T[illegible]ECT OF SPORE MIXTURES OF PHYSIOLOGIC RACES 9 AND 15 OF PUCCINIA RECONDITA ROB. EX DESM. ON THE INFECTION PROCESS ON TRITICUM SATIVUM

BY

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INTRODUCTION

The organism concerned in these studies, Puccinia recondita Rob. ex Desm., is the causal agent of the leaf rust disease of wheat; a universal and destructive disease found throughout the wheat growing areas of the world. At present the only economically feasible control for leaf rust is by the use of resistant wheat varieties. However, Johnson (10) has indicated that when resistant wheat varieties are released, their resistance is overcome or broken down in a relatively short time by the advent of new or previously undetected physiological races of the leaf rust fungus.

A susceptible alternate host of P. recondita has not been reported in areas of this country where leaf rust is prevalent. Thus, P. recondita must persist in the uredial stage, and any genetic variation that occurs must arise in the absence of hybridization.

Vakili and Caldwell (22) have demonstrated that, when urediospores of 2 or more races of P. recondita are mixed and inoculated on wheat leaves, new races, pathogenically different from the parental races, may be recovered. However, Milholland (14) was unable, for the most part, to produce similar results. The purpose of this study was to further explore the role of parasexualism as a source of variability in P. recondita, using single spore transfers and detached leaf cultures.

REVIEW OF LITERATURE

Johnson, 1953, (10) indicated that genetic variation in the form of new biotypes might occur by a nuclear exchange between different clones in the dicaryotic stage of rust. Fusions between germ tubes of mixed races of urediospores have been observed in P. graminis (13, 17, 26, 27) and in P. recondita (14) and the movement of cytoplasmic materials and nuclei between fused germ tubes also has been observed (14, 20, 26).

Nelson et al, 1955, (17) presented evidence that heterocaryosis was a basis for genetic variation in P. graminis var. tritici. Later, Nelson (16) mixed urediospore of 2 races of P. graminis var. tritici, inoculated them on wheat varieties, and reisolated new, more virulent, biotypes than either parental race. He recovered a trinucleated biotype which was unstable, but both parental races and the binucleate segreates were stable through many generations. Other workers have had similar results with P. graminis (3, 4, 5, 25) and with P. recondita (22). However, in 1949, Brown and Johnson (6), working with P. recondita, mixed urediospores of races 9 and 15, and races 9 and 5, and following inoculation of the mixtures on a susceptible wheat variety were able to reisolate only the parental races. Milholland (14) had similar results with one possible exception. He did find that race 9 would occasionally fruit (a type 2++ or 3- pustule) on the normally resistant variety Wabash x American Banner CI 12757, following inoculation with certain mixtures involving race 9, but when pure cultures of race 9 were used, no fruiting occured on that variety.

A detached leaf method of studing rust was first described by Farlow as early as 1885 (8). Clinton and McCormick, in 1924, (7) used detached leaves in Petri dishes to study rust infections but they observed that early deterioration of the leaves interfered with their results. Waters (24) used detached wheat leaves in Petri dishes to study teliospore and urediospore formation and also noted early death of the leaves. In 1946, Yarwood (29) reviewed the literature on detached leaf cultures. He described many media for maintaining detached leaves, but he found no media that would maintain the leaves of wheat over a prolonged period.

Person et al, (18, 19) described a media on which detached wheat leaves could be floated and yet retain their color and capacity to support growth of P. recondita and P. graminis for periods of at least one month. The media was merely a solution containing 30 to 100 PPM of benzimidazole. Wang (23) tested this media for its effect on the germination of urediospore of P. graminis tritici and concluded that there was no noticable effect on spore germination at a concentration of 50 PPM benzimidazole. An inhibitory effect on cell growth due to benzimidazole has been reported by Galston et al (9); Woolley (28) reported inhibition of colony growth with several yeasts and bacteria. Klotz and Mellody (12) reported inhibition of growth of Escherichia coli due to benzimidazole at concentrations as low as 50 PPM.

Milholland and Young, in 1959, (15) reported a method by which single urediospores of P. recondita could be picked freehand and placed on detached wheat leaves cultured on 40 PPM benzimidazole solution in a Petri dish where the rust could be cultured satisfactorily.

MATERIALS AND METHODS

The cultures of physiologic races 9 and 15 of P. recondita Rob. ex Desm. used in this study were selected because of their avirulent reaction on the seedling leaves of a selection of the common wheat cross Wabash x American Banner C. I. 12757[1]. These races both produced a zero fleck (0;) type reaction on Wabash x American Banner and no urediospores are produced from these infections.

Pure cultures of the races used were obtained by a modification of the single spore technique described by Milholland and Young (15) as follows. A ten day old primary leaf of the susceptible wheat variety Cheyenne C. I. 8885 was detached and then stripped by gently rubbing the leaf between the moistened thumb and fore-finger. The detached stripped leaf was placed in a Petri dish containing a divider with the cut end of the leaf submerged in a 40 PPM benzimidazole solution. The tip end of the leaf was supported over the solution by the divider. Two dissecting microscopes, and a small quantity of urediospores of one of the races, distributed over the surface of a sterile moistened glass slide, was placed under the adjacent dissecting microscope. By the use of a fine glass needle, and isolated spore on the glass slide was picked freehand and placed on a drop of water on the surface of the detached leaf. The Petri dish with the inoculated detached leaf then was incubated at 18-20 degrees C.

[1]C. I. refers to accession number of the Corps Research Division, Cereal Crop research Branch, United States Department of Agriculture.

pustules were used to mass inoculate Cheyenne leaves for further increase of the race. Each race was increased in an isolated temperature controlled room to avoid the possibility of contamination.

Germination and hyphal fusion rates of single spores of race 9 paired with single spores of race 15 were determined by tests made, in vitro, in the laboratory. Two dissecting microscopes were again placed side by side in a temperature controlled room. One microscope contained a glass slide covered with a film of 1.7 per cent potato-dextrose agar as described by Milholland and Young (15) and the other microscope contained two glass slides covered with a film of sterile water. Urediospores of race 9 were distributed over the surface of one of the moistened glass slides and urediospores of race 15 were distributed over the surface of the other. Using a thin glass needle, single spores of each race were picked freehand and paired with single spores of the other race on the slide containing the potato-dextrose agar film. The latter slides were placed in sterile Petri dishes and incubated for 12 hours at 18-20 degrees C. Spore germination and germ tube fusions were observed with a phase microscope.

Paired single spores and various combinations of multiple spore mixtures of races 9 and 15 were studied both on attached and detached leaves of the variety Wabash x American Banner C. I. 12757. The detached leaves were inoculated in the manner described previously for the purification of the rust race cultures except that Wabash x American Banner leaves were used in place of Cheyenne leaves. When attached leaves were used, single plants were grown in two inch pots. They were inoculated by the same method but the pots were incubated in moist chambers similar to those described by Stakman et al (21).

The effect of benzimidazole on urediospore germination was tested in the laboratory. A clean sterile glass slide was covered with a thin film of the benzimidazole solution to be tested and urediospores were distributed over the surface of the solution with care being taken to avoid spore concentrations that might result in the production of a self-inhibitor as described by Allen (1, 2). The glass slide incubated in a Petri dish containing moistened blotter paper at 18-20 degrees C. for 10 hours. Spore germination was counted with a phase microscope.

Fresh urediospores were used for each test. The increase of inoculum was made on the wheat variety Cheyenne C. I. 8885; chosen because it is highly susceptible to both race 9 and race 15. The original spore material was derived from the cultures used by Milholland (14) and, together with the seed of both wheat varieties used in these studies, was obtained from H. C. Young, Jr., Department of Botany and Plant Pathology, Oklahoma State University. Each time a culture was increased and each time a culture was used in a test, the identity of the culture was checked on the standard international wheat leaf rust differentials (Table 1, from Johnston and Mains (11)).

All of the tests were made in an isolated room where the temperature was maintained at 18-20 degrees C. Artificial light, both florescent and incadescent, with total intensity of 850 candles, was used with light and dark periods of 12 hours each.

TABLE I

REACTION OF *PUCCINIA RECONDITA* RACES 9 AND 15
ON THE STANDARD INTERNATIONAL WHEAT
LEAF RUST DIFFERENTIAL VARIETIES

Differential varieties	Reaction to race[1] 9	15
Malakof C. I. 4898	S	R
Carina C. I. 3759	R	R
Brevit C. I. 3778	R	R
Webster C. I. 3780	S	R
Loros C. I. 3779	S	R
Mediteranean C. I. 3332	R	S
Hussar C. I. 4843	R	R
Democrat C. I. 3384	R	S

[1] R indicates variety resistant; S indicates variety susceptible.

RESULTS

A. Tests Of Germination And Hyphal Fusion Rates

Tests were first made to determine if the mechanical handling involved in pairing of single urediospores of races 9 and 15 of P. recondita might effect germination rate and subsequently the hyphal fusion rate. The tests were made in vitro in the laboratory on glass slides with four replications for each of two treatments as follows: (1) mass urediospores of each race; and (2) paired single urediospores of each race. Dexterity and considerable time were involved in the isolation and manipulation of single spores, particularly in pairs. Consequently, since 800 single spores were involved, treatments could not be tested concurrently, the test was made over a period of 50 days. The rates of germination (Table II) and of hyphal fusion (Table III) were recorded and it was found that individual spores of the single spored pairs germinated at approximately one-half the rate of the spores in the mass inoculation. Both single spores germinated in only about 25 per cent of the pairs.

Hyphal fusions were observed in only 20 per cent of the pairs where both urediospores germinated or in only 5 per cent of the total paired spores (Table III). These results indicate that if a change in the normal infection processes of these races on a variety were to occur as a result of the proximity of two germinating spores of different races, such a change could be expected to occur in only 26 per cent of the cases. If such a change was the result of fusion, this phenomenon could be expected in a maximum of 5 per cent of the cases.

TABLE II

COMPARISON OF THE GERMINATION RATES OF UREDIOSPORES OF P. RECONDITA FOLLOWING BRUSH INOCULATIONS WITH MASSES OF SPORES AND MICRO-NEEDLE INOCULATIONS WITH SINGLE SPORES

Race	Treatment	Per cent Germination[1]
9	Brush inoculation[2]	89
15	Brush inoculation	96
9	Needle inoculation[3]	49
15	Needle inoculation	52

[1]Average of 4 replications of 100 spores each.

[2]Spores distributed on film of potato-dextrose agar on a glass slide with a camel hair brush.

[3]Spores isolated with a glass micro needle and placed on film of potato-dextrose agar on a glass slide.

TABLE III

THE FREQUENCY OF SIMULTANEOUS GERMINATION AND HYPHAL FUSIONS OF PAIRED SINGLE UREDIOSPORES OF RACES 9 AND 15 OF P. RECONDITA

Measurement	Per cent occurrence[1]
Simultaneous germination	26
Hyphal fusions	5

[1]Average of 4 replications of 100 pairs of spores.

Cytoplasmic movement between the fusion body and the germ tubes, as described by Rodenhiser and Hurd-Karrer (20, Wilcoxson et al (26), and Milholland (14), was observed frequently in this study.

B. Tests Of Host Response

It was evident from the foregoing studies that if any abnormalities were to be observed in the avirulent reaction of these two races on the wheat selection Wabash x American Banner as a result of the simultaneous germination or fusion of paired single spores then a considerable number of pairings would have to be made. Pairing spores on the wheat leaf was found to be even more time consuming than on the glass slide due to the difficulty of locating the position of the initial spore so that the second spore of the pair could be placed adjacent to it. As a result, only a maximum of 20 to 25 pairings could be accomplished in one day. Nevertheless, 1200 pairs of spores of races 9 and 15 were placed on leaves of Wabash x American Banner. These leaves were detached and inoculated, the cut ends were then placed in 40 PPM benzimidazole in a divided Petri dish, and incubated for 12 days. No fruiting pustules developed from any of these inoculations, although the normal avirulent reaction (0;) produced by these races was seen occasionally.

During the course of these studies, it was noted that the rate of germination of spores was even lower than the rate found for single spores on the glass slides. As a result, single spores of races 9 and 15 were paired on attached leaves of plants which had been grown in two inch pots to determine if the handling process with detached leaves had adversely affected germination of the spores. The attached leaves were maintained under the same temperature and light conditions as the detached leaves. Other than allowing the inoculated leaves to remain intact, the only modification was to incubate the plants in a moist chamber for 14 hours following inoculation. Over 200 single spore mixed pairs of races 9 and 15 were made on attached leaves but in no case were pustules observed.

However, there was evidence, through flect type infections, of increased spore germination on the attached leaves compared with detached leaves. Later, studies were made which indicated that the reduced spore germination on detached leaves may have been due to the effects of benzimidazole.

The negative results thus far obtained with single spore pairs led to the conclusion that perhaps combinations of more than single spores were required to produce the abnormal infection types reported by Milholland (14) in his studies with mass spore race mixtures. Also, with the reduced germination rates observed with single spores on detached leaves, pairings of more than single spores of each race would add to the chances for simultaneous germination and fusion. Therefore, by picking individual spores, various multiple spore combinations of races 9 and 15 were made in the combinations of 1:2, 1:3, 2:2, 2:3, and 3:3 spores of the respective races. These spore combinations were inoculated on the leaves of the wheat variety Wabash x American Banner which were then detached and cultured in 40 PPM benzimidazole. Although the multiple spore combinations involved even more time than the single spore pairings, 400 cultures were accomplished. After 12 days incubation, a total of 2 type 2++ pustules were found. These 2 pustules were produced by the following combinations: (1) 2 spores of race 9 combined with 3 spores of race 15 and (2) 3 spores of race 9 combined with 3 spores of race 15.

An attempt was made to increase these pustules by harvesting the urediospores and inoculating the variety Cheyenne using the glass slide inoculation technique described by Milholland (14). However, no infections resulted. A small quantity of spores was harvested from each of the 2 pustules for tests of spore viability. These tests were made in the laboratory on the surface of 3.5 per cent water agar on slides in the

previously described. No germination was observed and it was concluded that the spores were not viable. The spores were not examined for nuclear content.

Throughout these experiments, a check for race purity was made each time a culture was increased and each time a culture or lot of spores was used in an experiment. In no case was any contamination observed. In addition, whenever a race or combination of races was inoculated on the leaves of Wabash x American Banner by individual spores, a mass transfer of spores of each race to potted plants of this variety was also made as a check on the varietal reaction. However, although type 2 pustules were found on leaves otherwise showing only fleck type reactions. If fruiting pustules developed on the leaf at all, they were liberally distributed over the entire leaf. It was concluded that these plants with off-type reactions had arisen as a result of out-crossing in the variety or from a cytological instability.

Finally, mixtures of urediospores of races 9 and 15 were mass inoculated on leaves of Wabash x American Banner. In this test also, off-type plants were found, but off-type pustules on otherwise resistant plants were not seen, although the test was repeated twice.

C. Tests Of The Effect Of Benzimidazole On Urediospore Germination

Although the results obtained in the studies reported were negative or at best inconclusive, further exploration is warranted. However, it seemed advisable, first, to determine if benzimidazole at the concentration used affected urediospore germination.

Tests were made in the laboratory using glass slides covered with films of various concentrations of benzimidazole. Nine concentrations were used from 10 to 1000 PPM and 4 replications of each concentration was made. Urediospores were distributed on the surface of the benzimidazole solution. The slides were incubated at 18-20 degrees C. for 10 hours. Germination rates were established by counting the number of germinated spores in each 1000 for each replication of each concentration. These tests showed that benzimidazole inhibited urediospore germination from a level of 4 per cent at 10 PPM to complete inhibition at 1000 PPM (Table IV). The check on pure water germinated 94 per cent.

TABLE IV

A COMPARISON OF UREDIOSPORE GERMINATION ON VARIOUS CONCENTRATIONS OF BENZIMIDAZOLE

Benzimidazole[1] Concentration	Per cent of Germination[2]
0	93.7
10	89.7
20	86.7
30	84.5
40	68.8
60	56.3
80	44.0
350	2.0
500	0.5
1000	0.0

[1]Values expressed in PPM in water.

[2]Average of 4 replications of 1000 spores each.

no fruiting pustules of any kind were observed.

During the course of these studies, it was noted that spore germination rates on the detached leaves were even lower than the in vitro tests indicated. Consequently, 200 pairs of spores of the two races were placed on leaves of the variety Wabash x American Banner which were not detached from the plant. Spore germination was better, but no pustules were produced.

Combinations of individually placed multiple spore race mixtures resulted in 2 type 2++ pustules out of 400 such combinations made on the resistant variety Wabash x American Banner. However, the pathogenic identity of these pustules could not be determined because the urediospores produced were non-viable. In view of the fact that nuclear exchanges resulting in new pathogenic types or synergistic effects on the infect on potential of one race or the other possibly, or quite probably, are infrequent, it is understandable that such phenomena were not encountered with the justifiably small number of spores involved in this study. The 2 pustules resulting from certain multiple spore combinations may well have arisen as a result of germ tube fusions and the formation of a heterocaryotic condition. Indeed, the failure of the urediospores to germinate may have been caused by a heterocaryotic nuclear content, though the spores were not examined cytologically.

It does seem unusual that the pustules found rather readily by Milholland (14) following inoculation of Wabash x American Banner with certain race mixtures of masses of urediospores were not encountered from similar inoculations in this study. Some variation in inoculation or incubation procedures may have been responsible.

When it was noted that the germination of urediospores on detached

leaves ran considerably lower than on the attached leaves or in the *in vitro* tests an experiment was made to determine if benzimidazole might have an inhibitory effect on urediospore germination. The results indicated that benzimidazole inhibited urediospore germination as much as 4 per cent at 10 PPM to 100 per cent at 1000 PPM.

SUMMARY

1. The method of picking up single urediospores with a glass needle for single spore inoculation is effective but results in a rather serious reduction in germination.

2. Single urediospores of races 9 and 15 were paired *in vitro* and germination rates were recorded. Simultaneous germination occurred in 25 per cent of the pairs and germ tube fusions occurred in 5 per cent of the pairs. Movement of cytoplasmic materials between fused germ tubes of single spored pairs of races 9 and 15 often was observed.

3. When 1400 single urediospore pairs of races 9 and 15 were placed on attached leaves and detached leaves of the wheat variety Wabash x American Banner, C. I. 12757, no pustules were produced. If nuclear exchange or synergistic effects were produced in these pairs, they did not result in changes in the normal avirulent reaction of these races on Wabash x American Banner.

4. Two pustules were produced from 400 combinations of 1, 2, and 3 urediospores of each race inoculated on detached leaves of Wabash x American Banner. However, the urediospores produced by these pustules were nonviable and their pathogenic capabilities could not be identified.

5. Laboratory tests demonstrated that benzimidazole inhibited germination of urediospores of *Puccinia recondita*. The amount of inhibition varied from 4 per cent at a level of 10 PPM to 100 per cent at 1000 PPM of benzimidazole.

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