INFECTION OF WINTER WHEAT BY Puccinia recondita Rob. ex Desm. AT LOW TEMPERATURE

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Introduction

The disease caused by Puccinia recondita Rob. ex Desm. (formerly known as P. rubigo-vera (Eriks.) Carl. or P. triticina Eriks.) on winter wheat is known as leaf rust. This disease is found wherever wheat is grown in the United States. The "repeating stage" of this fungus is of great economic importance since it is able to produce extensive damage to the wheat crop. The annual loss due to this disease is counted in the millions of dollars.

The fungus is able to pass in the "repeating stage" from one crop to another infecting volunteer wheat between crop seasons and overwintering in the same stage in the new crops. Overwintering of the fungus can occur everywhere that winter wheat is grown but the amount of survival in the Northern States is so small that insufficient inoculum is provided to be of consequence in the epidemiology of the disease.

The amount of inoculum able to survive the winter in the Southern States is appreciable and after several generations in the spring the quantity of inoculum available for distribution northwards by the wind usually is quite high.

The latitude at which the present work was done is about the northern limit at which the fungus is able to survive the winter in appreciable quantity. The quantity of leaf rust that overwinters at this latitude is not constant each year but depends on the presence of susceptible wheat varieties, the minimum temperature and the free water available on the leaf surface either from dew or from rain.

The aim of the present study was to determine the amount of infection that Puccinia recondita is able to produce in winter wheat at minimal temperatures in relation to the length of the wetting period required to obtain it.

Literature Review

The series of phenomena that takes place in the infection of winter wheat by Puccinia recondita Rob. ex Desm. has been studied by a number of investigators. It is generally agreed that the success of the infection depends mainly on the following factors: humidity or moisture, temperature and light.

It has been reported by Mains (17) that 100 percent relative humidity is necessary to produce leaf rust uredospore germination. However, Stock (27) and Hemmi and Abe (12) reported that a very low percentage of leaf rust uredospores germinate in high percents of relative humidity and that free water, which is not always present at 100 percent relative humidity, is necessary to produce a profuse germination of the uredospores.

According to Stock (27) the cardinal temperatures for germination of uredospores of the leaf rust organism are as follows: minimum 2° - 3°C, optimum 5° - 20°C and maximum 29° - 30°C. Later, Bryzgalova (1) reported a minimum of 2°C, an optimum of 15° - 20°C, and a maximum of 26°C.

Several investigators have observed the influence of temperature on the reaction of the differential varieties used to identify physiologic races. These modifications in the reaction are obviously linked with modifications in the processes of infection. Roberts (23) stated that low temperatures have a tendency to increase resistance in varieties normally susceptible, and that varieties normally resistant showed

increased susceptibility with increased temperature. However, Johnson and Newton (14) found that at temperatures above 29°C Little Club wheat became resistant to physiologic races to which it was susceptible at ordinary room temperatures (20° - 24°C). Hassebrauk (11) showed that low temperatures, about 6°C, generally increased the susceptibility of the wheat plant to leaf rust though the reverse condition was true for some varieties. The same results were found by Naumov(20) who stated that the average critical temperature for leaf rust infection was 8.7°C.

The results obtained by Newton and Johnson (21) showed that any modification of the reaction of the differential varieties was dependant not only upon the variety but also on the physiologic race involved. They stated that the varieties Malakof and Democrat showed increasing susceptibility in direct relation with the descent of temperature. The reaction of Webster to most of the races was only slightly modified by changes in the temperature, although to some races this variety was susceptible at 18.2°C and resistant or moderately resistant at 24°C. The varieties Carina, Brevit and Hussar had an increase in their susceptibility with higher temperatures seemingly regardless of the race involved. The reaction of the variety Mediterranean was not well established but to certain races it was more susceptible at the higher temperatures. The reaction of the variety Loros did not seem to be affected by temperature.

Melander (18), Roberts (23) and Newton and Johnson (21) agree that low light intensities have a tendency to increase the resistance of

varieties normally susceptible. However, Hart and Forbes (10) found that darkness had no effect on the prevalence or severity of infection by Puccinia recondita (P. triticina).

Stomata have been found to play an important role in the infection of the wheat plant by stem rust and may also influence infection by leaf rust. Hart (9), working with Puccinia graminis tritici, found that the stem rust penetration tubes generally enter the host only through open stomata, and that the fungus does not seem able to force its way through closed stomata.

Caldwell and Stone (2) studying the stomatal function of wheat in relation to infection by leaf rust established that closed stomata offer no effective barrier to the entry of the penetration tube of this fungus.

Hussain (13) stated that in his studies at 4.4°C leaf rust infection did not occur unless the uredospores were actively germinating while the stomata were open.

Perusing the literature for a convenient method of studying the stomatal movements in the wheat seedlings it was found that many investigators have devised different systems of measuring stomatal activity in different species of plants. Some workers have related the movement of the stomata to the rate of flow of air through the leaf, as mentioned by Darwin and Pertz (4) or to the resistance to such flow, using the "Resistance Porometer". The latter method, or a modification of it, has been used by Gregory and Pearse (8), Wilson

(30), Volkerding (28), Freeland (6) and Williams (29).

Clark (3) related the movement of the stomata in corn to the rate of water-vapor loss from the leaves. The method was previously used by Meyer (19) and involves the use of Cobalt Chloride Paper for detecting the presence of water-vapor over a given length of time.

The systems mentioned above were not considered for this study because the methods of measurement were very indirect; that is to say, the determination of open or closed stomata depended largely on the exactness of the apparatus used. Also the porometers produced an abnormal condition within the leaf which might influence the stomatal movement.

A more convenient method was developed by Lloyd (15) who fixed strips of epidermis in absolute alcohol. This method proved satisfactory for many investigators although the possibility exists that some of the stomata may close between the time that the epidermis is stripped off and the time it is fixed in the alcohol. Also, removal of the epidermis of some leaves is not easily accomplished.

Sayre (24) and Scarth (25) observed stomatal movements directly on the plant (in situ), but such a method was impractical for the present work.

The system finally adopted was a modification of the method mentioned by Long and Clements (16) using collodion films. A modification of this same method was used successfully by Petersen (22). Further description of the method is given in the section on Materials and Methods.

Materials and Methods

For the present work race 9 of Puccinia recondita Rob. ex Desm. was selected because it has been one of the more prevalent races present in Oklahoma over the past several years and because in some respects it is superior to certain other races in survival ability (5).

The winter wheat variety Cheyenne C.I. 8885, was selected because of its susceptibility in the seedling stage to race 9 as well as to most other races.

All the tests were made in a temperature controlled room. Artificial light was provided for 12 hours at an intensity of 1800 to 2000 ft.c., an intensity which Gfeller and Goulden (7) found would produce satisfactory growth of wheat. All tests were initiated at 7:00 A.M., the time at which the light came on. During the light period the temperature was $5^{\circ} \pm 2^{\circ}C$ and the relative humidity averaged 90 percent. During the dark period the temperature was $4^{\circ} \pm 2^{\circ}C$ and the relative humidity averaged 94 percent.

Fifteen pots (4 in.) with 10 to 12 seedlings of the variety Cheyenne in each were grown for eight days in the greenhouse and brought into the cold room 48 hours before each test. In each case the tests were made when the seedlings were 10 days old. The plants were inoculated and distributed in 5 moist chambers similar to those described by Stakman et al (26). Three pots were placed in each chamber.

Fresh inoculum of race 9, approximately 1 mg per pot, was used. The inoculum was measured with a microscoop.

The inoculation was made using the dipping method described by Hussain (13). One ml of Photo-Flo in 500 ml of water was used as a surface tension breaker immediately prior to inoculation.

The pots were removed from the moist chambers after 4, 6, 8, 10 and 12 hours of wetting period. They were immediately placed in front of an electric fan for 15 minutes to dry them as rapidly as possible, after which they remained in the cold room for another 24 hours. Following this the pots were taken to a greenhouse where the temperature was controlled at approximately 22°C.

The viability of the inoculum was tested in two different ways: (1) on water-agar, and (2) on the wheat seedling. Spores were distributed with a camel hair brush on 3 percent water-agar contained in syracuse dishes. The dishes containing the water-agar were conditioned to the cold room temperature for 24 hours previous to the test. The germination of the spores was stopped after 4, 6, 8, 10, and 12 hours of wetting period by spraying the dish with a fungicide (Puratized at 0.5% by volume). The percent of the germinated spores was determined later by counting 250 to 300 spores in microscopic fields of 75 to 80 spores each.

The percent of germinated spores on the wheat seedling was determined with a modification of the method described by Long and Clements (16). Several collodion type solutions were tried and none of them was found to be satisfactory for low temperatures. Among a number of acetone soluble substances, Cellulose Acetate (Eastman Kodak Co., Low Medium Viscosity, High Acetyl) was selected. A solution was

made by dissolving 10 grams of Cellulose Acetate in 100 ml of acetone. This solution was found to be most satisfactory because its viscosity or thickness could be modified by the addition of either acetone or cellulose according to the necessity of the work.

Immediately after each set of plants had passed the prescribed wetting period and was dried as previously described, 10 films of each set were made. Each film was made by applying the solution to the upper third of the lower surface of the leaf with single strokes of a camel hair brush. After a period of 10 to 15 minutes the films were dry and were taken off the leaf with forceps and stored between two standard microscope slides. Later these films were dry mounted on a single slide with a cover glass which was fastened to the slide with Duco cement at the edges. The percent of germinated spores was determined by counting 500 to 1,000 spores from each set of films. All observations were made with a phase microscope. The same films were used to measure the percent of open stomata. In these computations a total of about 300 stomata were observed for each set of 10 films.

Results

The results of the tests for germination of the uredospores on water-agar were utilized to establish a basis for the length of time that the wheat seedlings should remain in the moist chambers to acquire the leaf rust infection at low temperature (about 5°C). The results of the water-agar germination tests are summarized in Table I.

Table I. Germination of Uredospores of Puccinia recondita Rob. ex Desm. Race 9, on 3 percent water-agar, at 5° ± 2°C., and under 1800 to 2000 ft.c. of Artificial Light.

Germination after:	Percent of Germinated Uredospores Test Number			
	1	2	3	Average
4 hrs.	77	28	90	65
6 hrs.	80	87	94	87
8 hrs.	92	88	96	92
10 hrs.	90	85	95	90
12 hrs.	90	88	95	91

A satisfactory germination could be obtained after 4 hours of wetting at this temperature, however after 8 hours the germination was more uniform between the three tests. For some reason the germination after 4 hours of wetting in the second test was much less than in the other two tests and in general the germination throughout the second test was somewhat less than the other tests.

After the 4 hour wetting period at 5°C the germ tube was not well developed, the length varying between 30 to 90 microns. After 6 hours the percent of germination had increased and the germ tubes were better developed than after 4 hours, the length of the germ tube varying

between 45.5 to 182 microns. After 8 hours of wetting period at this temperature, the germination reached a maximum level and likewise the germ tube reached maximum development. The longer periods of wetting brought no increase in either the percent of germination or in germ tube growth.

In the wheat seedling infection tests, the plants were brought out of the moist chambers after 4, 6, 8, 10 and 12 hours of wetting period, the same as the time periods in the spore germination tests, in order to compare the results. The results of the seedling infection tests are given in Table II.

Table II. Number of Pustules per 100 Leaves Inoculated, After Different Wetting Periods at 5° ± 2°C and under 1800 to 2000 ft. c. of Artificial Light.

Wetting period	Pustules per 100 Leaves			
	Test Number			
	1	2	3	Average
4 hrs.	4	2	3	3
6 hrs.	9	0	9	6
8 hrs.	0	16	5	7
10 hrs.	Infinite[1]	Infinite	Infinite	Infinite
12 hrs.	Infinite	Infinite	Infinite	Infinite

[1] The term "Infinite" was used in the beginning to indicate satisfactory rust development. Later, however, more precise observations indicated that the term "Infinite" had been applied where each leaf had from 40 to 125 pustules, averaging about 55 pustules per leaf.

A few rust pustules developed on the wheat seedlings with as little as 4 hours of wetting, but satisfactory infection required a minimum of 10 hours of wetting. Even though the results of the uredospore

germination test indicated that a satisfactory germination could be obtained with as little as 4 hours of wetting, the infection obtained on wheat seedlings that remained in the moist chamber for as long as 8 hours, was extremely low.

The germination of the uredospores and growth of the germ tube was then observed on the wheat seedlings themselves. The results of these observations are given in Table III.

Table III. Germination of Uredospores of Puccinia recondita Rob. ex Desm., Race 9, on the Leaves of the Wheat Seedling, at Low Temperature (5°C).

Period of Wetting	Percent of Germinated Uredospores Test Number			
	1	2	3	Average
8 hrs.	0.	4.5	4.2	2.9
10 hrs.	4.	7.7	3.9	5.2
12 hrs.	9.4	10.8	7.3	9.2

The percent of germination observed on the wheat seedlings was not comparable with the germination observed on water-agar. The maximum germination obtained on the wheat seedlings was 10.8 after 12 hours of wetting whereas the maximum germination obtained on water-agar was 96 percent after only 8 hours of wetting. Furthermore the difference between the percent of germination after 8 hours and 10 hours of wetting is not believed to be sufficient to explain the differences in total infection following these two wetting periods.

The length of the germ tubes of the uredospores germinated on the wheat seedling leaves was carefully measured. The length of the germ tube expressed in microns is recorded in Table IV.

Table IV. Length in Microns of the Uredospore Germ Tube of Puccinia recondita Rob. ex Desm., Race 9, Germinated on Leaves of Wheat Seedlings, at Low Temperature (5°C).

Period of Wetting	Length of the Germ Tube in Microns /1 Test Number			
	1	2	3	Average
8 hrs.	67.8	53.4	40.2	53.8
10 hrs.	129.9	138.0	124.1	130.6
12 hrs.	155.8	188.6	155.2	166.5

/1 Average of 30 germinated spores

The average length of the germ tubes of the germinated uredospores after 8 hours of wetting at 5° ± 2°C was only 53.8 microns. An additional two hours of wetting (10 hrs.) at that temperature almost tripled the length of the germ tubes. A further two hour increase in the wetting period (12 hrs.) brought about only a fractional increase in germ tube length. This study indicated a definite break between 8 and 10 hours of wetting, quite similar to the break observed in infection between 8 and 10 hours of wetting at this temperature.

The percent of open stomata also was observed after different lengths of the wetting period. The results of these observations are recorded in Table V.

Table V. Percent of Open Stomata of Cheyenne Winter Wheat, After Different Periods of Wetting at Low Temperature (5°C).

Period of Wetting	Percent of Open Stomata /1 Test Number			
	1	2	3	Average
8 hrs.	23	11	27	20.3
10 hrs.	11	14	21	15.3
12 hrs.	7	17	11	11.6

/1 Observations were made on the dorsal side of the distal one-third of the leaves where the stomata averaged 2005 per square centimeter.

The leaves on which these observations were made were held in darkness for 12 hours prior to the inoculation, after which they were held under 1800 and 2000 ft. c. of artificial light. Eight hours after inoculation it was found that 20 percent of the stomata were open or approximately 400 per square centimeter in the measured area. (distal one-third of leaf, dorsal side). As the length of time following inoculation increased the percent of open stomata decreased and at 12 hours only 11.6 percent of the stomata were open. This is illustrated graphically in Figure 1.

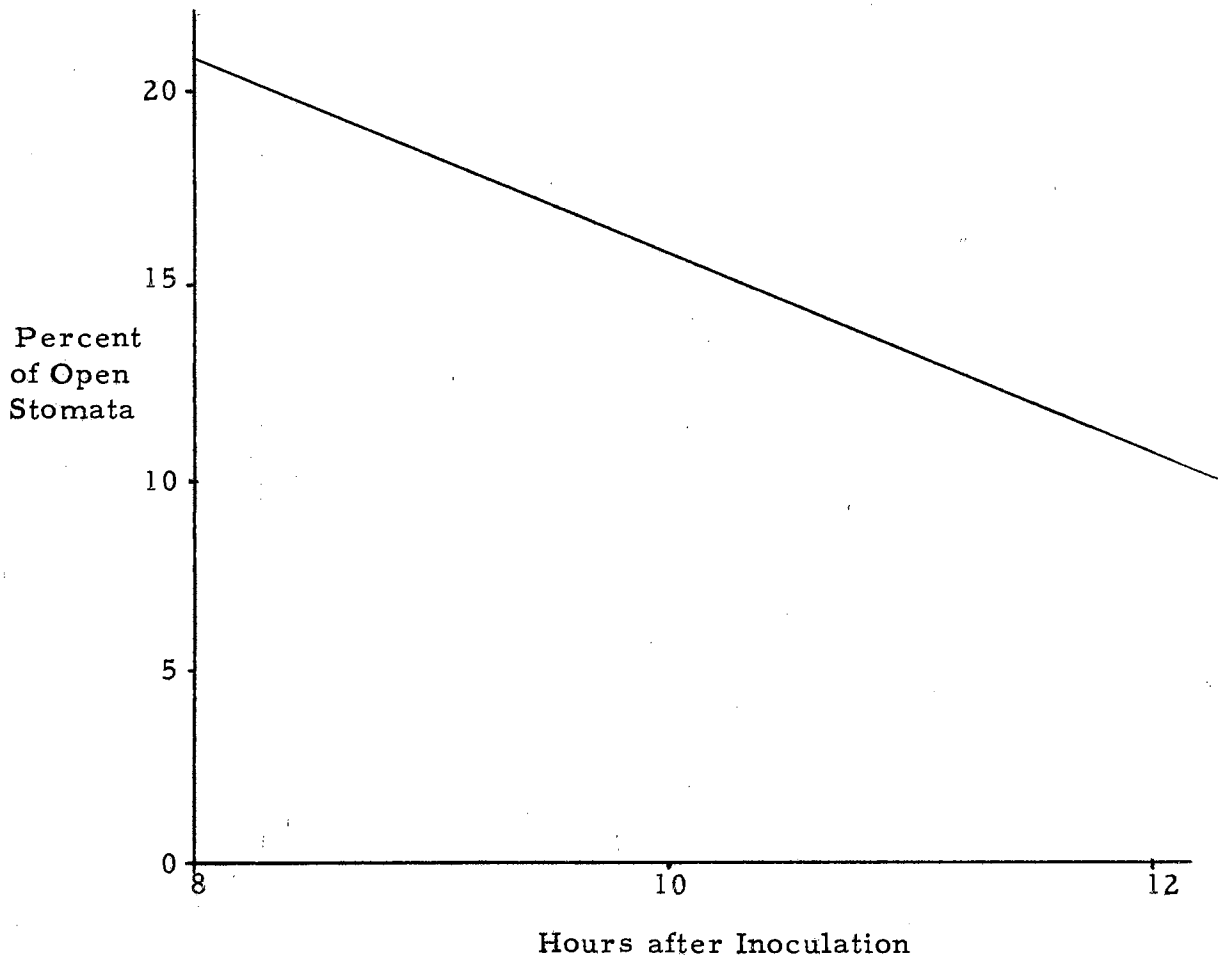

Figure 1. Average Percent of Open Stomata of Cheyenne Winter Wheat at Intervals During the Wetting Period. Plants were held for 12 hours in darkness, inoculated and then held under 1800 to 2000 ft. c. of artificial light of artificial light while in the moist chamber.

If open stomata were the critical factor in infection, then these results would indicate that a higher degree of infection would occur following 8 or 10 hours of wetting than at 12 hours of wetting. Since this is not the case it must be concluded that the percent of open stomata was not the critical factor in these studies.

Discussion

The percent of germination of uredospores of leaf rust on artificial media was found to be high under the conditions established for the present study. However, under the same environmental conditions, the percent of germination of uredospores germinated on the wheat seedlings, was extremely low. Though low, the percent of uredospore germination on the wheat seedlings, was enough to produce (after 10 hours of wetting) an infection of 35 percent (Cobb scale).

While there was no appreciable difference in the percent of germination of the uredospores on the wheat leaf after different lengths of the wetting period, there was a definite difference in the growth of the germ tube. After 8 hours of wetting, the germ tubes had grown only an average of 54 microns in length, but after 10 hours of wetting, almost 3 times as much growth had taken place. This difference in growth can be directly correlated with the differences in the amount of infection produced during these two wetting periods; i.e. a trace after 8 hours and 30 to 35 percent severity after 10 hours.

A rough estimation of the number of spores contained in 1 mg would be approximately 1 1/4 million. Using this inoculum for approximately 10 seedlings and estimating that the seedlings picked up 3/4 of the inoculum, approximately 10,000 spores would be deposited on each square centimeter of leaf surface. Considering then

a germination of 5 percent, approximately 500 spores per square centimeter would be germinated after 10 hours of wetting. From these 500 spores only 40 to 50 pustules were produced under the conditions of the present study.

It is interesting to compare the total number of open stomata per square centimeter after 10 hours of wetting with the number of pustules developed per square centimeter in this same period. There were 300 open stomata and about 500 germinated spores, but only 40 to 50 pustules were obtained. Though the percent of open stomata was low, the actual number of open stomata per square centimeter certainly presented ample opportunity for penetration through these organs if it is necessary for the organism to enter in this manner. In this study it was not possible to determine whether or not the movements of the stomata affected the severity of infection by leaf rust.

Summary

1. Satisfactory germination of uredospores of Puccinia recondita, race 9, on 3 percent water-agar was obtained when tested at $5^{o} \pm 2^{o}C$, under 1800 to 2000 ft. c. of artificial light. After 8 hours of wetting period at this temperature the germination reached a maximum level and the germ tubes reached a maximum development. Longer periods of wetting brought no increase in either percent of germination or in germ tube growth.

2. Satisfactory infection of the wheat seedlings required a minimum of 10 hours of wetting. A longer wetting period (12 hrs.) brought no appreciable increase in the severity of the infection. Shorter wetting periods (less than 8 hrs.) produced extremely poor infection.

3. On the wheat seedlings, the maximum uredospore germination was 10.8 percent after 12 hours of wetting under the temperature and light conditions mentioned above.

4. An active development of the germ tube of uredospores germinated on the wheat seedlings was obtained after 10 hours of wetting. Further increase in the wetting period (12 hrs.) brought only a fractional increase in the germ tube length. With a shorter wetting period (8 hrs.) only about a third of the growth obtained after 10 hours was accomplished.

5. The maximum percent of open stomata (20.3) was observed after 8 hours of wetting. The percent of open stomata decreased with longer wetting periods.

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