EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF FOUR RACES OF THE LEAF RUST FUNGUS ON SEEDLINGS OF THREE CULTIVARS OF WHEAT

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CHAPTER I

INTRODUCTION

Wheat, the "Staff of Life", is grown throughout the world. It forms the staple diet of millions of people and supports other millions directly or indirectly through the many different avenues of employment associated with its production, distribution and utilization. Wheat acreage and production throughout the world exceeds that of any other grain crop. An estimated 575 million acres of the world's cropland produces over 8 billion bushels annually (20). Wheat provides almost 20% of the total food calories for the people of the world. It ranks second only to rice in order of food crop importance (20).

Over 90% of the wheat producing areas of the world are in the northern hemisphere and in that hemisphere the U.S., with an estimated 1.2 billion bushels harvested annually, ranks second only to the U.S.S.R. in production.

Most wheat of the world is of the common or hexaploid type (Triticum aestivum L. em. Thell.). The grain may be either hard or soft in texture; brownish-red or white in color. Hard textured wheats are commonly used for bread, or in some cases, semolina, while the softer wheats are used for crackers, pastry, and other sweet goods.

The yield per acre of wheat in the United States has increased markedly over the last 25 years. This increase in production is multifarious. Changes in agricultural practices, higher yielding cultivars,

better soil management, increased use of chemical fertilizers, and disease resistance are only a few of the many things contributing to the increased yields (23).

An important phase of wheat production is the pest problem; diseases, insects and weeds, many of which can be controlled by the use of pesticides. Even though such controls are available, they not always are effective or economical. Pests such as the rusts, for example, usually cannot be controlled adequately economically with pesticides. Such diseases have been most effectively controlled by means of resistant cultivars (25). Resistance, however, is not always fully effective either or lasts only for a short time because of constantly changing genotypes of the attacking pests (8).

Leaf rust, one of the most destructive and widely distributed diseases of wheat, is co-extensive with wheat cultivation. More prevalent in some parts of the world than in others, it is most prevalent in the wheat-growing areas of the U.S. east of the Rocky Mountains (12).

The pathogen which causes leaf rust of wheat has been known by many different names, both common and scientific. Called leaf rust in the U.S., it is known as brown rust throughout most of the rest of the world. The one most widely used scientific name in the first half of the century was Puccinia triticina Erikss., first used by Eriksson in 1899. However, in 1932 it was pointed out that the name P. rubigo-vera had been used as early as 1892 and therefore, that name had precedence and was used from 1932 until 1956. Then it was found that P. recondita Rob. ex Desm. had been used at an even earlier date (7), and it is the name most widely used today.

This study was conducted to determine temperature effects on the host-pathogen interaction of certain resistant and susceptible wheat cultivars or lines and cultures of certain races of the rust fungus virulent and avirulent on them. Three cultivars or lines with known leaf rust resistance genotypes were tested at different temperatures with cultures of races of the pathogen whose virulence on those host genotypes was known.

CHAPTER II

LITERATURE REVIEW

Leaf rust, Puccina recondita Rob. ex Desm. f. sp. tritici, Ericks. and E. Henn., occurs on wheat wherever wheat is grown, attacking the leaves and leaf sheaths (12). With proper environmental conditions severe epidemics have occurred over the years and this disease has plagued man for centuries by cuasing world wide losses.

Damage caused by leaf rust has been associated with retarded growth and water loss due to excessive transpiration (6). Disease symptoms include premature leaf death associated with excessive development of fungal truiting structures, called sori, which contain the asexual reproductive urediospores.

Damage to the plant by leaf rust may occur in the early stages of wheat growth, and reduce the forage potential for winter grazing. Even more drastic are grain yield losses that occur as a result of this disease. Reductions in yield as high as 70% have been recorded when severe levels of infection occur at jointing stage or before and persist to maturity (12).

Chemical control measures have been investigated and proven effective but costly (8). The most desirable and practical control method today is the use of resistant cultivars. Specific genes for resistance to leaf rust have been incorporated into desirable plant types offering protection to specific races. Such resistance, however,

is not often a lasting control for this disease (29). The leaf rust fungus, like most living organisms mutates, and when selection pressure is applied to the population through host resistance, races possessing genes for virulence to that resistance gene will increase in prevalence (29). Therefore, breeding for rust resistance must be a continuing process (27).

As late as 35 years ago, resistance to leaf rust was thought to be due to some morphological characteristic or physiological composition of the host which limited growth of the pathogen. Such resistance was considered strictly a matter of host genetics and when the resistance of a host "broke down" it was attributed to some genetic change in the host.

The first work concerned with physiological specialization in this parasite was published in 1922 by Mains and Jackson (17). It was expanded in 1932 by Johnston and Mains (14) and accepted internationally. Units of the leaf rust fungus population called physiological races, were identified with eight differential varieties. The list of races of this pathogen so identified has been revised six times. An infection type classification similar to that proposed by Stakeman et al. (26) was used in this identification system. In 1956, Johnston (13) proposed that physiological races be consolidated into "unified" groups. Basile (1) devised a diagnostic key to facilitate identification of such unified groups based on the response of five of the original eight differential varieties. This method of identification is used by many researchers today.

Not until the mid-1940's did any significant work with host-pathogen interactions in this or other diseases come about. Flor (9)

was the first to study the genetics of both members of a host-parasite system using flax and the flax rust organism. His research led to what is now known as the "gene for gene" hypothesis, which states, in general, that for each gene conditioning resistance or susceptibility in the host there is a corresponding gene in the pathogen conditioning virulence or avirulence. This concept has spurred further investigations by many researchers. Person (19) discussing Flor's proposed hypothesis, stated that specific gene for gene relations may well occur as the rule rather than the exception in host-parasite systems. Rowell and Loegering (22) most clearly defined the role of host and parasite in the development of what they termed "high" and "low" infection types. Loegering and Powers (16) classified the interactions between genes of host, of parasite and host and parasite into four categories: (I) interactions between alleles of one organism or the other; (II) interaction between genes of one organism or the other; (III) interaction between genes of the organisms; and (IV) interactions between different category III interactions.

In 1971, Browder (3) proposed a new system for coding infection types of the cereal rusts. He stated that infection type in the cereal rusts is the phenotype of genotypic interaction between a specific host plant and a specific parasite culture in a specific environment. Within these limits, infection type is a non-variable, qualitative character. Use of an infection type coding system would give a description of phenotypes in experiments involving variation in host, parasite, or environment. This system was later modified by Browder and Young (5).

The degree of environmental affects on host-parasite interactions has been investigated by many researchers. Williams and Johnson (28) reported in 1965 that leaf rust infection types on certain differential varieties were affected greatly by different average temperatures. They reported there was a change in host response from resistance at lower temperatures to susceptibility at higher temperatures.

In 1931, Gassner and Straib ((10), as cited by Newton and Johnson (18)) showed that the response of certain host varieties varied from a low infection type at 18.7 C to a high infection type at 6 C and lower. However, this response was not clearly characteristic of all resistant cultures. Roberts (21) stated that the effects of low temperature and low light intensity were similar in that both tended to increase resistance of normally susceptible cultivars. Resistant cultivars often showed increased susceptibility with increased temperature and light intensity.

Hassebrauk (11) showed that lowering temperatures to about 6 C generally increased susceptibility though the reverse was true for some cultivars.

Newton and Johnson's (18) experiments, in 1941, showed a pronounced varietal response to temperature. The leaf rust differential varieties Malakof and Democrat showed increased susceptibility with low temperatures whereas the reaction of Webster to most races was not greatly influenced by temperature. To some races, however, Webster was susceptible at low temperature and resistant or moderately resistant at high temperature. The varieties Carina, Brevit, and Hussar showed increasing susceptibility with higher temperature. They stated that temperature must clearly be taken into consideration when differential

varieties for identification of physiological races of the pathogen. In several instances, the same culture of rust appeared to be a different physiological race because of changes in the responses of differential varieties to changes in temperature.

CHAPTER III

MATERIAL AND METHODS

Three cultivars or lines of wheat were used in this study:

1. Sage (CI 17277), a cultivar with one known specific gene for resistance to leaf rust, LR24;

2. 5* WI/TF(2), a line selected from a cross of the variety Transfer (CI 13373) with the cultivar Wichita (CI 11952) and back-crossed to Wichita four times, with one known specific gene for resistance to leaf rust, LR9; and

3. Sage//5*WI/TF (CI 17908), a selected line from a cross of the above cultivar and line and known to have both LR9 and LR24 leaf rust resistance genes.

Cultures of four races of Puccinia recondita f. sp. tritici were used. A culture of race UN2, locally designated 2AAG, was chosen because it is virulent on LR24 and avirulent on LR9 (Table I). A culture of UN3, locally designated TF, conversely, is virulent on LR9 but avirulent on LR24. A culture of UN17, locally known as CAN-A, has four known genes for virulence. While a culture of race UN13, locally known as CAN-C, has seven genes for virulence at other loci. None of these races, or any other known race, were virulent at both the LR9 and LR24 loci. Cultures of the first two races were isolated originally from collections made in wheat disease observation plots in Oklahoma. Cultures of the latter two races were obtained from Dr. D. J. Samborski,

Rust Research Laboratory, Canada Department of Agriculture, 25 Dafoe Road, Winnipeg, Manitoba, Canada. All four races were identified and their virulence formula determined by their infection types on differential varieties suggested by Basile (1) and the additional cultivars, Agent (LR24) (CI 13523), Transfer (LR9) (CI 13373).

TABLE I

CULTURES OF RACES OF PUCCINIA RECONDITA TRITICI USED AND THEIR PATHOGENICITY RELATIVE TO THIS STUDY

Local Culture Designation	UN Race	Avirulence/ Virulence Formulae
2AAG	2	LR1, 2A, 2C, 3A, 9, 16, 17, 19/ LR3, 10, 24
TF	3	LR1, 2A, 3A, 16, 17, 19, 24/ LR2C, 3, 9, 10
CAN-A	17	LR1, 9, 10, 16, 17, 19, 24/ LR2A, 2C, 3, 3A
CAN-C	13	LR9, 17, 19, 24/ LR1, 2A, 2C, 3, 3A, 10, 16

Over the past few years the culture 2AAG has been one of the most prevalent in Oklahoma. A culture virulent on LR9 was produced by Samborski (24) in greenhouse culture. Such virulence has since been found in the field but only rarely in Oklahoma. The two cultures CAN-A and CAN-C have been isolated only in Canada (24).

Urediospores of these cultures were provided by Dr. Francis Gough and Dr. Harry C. Young, Jr., Department of Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

Glass tubes containing urediospores of each culture were removed from liquid nitrogen storage (15) and heat treated at 40 C for five minutes. Each culture was increased initially on the near-universal susceptible cultivar Danne (CI 13876) using the oil technique described by Browder (3). To obtain sufficient urediospores to inoculate experimental plants, a second increase was made using the brushing technique (3). During the course of the experiments, eight pots of Danne were planted with approximately 20 seeds each every day for subsequent inoculation to insure that fresh inoculum would be ready when the test plants had reached the desired size.

All plants to be tested were grown in 5 cm by 5 cm plastic pots with 20 seedlings per pot. At seven to ten days of age, these plants were inoculated using the brushing technique and placed in moist chambers. Separate chambers were used for each culture to avoid possible contamination. The plants of each cultivar or line were inoculated on the same day. The morning after inoculation, the plants were moved from the moist chambers and placed in growth chambers (Percival Model E-30B).

Four pots of each cultivar were placed in each of three different growth chambers programmed for temperatures of 15, 20, and 25 C. These temperatures were maintained on a 24-hour basis with a 12-hour day length of approximately 21,528 lux light intensity during the light cycle. At ten to 14 days after inoculation, evaluation of infection types were made based on both the classical system proposed by

Stakman et al. (26) and the three-digit system of Browder (4) and Browder and Young (5). The infection types for any given cultures were evaluated on all cultivars or lines on the same day. The experiment was repeated twice.

CHAPTER IV

RESULTS

In the first experiment results with culture 2AAG were predictable (Table II): Sage was susceptible with a type 4, or in Browder and Young's scale a 5 to 6-P infection type; the line 5*WI/TF was immune, as was the selection from the cross. Pustules on Sage were small in the growth chambers (only 5 to 6 on Browder and Young's scale compared with 7 to 8 usually observed in the greenhouse) with a slight tendency for increased size with increased temperature. Otherwise, no effect of different temperatures on infection types was observed.

The results with culture CAN-A also were predictable (Table III). The infection type on Sage was 0; or 0-3-C on Browder and Young's scale, while on both 5*WI/TF and the selected line from the cross the infection type was 0, or 0-0-0, indicating an immune host response. In all cases, the infection types were stable over the range of temperatures. The results with both cultures CAN-A and 2AAG, strongly indicated a category II interaction in the host (LR9 was epistadic to LR24), but no apparent category IV interactions.

The results with cultures TF and CAN-C were not so predictable (Tables IV and V). With culture TF Sage gave the expected 0, or 0-3-C response only at 15 C. At 20 and 25 C an X, or 5-6-X infection type was observed. Such a response has been observed occassionally before in various greenhouse tests with this particular host-parasite combination

TABLE II

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED WITH CULTURE 2AAG OF RACE UN2 OF P. RECONDITA TRITICI AND HELD AT THREE DIFFERENT POST-INOCULATION TEMPERATURES

Cultivar or Line	Temp.	Classical Infection Type[1]	Three Digit Infection Type[2]		
Sage	15	4	5	5	P
	20	4	6	6	P
	25	4	5	6	P
5*WI/TF	15	0	0	0	0
	20	0	0	0	0
	25	0	0	0	0
Sage//5*WI/TF	15	0	0	0	0
	20	0	0	0	0
	25	0	0	0	0

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

TABLE III

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED WITH CULTURE CAN-A OF RACE 17 OF *P. RECONDITA TRITICI* AND HELD AT THREE DIFFERENT POST-INOCULATION TEMPERATURES

Cultivar or Line	Temp.	Classical Infection Type[1]	Three Digit Infection Type[2]		
Sage	15	0;	0	3	C
	20	0;	0	3	C
	25	0;	0	3	C
5*WI/TF	15	0	0	0	0
	20	0	0	0	0
	25	0	0	0	0
Sage//5*WI/TF	15	0	0	0	0
	20	0	0	0	0
	25	0	0	0	0

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

TABLE IV

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED WITH CULTURE TF OF RACE UN3 OF *P. RECONDITA TRITICI* AND HELD AT THREE DIFFERENT POST INOCULATION TEMPERATURES

Cultivar or Line	Temp.	Classical Infection Type[1]	Three Digit Infection Type[2]		
Sage	15	0;	0	2	C
	20	X	5	6	X
	25	X	5	6	X
5*WI/TF	15	4	6	6	P
	20	4	7	7	P
	25	4	7	7	P
Sage//5*WI/TF	15	0;	0	2	C
	20	0;	0	2	C
	25	0;	0	3	C

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

TABLE V

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED WITH CULTURE CAN-C OF RACE UN13 OF *P. RECONDITA TRITICI* AND HELD AT THREE DIFFERENT POST-INOCULATION TEMPERATURES

Cultivar or Line	Temp.	Classical Infection Type[1]	Three Digit Infection Type[2]		
Sage	15	0;	0	2	C
	20	0;	0	3	C
	25	0;	0	3	C
5*WI/TF	15	4	6	6	P
	20	4	7	7	P
	25	4	7	8	P
Sage//5*WI/TF	15	0	0	0	0
	20	0	0	0	0
	25	0	0	0	0

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

(H. C. Young, Jr., personal communication). The line 5*WI/TF was susceptible as expected, and again there was a tendency for increased pustule size with increased temperature. The response of the cross was indicative of a category II interaction between genes LR9 and LR24. In this case, with the effect of the LR9 gene removed by the culture being virulent on that gene, the response was typical of that expected when this culture interacts with a line carrying LR24 alone, namely a 0;, or 0-3-C infection type.

Culture CAN-C produced a high infection type on the parent line 5*WI/TF which carried resistance gene LR9. This was totally unexpected. The response of Sage (0;) was normal, as was that of the selection of the cross (0). Temperature had no effect on these infection types except that pustule size with the high infection type and size of the lesions in the 0; interaction types increased slightly with an increase in temperature. The response of these three host lines to CAN-C was not normal in another respect. If, indeed, culture CAN-C was virulent on LR9, as indicated by the response of the parent line 5*WI/TF, then the response of the selection from the cross carrying both LR9 and LR24 should have been 0;, as was the case with culture TF. Instead, the response of the cross was 0.

Consequently, the experiment was repeated in its entirety except that different growth chambers were used for each temperature. The results with cultures 2AAG and CAN-A were the same as in the first trial except that pustule and/or lesion size on Sage varied slightly (Table VI). Culture CAN-C also produced the same results, i.e., it was virulent on 5*WI/TF (Table VII), but culture TF was different in that

TABLE VI

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED SEPARATELY WITH CULTURES 2AAG AND CAN-A OF RACES UN2 AND UN17 OF P. RECONDITA TRITICI AND HELD AT THREE DIFFERENT POST INOCULATION TEMPERATURES (EXPERIMENT II)

Cultivar or Line	Temp.	Classical Infection Type[1] with Cultures 2AAG	CAN-A	Three Digit Infection Type[2] with Cultures 2AAG	CAN-A
Sage	15	4	0;	5 5 P	0 2 C
	20	4	0;	6 6 P	0 3 C
	25	4	0;	6 6 P	0 3 C
5*WI/TF	15	0	0	0 0 0	0 0 0
	20	0	0	0 0 0	0 0 0
	25	0	0	0 0 0	0 0 0
Sage//5*WI/TF	15	0	0	0 0 0	0 0 0
	20	0	0	0 0 0	0 0 0
	25	0	0	0 0 0	0 0 0

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

TABLE VII

THE INFECTION TYPE ON THE PARENT WHEAT CULTIVAR SAGE, THE 5*WI/TF LINE AND A SELECTION OF SAGE//5*WI/TF INOCULATED SEPARATELY WITH CULTURES TF AND CAN-C OF RACES UN3 AND UN13 OF P. RECONDITA TRITICI AND HELD AT THREE DIFFERENT POST-INOCULATION TEMPERATURES

Cultivar or Line	Temp.	Classical Infection Type[1] with Cultures TF	CAN-C	Three Digit Infection Type[2] with Cultures TF	CAN-C
Sage	15	X	0;	5 6 X	0 2 C
	20	X	0;	6 6 X	0 3 C
	25	X	0;	6 7 X	0 5 C
5*WI/TF	15	4	4	4 3 P	5 5 P
	20	4	4	5 6 P	6 7 P
	25	4	4	6 6 P	7 7 P
Sage//5*WI/TF	15	0;	0	0 3 C	0 0 0
	20	0;	0	0 5 C	0 0 0
	25	0;	0	0 5 C	0 0 0

[1]After Stakman et al. (26).

[2]After Browder and Young (5).

an X infection type was produced on Sage at all temperatures instead of just at 20 and 25 C.

To verify the discrepancy between experiments one and two, the entire experiment was conducted a third time. The results, with minor variations in lesion and pustule size, were the same as those found in the second experiment and are not presented in table form.

CHAPTER V

CONCLUSIONS

Any parasitic plant disease is an interaction of host, parasite and environment (9). Each of these factors may introduce variables into that interaction; host and/or parasite in the form of genetics, the environment in the form of variations in temperature, moisture, humidity or a number of other characteristics of environment. The purpose of this experiment was to test the effect of variable temperature on certain host-parasite genes and a host with a combination of those genes. It is evident that of the eight host-parasite gene combinations studied, seven were exceedingly stable over a range of 10 C in temperature. Compared with the results of Williams and Johnston (28), and others (10, 11, 18, 21, 28), these results could be considered unusual, because using different host-parasite gene combinations, the other researchers found much greater infection type responses to variations in temperature.

The combination of host gene LR24 and the corresponding genes in the parasite culture 2AAG was responsive to temperature. The expected infection type of 0; was found only at 15 C, and that in only one of three trials.

A category II interaction (16), between host-genes LR9 and LR24 was evident. The expression of resistance by LR9 was epistatic to the expression of LR24. Both cultures virulent on LR9 in this study (TF

and CAN-C) produced a 0; infection type on a selection from a cross containing both LR9 and LR24, whereas other cultures avirulent to LR9 produced a 0 infection type on that cross, including culture CAN-C which was virulent on LR9 in this study.

Virulence of culture CAN-C used in these experiments on the line 5*WI/TF has no ready explanation. The response of the other hosts used indicated that the culture was indeed culture CAN-C of race UN13 (Table I). Also, response of the host line 5*WI/TF to cultures 2AAG and TF clearly indicated that this line contains the host resistance gene LR9, yet this is the first occassion where that culture has been known to produce a high infection type on any line or cultivar containing only the resistance gene LR9. These facts obviate the possibility of contamination of either host or parasite. A further complication was the fact that unlike culture TF which developed a 0; infection type on the cross containing both LR9 and LR24, culture CAN-C developed only a 0 infection type on that cross.

CHAPTER VI

SUMMARY

Three host lines, two containing a single leaf rust resistance gene each and one containing a combination of those two genes were tested with cultures of four races of P. recondita tritici at three different temperatures. The observed results were as follows:

1. The only effect of temperature on these various host-pathogen combinations was a slight increase in pustule size with an increase in temeprature where high infection types were involved and a slight increase in lesion size with an increase in temperature where low infection types were involved.

2. Variation in temperature had no effect upon the infection type of the combination of host resistance gene LR9 and cultures of races avirulent at that locus. In all cases the infection type was 0, i.e., an immune host response.

3. The host resistance gene LR9 was epistatic to host resistance gene LR24--a typical category II interaction.

4. The culture CAN-C of race UN13 used in these studies was virulent on the host line containing the resistance gene LR9, but produced only a 0 infection type on the cross containing both LR9 and LR24 which was typical only of races avirulent on LR9.

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