resistance in the progeny of a cross between Thatcher and Triunfo wheat cultivars. Jones and Ausemus (39) also reported no linkage between leaf rust resistance in a Frontana selection and stem rust resistance in a Kenya derivative selection. Resistance genes to both leaf and stem rust from the two reports mentioned previously were found to be inherited independently and they could be combined in a single wheat stock to provide protection against both pathogens.

On the other hand, McKintosh and Luig (62) reported that Lr16 for resistance to leaf rust was closely linked in coupling stage with Sr23 for resistance to stem rust. Another study conducted by McKintosh et al. (63) located genes Lr24 and Lr19 for resistance to leaf rust on chromosomes 3D and 7D of the cultivars Agent and Agatha respectively. Gene Lr24 was found to be closely linked with Sr24 for resistance to stem rust and gene Lr19 was also found to be closely linked with Sr25. Linkage between resistance to leaf rust, stem rust, and powdery mildew was demonstrated. Watson and Baker (97) reported that Thew and Kenya 744 wheats were resistant to both race 1 of powdery mildew and race 95 of leaf rust because the genes for resistance to these two diseases in each variety were closely linked. McKintosh et al. (60) reported three linked genes for resistance to leaf rust, stem rust, and powdery mildew on chromosome 7B of the Hope cultivar of wheat. The gene for resistance to leaf rust designated Lr14 was incompletely dominant. The gene for resistance to stem rust designated sr17 was recessive and the gene resistance to powdery mildew also was recessive. Indications of linkage relationships from these latter reports were considered to be undesirable because such linkage would upset the frequency of various possible combinations of genes.

Despite many studies on linkage between resistance to leaf rust and reaction to other diseases, only one study on the relationship between leaf rust resistance and SBWMV resistance was found. Shaalan et al. (81) conducted a study on breeding wheat for resistance to several disease agents including SBWMV and leaf rust. Progenies of the wheat cross Ottawa X Bison were studied for reaction to SBWMV and leaf rust race 9. He reported that the resistance to SBWMV was conferred by two partially dominant genes, and the resistance to leaf rust was conferred by a single dominant gene. He concluded that since there was no linkage detected between the two resistances and their combination could be bred into a single desired cultivar. McNair 701 wheat possessing genes for resistance to SBWMV, leaf rust and powdery mildew was developed from a similar multiple disease control breeding program in Florida (43).

CHAPTER III

MATERIALS AND METHODS

The experiments reported in this paper was conducted in 1981-1982 in both the greenhouse and the field at Oklahoma State University, Stillwater. Two cultivars of hard red winter wheat (Triticum aestivum L. em Thell) were the parents of the F_2 progeny used in this study. The female parent was a selection of the cross Loros/5*Comanche and is designated in this study as LR2C(CMN) and the male parent was the cultivar Payne (C. I. 17717).

LR2C(CMN), contains the LR2C gene for resistance to leaf rust (16, 103), and has a resistance to SBWMV derived from the Comanche parent. Cultivar Comanche was grown extensively for wheat-production in Kansas, Texas, Colorado, Oklahoma, and New Mexico (73), but is susceptible to leaf rust (90, 103).

Payne, a semidwarf hard red winter wheat, containing the LR24 gene for resistance (16, 103), was developed cooperatively by the Oklahoma Agri. Exp. Sta. and AR-SEA-USDA and was released in 1977 (88). It is susceptible to SBWMV (88).

The cross LR2C(CMN)/Payne was made in 1979-1980 and the F_1 plants were grown in the field in 1980-1981. Seeds from the F_2 generation and seeds of LR2C(CMN) and Payne parents were grown and tested for leaf rust reaction in the greenhouse and then transferred to a naturally SBWMV-infested area on the Plant Pathology farm to be tested for SBWMV reaction in 1981-1982.

Pure cultures of two races of the leaf rust fungus, *P. recondita* f. sp. *tritici*, designated in this study as 2AAG and 6B were used in this study. Race 2AAG has constituted approximately one half of the leaf rust population in Oklahoma for several years. Race 6B, although detected in the early 1950's, is rarely found (103). SBWMV is most prevalent in the central and eastern areas of the southern Great Plains region including Oklahoma (102).

The leaf rust cultures were supplied by Dr. Francis J. Gough and Dr. Harry C. Young, Jr., Department of Plant Pathology, Oklahoma State University, Stillwater. The cultures of both races were originally isolated from field collections made in commercial wheat fields or disease observation plots in Oklahoma. They were identified and classified on the basis of 8 differentials selected by Johnston and Mains (36) and the additional supplemental differentials Agent (C.I. 13523) containing LR24, Transfer (C. I. 13296) containing LR9, Wesel (C.I. 13090) containing LR10 and at least one other unknown resistance gene, and Westar (C.I. 12110) containing LR10. Purified uredospores of both races had been stored in separate glass tubes in liquid nitrogen (45).

The initial inoculum of each leaf rust culture was removed from storage, treated with warm water at 40°C for five minutes, left in a few drops of water for two hours and then inoculated on the ten-day-old wheat seedling of universally susceptible cultivar Danne (C.I. 13876) by the "spatula technique" (12). After inoculation seedlings were maintained overnight in a moist chamber before being placed on a greenhouse benches at 20± 3° C. Subsequent increase of inoculum for each race was made by using the "brushing technique" (12) on eight 10 cm pots, each containing 25 seedlings of the cultivar Danne (C. I. 13876). The two cultures were maintained separately and when uredospores were fully developed, approximately 12-14 days after inoculation, they were ready to serve as sources of inocula for the wheat parents and the F_2 progeny used in the test.

The greenhouse experiment was divided into segments and conducted during August and September, 1981, to study the leaf rust seedling reaction of the parents and F_2 generation of the cross. The first segment involved inoculating 10 plants of each parent and 240 F_2 plants with race 2AAG. The second and third segments involved inoculating the same number of parent and F_2 seedlings with race 6B and a 50-50 mixture of races 2AAG and 6B respectively.

Six wooden boxes each 40 X 52 X 8 cm in size were filled with 780 of 4 X 4 X 6 cm plant bands arranged into 13 rows and 10 columns for each box. These plant bands were then firmly packed with a 1:1:1 mixture of soil, sand and peat moss. Five Arasan treated seeds of each parental cultivar were sown, one seed per plant band, in the first row of the box. One hundred and twenty Arasan treated seeds of the F_2 population were sown in the remainder of the 120 plant bands of each box (Figure 1). All of these seedlings were inoculated 10 days after they were sown.

Each box was placed in separate moist chamber and the seedling leaves were moistened by spraying with a solution of tap water and 3-4 drops/1000 ml of the surfactant Tween 20 (Polyoxyethelene 20 sorbitanmonolaurate). Plants of the cultivar Danne containing uredospores each of races 2AAG and 6B were used individually to brush the leaves of the plants to be inoculated in the most chambers. Two pots of plants of each race were used for each box. Each box to be inoculated with both races was first brushed with two pots of race 2AAG and then brushed with two pots of race 6B. The inoculated plants were sprayed again with the surfactant solution, and incubated in the moist chambers overnight. Each box was then placed in separate cloth cage on the greenhouse bench at $20 \pm 3^{\circ}$ C. About 10 to 12 days after inoculation, the rust infection types were recorded on an individual plant basis according to the method first described by Stakman et al. (92), and also according to the coding system described by Browder (11) and Browder and Young (13). After scoring for rust reaction, the rusted leaves were removed and the plants were fertilized. They

Figure 1. Seedlings of LR2C(CMN) Wheat Line and Payne Wheat Cultivar and of a Cross Between Them Planted in a Wooden Box for Leaf Rust Resistance Test in the Greenhouse

were maintained in the greenhouse for 10 days before transplanting into the field.

The field experiment was arranged so as to investigate the relationship between leaf rust reaction and SBWM reaction on the same plant in this F_2 population. Plants previously tested for leaf rust reaction were transplanted to the soil known to be infested with SBWMV on the Plant Pathology Farm, Oklahoma State University, Stillwater, Oklahoma. The plant bands were removed and the plants then transplanted into a 3.6 X 9.0 m plot in precisely the same order as they were in the boxes. Spacing between plants was 15.2 cm in rows 30.4 cm apart.

The reading of SBWMV reaction was made on a single plant basis between March 7, and April 7, 1982, when maximum leaf mottling occurred. The reactions to SBWMV were classified into two groups; resistant, showing normal growth and no trace of mosaic symptoms, and susceptible, characterized by the presence of mottling and yellowing of the leaves and stunted growth.

Notes taken on reactions to leaf rust and SBWMV were assembled and the data were summarized for statistical analysis of the relationship between the reaction to these two diseases. Chi-square tests of goodness of fit were made for segregation ratios and chi-square tests for independence were made for joint segregations to detect linkage (5,52). Fits were considered satisfactory when P values were 0.05 or higher.

CHAPTER IV

RESULTS

Parental Reaction to Soil-borne Wheat Mosaic Virus

The reaction to SBWMV of the F_2 plants were classified into resistant and susceptible groups according to the typical parental symptoms. Payne exhibited a completely susceptible reaction to SBWMV as shown in Table I, II and III. Most of LR2C(CMN) plants exhibited a resistant reaction, but 23 per cent of them were found to be susceptible. This is probably the result of impure seed since the seed used to represent the actual parent plant had been grown for many years and tested only for leaf rust reaction.

Parental Reaction to Leaf Rust

LR2C(CMN) exhibited a resistant reaction (type 0;-2) to leaf rust race 2AAG and a susceptible reaction (Type 3-4) to race 6B (Tables IV and V). Payne exhibited a resistant reaction (type 0;) to leaf rust race 6B and a susceptible reaction (type 4) to race 2AAG (Tables IV and V). The reactions of LR2C(CMN) and Payne to each race of leaf rust

TABLE I

REACTION TO SOIL-BORNE WHEAT MOSAIC VIRUS OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE PREVIOUSLY TESTED WITH LEAF RUST RACE 2AAG

Parent or cross	No. of parental or F_2 plants classified as:			Chi-square Test		
	Resistant[1]	Susceptible[2]	Total	Expected ratio	X^2	P
LR2C(CMN)	8	1	9			
LR2C(CMN)/PAYNE, F_2	49	176	225	1:3	1.246	.25-.50
PAYNE	-	9	9			

[1] Resistant = No disease symptom.

[2] Susceptible = Yellowing, leaf mottling and stunting.

TABLE II

REACTION TO SOIL-BORNE WHEAT MOSAIC VIRUS OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE PREVIOUSLY TESTED WITH LEAF RUST RACE 6B

Parent or cross	No. of parental or F_2 plants classified as:			Chi-square Test		
	Resistant[1]	Susceptible[2]	Total	Expected ratio	X^2	P
LR2C(CMN)	7	2	9			
LR2C(CMN)/PAYNE, F_2	83	150	233	1:3	14.021	<.005
PAYNE	-	9	9			

[1] Resistant = No disease symptom.

[2] Susceptible = Yellowing, leaf mottling and stunting.

TABLE III

REACTION TO SOIL-BORNE WHEAT MOSAIC VIRUS OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE PREVIOUSLY TESTED WITH A MIXTURE OF LEAF RUST RACES 2AAG AND 6B

Parent or cross	No. of parental or F_2 plants classified as:			Chi-square Test		
	Resistant[1/]	Susceptible[2/]	Total	Expected ratio	X^2	P
LR2C(CMN)	5	3	8			
LR2C(CMN)/PAYNE, F_2	38	174	212	1:3	5.660	.01-.02
PAYNE	-	6	6			

[1/] Resistant = No disease symptom.

[2/] Susceptible = Yellowing, leaf mottling and stunting.

TABLE IV

REACTION TO LEAF RUST RACE 2AAG OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Parent or cross	No. of parental or F_2 plants classified as:			Chi-square Test		
	Resistant[1]	Susceptible[2]	Total	Expected ratio	X^2	P
LR2C(CMN)	10	-	10			
LR2C(CMN)/PAYNE, F_2	177	63	240	3:1	0.201	.50-.75
PAYNE	-	10	10			

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[1] Resistant reaction in LR2C(CMN) to race 2AAG = Infection type 0;-2.
Resistant reactions in the F_2 population to race 2AAG = Infection types 0;, 0;-1, 0;-2, and 2.

[2] Susceptible reaction in Payne to race 2AAG = Infection type 4.
Susceptible reactions in the F_2 population to race 2AAG = Infection types 3 and 4.

TABLE V

REACTION TO LEAF RUST RACE 6B OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Parent or cross	No. of parental or F_2 plants classified as:			Chi-square Test		
	Resistant[1]	Susceptible[2]	Total	Expected ratio	X^2	P
LR2C(CMN)	2	8	10			
LR2C(CMN)/PAYNE, F_2	176	64	240	3:1	0.356	.50-.75
PAYNE	7	2	9			

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[1] Resistant reaction in Payne to race 6B = Infection type 0;.
Resistant reactions in the F_2 population to race 6B = Infection types 0;, 0;-1, 0;-2, and 2.

[2] Susceptible reaction in LR2C(CMN) to race 6B = Infection type 3-4.
Susceptible reactions in the F_2 population to race 6B = Infection types 3 and 4.

were distinct, but both parents had a few plants with erratic reactions to race 6B.

When a mixture of the two races was inoculated on each parent, nine of the Payne plants had a uniform mixed infection type of 0;-4 as would be expected, but one plant was more resistant with the 0;-3 infection type. The LR2C(CMN) parent was variable. Most plants had infection types of 0;-2 or 0;-3 and only two plants had the expected 0;-4 infection type (Table VI). Again, the deviation of some reactions of the parental plants to individual races of leaf rust and to the mixture of races indicates the possibility of a mixture of seeds within individual unpurified seed lots which were used as representatives of the real parents of the cross.

Reaction of F_2 Plants from the LR2C(CMN)/ Payne Cross to Soil-borne Wheat Mosaic Virus

Analysis of the total F_2 population tested showed that the segregation in the LR2C(CMN)/Payne cross fit a 1:3 ratio, indicating a single recessive gene for resistance to SBWMV in LR2C(CMN). A chi-square value of 0.036 indicated a satisfactory fit to the expected 1:3 ratio with a probability between 0.75 and 0.90 (Table VII). Analysis of individual segments of the population; i.e., those tested with each leaf rust race individually and the mixture of races gave chi-square values ranging from 1.246 to 14.021

TABLE VI

REACTION TO A MIXTURE OF LEAF RUST RACES 2AAG AND 6B OF PARENTS AND A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Parent or cross	No. of parental or F_2 plants classified as:				Chi-square Test		
	Res.	Mod.	Sus.	Total	Expected ratio	X^2	P
LR2C(CMN)	8	2	-	10			
LR2C(CMN)/PAYNE, F_2	127	93	19	239	9:6:1	1.643	.25-.50
PAYNE	1	9	-	10			

Res. = Resistant reactions to the mixed culture of leaf rust = Infection types 0;-2, 0;-3.

Mod. = Moderately susceptible reaction to the mixed culture of leaf rust = Infection type 0;-4.

Sus. = Susceptible reaction to the mixed culture of leaf rust = Infection type 4.

TABLE VII

DISTRIBUTION OF RESISTANCE AND SUSCEPTIBILITY TO SOIL-BORNE WHEAT MOSAIC IN AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Reaction to soil-borne wheat mosaic		Total	Value of X^2 for a 1:3 ratio	P
No. Plants Resistant[1]	No. Plants Susceptible[2]			
170	500	670	0.036	.75-.90

[1] Resistant = No disease symptom.

[2] Susceptible = Yellowing, leaf mottling and stunting.

with probabilities ranging from .005 to 0.25-0.50 (Table VIII, IX and X).

Reaction of F_2 Plants from the LR2C(CMN)/ Payne Cross to Leaf Rust

Seedlings of the F_2 progeny from the cross between LR2C(CMN) and Payne were tested with leaf rust races 2AAG and 6B and a mixture of both races. Reactions to races 2AAG and 6B individually were grouped for genetic analysis with infection types 0;, 0;-1, 0;2; and 2 in the resistant group and types 3 and 4 in the susceptible group. Reactions to the mixture of races were classified as resistant (types 0;, 0;-1, 0;-2 and 0;-3), moderately susecptible (type 0;-4) and susceptible (type 4).

Segregation of a single factor for resistance to the F_2 progeny tested with race 2AAG had 177 resistant and 63 susceptible plants which gave a chi-square value for goodness of fit to the 3:1 expected ratio of 0.201 with a probability of between 0.50-0.75 (Table IV). The F_2 population tested with race 6B had 176 resistant and 64 susceptible plants which also satisfactorily fitted a 3:1 ratio (chi-square value = 0.356) with a probability of 0.50-0.75 (Table V).

The F_2 population tested with a mixture of leaf rust race 2AAG and 6B had 127 resistant, 93 moderately susceptible, and 19 susceptible plants which fitted a 9:6:1

TABLE VIII

JOINT REACTION TO LEAF RUST RACE 2AAG AND SOIL-BORNE WHEAT MOSAIC VIRUS OF PLANTS OF A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Reaction to soil-borne wheat mosaic virus	Reaction to leaf rust race 2AAG		Total
	Resistant	Susceptible	
Resistant	40	9	49
Susceptible	129	47	176
Total	169	56	225

X^2 for goodness of fit to a 3:1 ratio for resistance to leaf rust race 2AAG = 0.001; P = .90-.95.

X^2 for goodness of fit to a 1:3 ratio for resistance to soil-borne wheat mosaic virus = 1.246; P = .25-.50.

X^2 for independence of resistance to leaf rust race 2AAG and resistance to soil-borne wheat mosaic with a 3:1:9:3 ratio = 1.425; P = .10-.25.

TABLE IX

JOINT REACTION TO LEAF RUST RACE 6B AND SOIL-BORNE WHEAT MOSAIC VIRUS OF PLANTS OF A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Reaction to soil-borne wheat mosaic virus	Reaction to leaf rust race 6B		Total
	Resistant	Susceptible	
Resistant	59	24	83
Susceptible	115	35	150
Total	174	59	233

X^2 for goodness of fit to a 3:1 ratio for resistance to leaf rust race 6B = 0.013; P = .90-.95.

X^2 for goodness of fit to a 1:3 ratio for resistance to soil-borne wheat mosaic virus = 14.021; $P < .005$.

X^2 for independence of resistance to leaf rust race 6B and resistant to soil-borne wheat mosaic with a 3:1:9:3 ratio = 0.881; P = .25-.50.

TABLE X

REACTOPM TO A MIXTURE OF LEAF RUST RACES 2AAG AND 6B AND SOIL-BORNE WHEAT MOSAIC VIRUS OF PLANTS OF A SEGMENT OF AN F_2 PROGENY OF THE CROSS LR2C(CMN)/PAYNE

Reaction to soil-borne wheat mosaic virus	Reaction to leaf rust races 2AAG and 6B			Total
	Resistant	Moderately Susceptible	Susceptible	
Resistant	19	14	5	38
Susceptible	98	66	10	174
Total	117	80	15	212

X^2 for goodness of fit to a ratio of 9:6:1 for resistance to a mixture of leaf rust races 2AAG and 6B = 0.277; P = .75-.90.

X^2 for goodness of fit to a ratio of 1:3 for resistance to soil-borne wheat mosaic virus = 5.660; P = .01-.025.

X^2 for independence of resistance to leaf rust race 2AAG, leaf rust race 6B and resistance to soil-borne wheat mosaic with a ratio of 9:6:1:27:18:3 = 2.657; P = .25-.50.

ratio with a chi-square of 1.64 and P value of 0.25-0.50 (Table VI). This ratio would be expected for segregation involving two independent dominant factor pairs in the presence of two races, with each host gene giving resistance to only one race.

Tests for Independence of a Gene for Resistance to Soil-borne Wheat Mosaic and Two Individual Genes for Resistance to Leaf Rust

Segregation among the F_2 plants for resistance to both SMWV and leaf rust indicated that there was no genetic association between any of the three genes for resistance to these two organisms (Tables VIII, IX and X).

Both the LR2C gene for resistance to leaf rust race 2AAG and the LR24 gene for resistance to leaf rust race 6B were found to segregate in a 3:1 ratio in the presence of individual races and to a 9:6:1 ratio in the presence of both races. Chi-squares of 0.001 and 0.013 for segregation of each individual resistance gene gave a highly satisfactory fit to a 3:1 ratio, both with P values between 0.90 and 0.95 (Tables VIII and IX). The chi square of 0.277 for segregation of these two resistance genes to a mixture of both races also gave a highly satisfactory fit to a 9:6:1 ratio with a P value between 0.75 and 0.90 (Table X).

The gene for resistance to SBWMV in LR2C(CMN) was found to be recessive in the cross with Payne and segregation in the F_2 fitted a 1:3 ratio with a chi-square value of 1.246 and a P value between 0.25 and 0.50 (Table VIII).

Although there were some indications of departure from a 1:3 ratio for SBWMNV reaction in the segments of the experiment tested with race 6B and the mixture of races (Table IX and X), the cause for this deviation could not be ascribed to linkage because the chi-square values for independence in these segments, as well as the segment tested with race 2AAG, were still small enough (probabilities between 0.10-0.25, 0.25-0.50 and 0.25-0.50 respectively) to show statistical independence of this relationship.

CHAPTER V

DISCUSSION

The expression of SBWMV under Oklahoma conditions in which the parents and the F_2 segregating generation of the cross LR2C(CMN)/Payne was studied showed up in early March when active spring growth started. Field symptoms, disease development and severity were similar to those of SBWMV found in Kansas and Nebraska (83). The rosette reaction has not been found in these states. The symptoms used as the criteria to determine the susceptible reaction were the typical of the Payne parent, characterized by the presence of yellow and green mosaic on the leaves, accompanying by mottling, streaking and stunting. The immune reaction which was typical of the LR2C(CMN) parent was used as a criteria for resistant reaction. Distribution of SBWMV was observed to be uniform throughout the field.

The results obtained from this report indicated that one recessive gene governed resistance to SBWMV in this cross. This result is somewhat similar to work reported in Kansas by Shaalan et al. (81) who found a single partially dominant gene (with a 1:2:1 ratio) conditioning resistance to SBWMV in the cultivar Ottawa found in one of three families of an Ottawa/Bison cross. They classified reactions to SBWMV into three groups according to the typical parental resistant and susceptible reactions and a heterozygous intermediate reaction. However, they also reported two dominant genes conditioning resistance to SBWMV in two other families of the Ottawa/Bison cross with a ratio 1:14:1. The results from the study reported here do not agree either with results from work in Japan (64, 65, 67, 68) where both yellow and green strains of SBWMV were involved, or with results from other work in the United States (24) where both mosaic and mosaic-rosette strains were involved. In Oklahoma, only the green mosaic strain is present.

The mode of inheritance of leaf rust resistance gene LR2C from the line LR2C(CMN) to race 2AAG and of gene LR24 from Payne to race 6B were determined in the F_2 generation of a cross of these parents. Both resistance genes were inherited in a simple dominant monogenic Mendelian fashion. These results agree with those reported for gene LR2C in Brevit and Loros by Soliman et al. (90) and Dyck and Samborski (26), and for gene LR24 in Agent by McKintosh et al. (63). The result of testing F_2 progenies of the LR2C (CMN)/Payne cross containing both LR2C and LR24 genes to a mixture of races 2AAG and 6B gave a good fit to a 9:6:1 segregating ratio. The interaction betwen both complete dominants gave rise to a phenotype classified into a moderately susceptible group.

Tests for independence of SBWMV and leaf rust resistance genes indicated that there was no significant association between them. It appeared that either or both the leaf rust resistance gene LR2C in LR2C(CMN) and the gene LR24 in Payne can be combined with the resistance gene to SBWMV. The results reported here agree with the work of Shaalan et al. (81) in Kansas who found no linkage between resistance to SBWMV and resistance to leaf rust race 9 in the cultivar Ottawa.

CHAPTER VI

SUMMARY

1. The F_2 progenies from a wheat cross, LR2C(CMN)/Payne, were used to study the relationship between SBWMV resistance and two leaf rust resistance genes: LR2C(CMN), having the LR2C gene for resistance to leaf rust race 2AAG and a gene for resistance to SBWMV, but susceptible to race 6B, was used as the maternal parent; Payne, having the LR24 gene for resistance to leaf rust race 6B, but susceptible to race 2AAG, was used as the paternal parent.

2. Two races of leaf rust named 2AAG and 6B and a mixture of them were used for leaf rust resistance evaluation in the greenhouse, while a naturally SBWMV-infested field nursery was used for SBWM resistance evaluation.

3. LR2C(CMN) was found to be resistant to SBWMV with the immune type of reaction and Payne was susceptible with typical leaf mottling, yellowing and stunting characteristics. The rosette form was not detected.

4. LR2C(CMN) exhibited a resistant reaction (type 0;-2) to leaf rust race 2AAG and a susceptible reaction (type 3-4) to race 6B. Payne exhibited type 0; for

resistance to race 6B and type 4 for susceptibility to race 2AAG.

5. Segregation of the F_2 progeny from the cross LR2C(CMN)/Payne to SBWM resistance gave a satisfactory 1:3 ratio, indicating that a single recessive gene governed the resistance to SBWMV in the LR2C(CMN) parent.

6. The segregation ratios of segments of the F_2 progeny from the LR2C(CMN)/Payne cross to leaf rust races 2AAG and 6B individually each gave a satisfactory fit to a 3:1 ratio, indicating that both the LR2C gene in LR2C(CMN) and the LR24 gene in Payne are single completely dominant genes. Also, the segregation ratio of the segment of the F_2 progeny tested with the mixture of races 2AAG and 6B showed good fit to a 9:6:1 ratio indicating two independent completely dominant genes.

7. Joint distribution for the two diseases in the F_2 progeny satisfactorily fitted a 3:1:9:3 ratio showing independence of individual leaf rust resistance genes and SBWMV when tested with single races and a 9:6:1:27:18:3 ratio showing independence of both leaf rust resistance genes and SBWMV, indicating no linkage between the two leaf rust resistance genes and the resistance to soil-borne mosaic.

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