AN INVESTIGATION OF THE PATHOGENICITY OF RACE MIXTURES OF Puccinia recondita Rob. ex Desm.

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INTRODUCTION

Throughout most of the grain growing areas of the country susceptible species of the genera Thalictrum and Isopyrum, the alternate hosts for wheat leaf rust, do not occur and the leaf rust fungus, Puccinia recondita Rob. ex Desm., persists in the uredial stage. The uredial stage is able to pass from one crop to another infecting volunteer wheat between seasons or being blown north with the crop, and in the same stage overwintering on the new crop. In this manner sufficient inoculum is provided so that the wheat crop may be damaged extensively making leaf rust of significant economic importance.

The organism concerned with the present studies, P. recondita, is one of the most highly specialized of the cereal rusts. Resistance has long been used in attempts to control the disease but, according to Johnson (8), it has been shown that wheat varieties which were resistant to leaf rust when released have become, year by year, more susceptible. This apparent breakdown in resistance is brought about by the appearance of new or previously undetected physiologic races. In general, most races of the various cereal rusts remain constant in their pathogenic properties and the sudden appearance of a new race sometimes simply depends upon a change in the predominant host variety. This, in turn, may change the race population and a minor or previously undetected race may suddenly become prominant following its origin by hybridization, or occasionally by mutation (13). Determining the cause and mechanism of variation in pathogenic potentialities has been one of the most important problems confronting investigators of the cereal rusts.

The effect of known mixtures or combinations of rust organisms on wheat has been studied appreciably only in the last few years. From more

recent studies made on the development of new races from a mixture of races of rust on wheat, it has been shown that races more virulent than either of the parental types may arise by heterocaryosis, indicating still another source or mechanism of variation.

The aim of the present study was to determine the effect of race mixtures of Puccinia recondita on different varieties of wheat.

LITERATURE REVIEW

In 1953, Johnson (8) suggested that new biotypes may arise by a nuclear exchange in the dicaryotic stage between different clones of a rust. Actually, fusion between germ tubes and hypha arising from urediospores of the cereal rusts has been observed by a number of investigators (10, 12, 14, 18, 19). Nelson, Wilcoxson, and Christensen (12), presented evidence that the association of more than two genetically different kinds of nuclei in a vegetative cell or spore (heterocaryosis), is a basis for variation in Puccinia graminis var. tritici, and that new races of this rust may arise by this method. They found hyphal fusions occurring between races of P. graminis var. tritici and the exchange of nuclei resulted in the production of races that were more virulent than the parental races. Cytological investigations indicated that there was considerable variation in the nuclear condition among sori. Some of the urediospores, pedicels, and hyphal cells of the virulent race were uniformly binucleate, whereas others were 3- or 4- nucleate. It was also pointed out that a multinucleate condition in urediospores is unstable.

The results obtained by Watson (17) and Bridgmon (2) established further evidence for the production of new virulent races by combining two different races of the stem rust fungus on wheat seedlings.

By combining two physiologic races that differed in color and pathogenicity, Nelson (11) was able to show that the factors involved in urediospore color could be transferred between biotypes of Puccinia graminis var. tritici by means of nuclear exchange between vegetative hyphae.

Similar results were found to occur between uredial clones of Puccinia recondita (16). However, in an attempt to determine to what extent nuclear interchange occured when dicaryotic mycelia of known races of leaf rust came into contact, Brown and Johnson (4) made infection studies with

mixtures of wheat leaf rust races 9 and 15, and 9 and 5, by infecting a susceptible wheat (Little Club). The results obtained were entirely negative. Only the races used in the mixture were reisolated from it and evidence of interactions between the two races was not found.

The dicaryotic condition of mycelium and spores of Puccinia recondita has been definitely established by several workers; however, variations in the number of nuclei have been reported in nearly all stages of the life cycle of this rust fungus (1).

In the autoecious rust Puccinia helianthi Schw. the process of "diploidization" described by Brown (3) is another possible means of bringing the genetic elements of the different races of rust together.

It has been demonstrated many times that one fungus may be stimulated by the presence of another to produce effects or changes that neither could produce alone. In one instance Fawcett (6) found that Diplodia natalensis and Colletotrichum gloeosporioides together produced much greater effects on citrus bark than either one of the pair alone could produce. Watson (17) stated that race 111, of the wheat stem rust fungus, when grown in association with race NR-2, sporulates on the variety Einkorn. He stated that a synergistic effect must have taken place since pustules of race 111 had not been found previously on this variety.

Antagonistic effects between rust organisms also have been demonstrated (9, 20). The results obtained by Johnston and Huffman (9) indicated evidence of local antagonism between two cereal rust fungi. By inoculating wheat seedlings with urediospores of the oat crown rust fungus (Puccinia coronata Cda. var. avenae Fraser et Led.) prior to inoculation with the wheat leaf rust fungus, the pustules of the leaf rust that developed were fewer in number and smaller in size than were those where only

the leaf rust organism was used. They stated that the local antagonism was due to the action of substances produced by the mycelium of the oat crown rust organism which was not able to establish itself parasitically, or by plugging a number of the possible infection courts.

MATERIALS AND METHODS

The leaf rust races used in this study were pure cultures of physiologic races 5, 9, 9A, 15, 105 and 105B. These races were selected, either because of their prevelance in Oklahoma over the past several years, or because of their pathogenic reaction to certain of the varieties of wheat seedlings being tested. Fresh inoculum of each race used in these studies was obtained from single pustule isolations on the leaf-rust-susceptible variety Cheyenne C.I. 8885./1 Urediospores of each race were tested for at least five uredial generations on varieties of the differential series. Each race was found to repeatedly produce a consistent type of reaction on the differential varieties used (Table I).

Table I. The reaction of certain differential wheat varieties to the races of Puccinia recondita used in the studies of race mixtures.

Differential varieties	Response to race: /a					
	5	9	9A	15	105	105B
Democrat	S	R	R	S	S	S
Malakor	S	S	S	R	S	S
Webster	R	S	S	R	R	R
Loros	R	S	S	R	S	S
Westar	R	R	S	R	R	S
Wesel	R	R	R	R	R	S
Wabash x American Banner	R	R	R	R	R	R

/a R indicates variety was resistant; S indicates variety was susceptible.

/1 C.I. refers to the accession number of the Cereal Crops Research Branch, Crops Research Division.

To determine the extent of hyphal fusions that occured between the different races, in vitro tests were set up in the laboratory. A thin

film of PDA was placed on sterilized glass slides. Urediospores of one race were sown over 3.5% water agar in a petri-dish. The same procedure was followed with urediospores of another race. By using a sterilized glass needle, urediospores of each race were picked from the petri-dishes and placed on the glass slides in parallel lines approximately 150-200 microns apart. In order to prevent contamination the slides were then placed in sterilized petri-dishes. These petri-dishes were placed in an incubating chamber and allowed to incubate between 12 and 16 hours at 20 degrees C. and the slides were then examined with a phase microscope.

All pathological studies were conducted in a closed room. The temperature of the room was maintained at 18-20 degrees C. for all tests and artificial light, both florescent and incandescent, was provided for 12 hours of each day.

Resistance was considered a factor which might influence hyphal fusion and the exchange of nuclei between different races of the leaf rust fungus. Consequently, both resistant and susceptible wheat varieties were used. Cheyenne C.I. 8885 was selected because of its susceptibility to all races of the leaf rust organism. Selections of the crosses Wabash x American Banner C.I. 12757 and Chinese + Aegilops umbellulata C.I. 13483 were used because of their resistance to most or all of the races prevelant in Oklahoma. Pure seed of these three varieties was obtained from Dr. H. C. Young Jr., Department of Botany and Plant Pathology, Oklahome State University. Approximately 20,000 wheat seedlings were used in these studies.

For each test, seed was planted and grown in ten 4 inch pots with 15-20 seedlings in each pot. In all cases the plants were inoculated when

they were ten days old.

Seedlings of the particular variety being used, along with the differential varieties of wheat used in the identification of races of the leaf rust fungus, were inoculated with the single races which composed a mixture to serve as checks with each mixture that was tested.

Approximately 3mg. of urediospores of each physiologic race were used to constitute the mixture.

Inoculation was accomplished by dipping the seedlings into a beaker containing 1 ml. of Photo-Flo in 500 ml. of water to break the surface tension; the plants were then dipped into a second beaker containing 500 ml. of plain water to remove the excess Photo-Flo solution; and finally dipping the plants into 500 ml. of water containing the urediospores dispersed on the surface. After inoculation, the pots were distributed in moist chambers similar to those described by Stakman et al (15). The seedlings were removed from the moist chambers after 24 hours and allowed to incubate for ten days. All of this was done within the closed room described above.

The method used to increase single pustule isolations follows. The plants were prepared for inoculation by stripping the primary leaf of ten day old seedlings between the moistened thumb and fore-finger. The urediospores from the single pustule were picked off with a sterilized needle and placed in a drop of water on a clean glass slide. By running the slide up and down the primary leaf several times, the urediospores were evenly distributed over the leaf surface. After inoculation each pot was placed in a seperate moist chamber. Ten days later, the inoculum produced on these plants was brushed on a set of differential varieties and identified in the usual way.

RESULTS

To determine if genetic variation might result from the mixing of different races of Puccinia recondita on wheat, studies were first made in the laboratory to establish whether or not fusion of germ tubes would occur between certain races of the leaf rust fungus. Germination of urediospores of mixtures of races 9 and 15, and 9 and 5 were observed under the phase microscope.

After 16 hours of incubation fusion between hyphal branches of the germ tubes of the two races were observed quite frequently. Such hyphal fusions between the different races were determined by tracing back from the point of fusion to the urediospores. On several occasions, when urediospores of the two races were germinated on PDA, round bodies such as those described by Rodenhiser and Hurd-Karrer (14), formed on the ends of some of the germ tubes. A few of these bodies were seen fused with hyphae from a different race (Fig. 1). On one occasion, when one of the round bodies fused with a hypha from a different race, protoplasmic material, such as that described by Rodenhiser and Hurd-Karrer (14), was observed passing into the fusion body.

Since fusion of hyphae from two different races of Puccinia recondita was obtained in culture, experiments were designed in the greenhouse to determine if some variability in pathogenicity might be produced by mixing different races of leaf rust and infecting wheat with the mixture.

The race mixtures were used to inoculate both a resistant variety (Wabash x American Banner C.I. 12757) and a susceptible variety (Cheyenne C.I. 8885). When the resistant variety was used the plants were held for ten days after inoculation and then examined for pustule development.

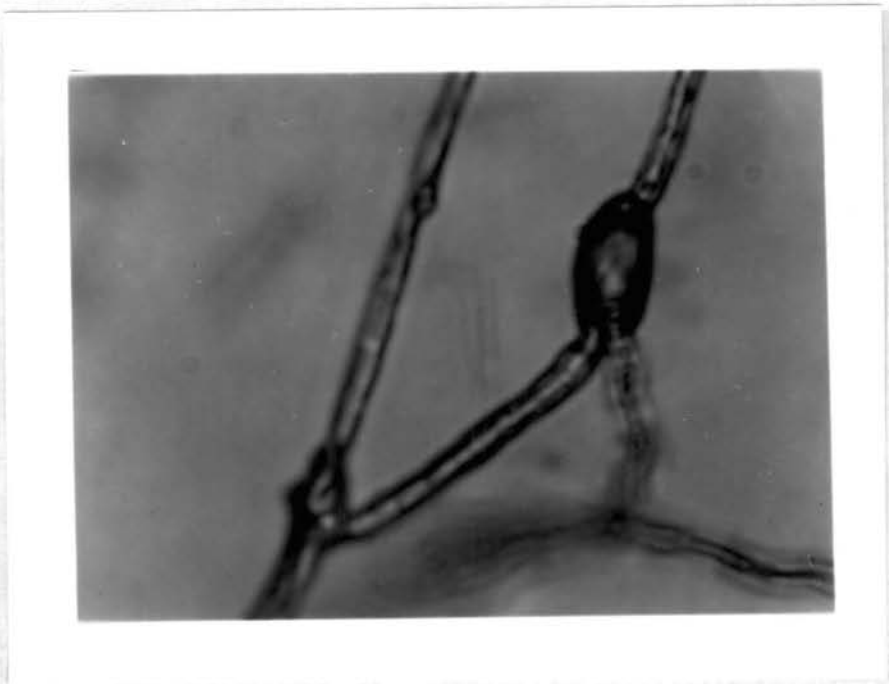

Figure 1. Fusion of a hyphal branch of a germ tube and a fusion body involving urediospores of races 9 and 15 of Puccinia recondita on potato dextrose agar.

As a result of inoculations with mixtures of urediospores of races 9 and 15 on the wheat variety Wabash x American Banner a susceptible type pustule was obtained only once from some 15 different trials. This pustule was increased and later identified as race 35. The reactions of these three races on certain differential varieties used in the identification of leaf rust races in these studies are illustrated in Table II.

Table II. Reaction of certain differential wheat varieties to three races of Puccinia recondita.

Differential varieties	Varietal reaction to races: /a		
	9	15	35
Democrat	R	S	S
Malakof	S	R	S
Webster	S	R	S
Loros	S	R	S
Westar	R	R	R
Wesel	R	R	R
Wabash x American Banner	R	R	S

/a R indicates variety was resistant; S indicates variety was susceptible.

Both races 9 and 15 were run through 5 uredial generations and identified on the varieties of the differential series to be sure of purification. There had been no previous culture of race 35 brought into the greenhouse and all possible means of keeping out contamination had been followed.

During the infection studies with mixtures of races 9 and 15 on the resistant variety Wabash x American Banner, a type-2 pustule was produced on several occasions on the resistant variety (Fig. 2). Used alone, both race 9 and 15 produce only a slight flecking reaction on Wabash x American Banner. Later, these type-2 pustules which developed on Wabash x American

Banner were increased on the leaf rust susceptible variety Cheyenne. The inoculum produced on the variety Cheyenne was brushed on a set of differentials for the purpose of identification. In each case a pure culture of race 9 was recovered.

When the race mixture was used to inoculate the susceptible variety, the inoculated plants were held 12 days to insure full pustule development. Then these infected plants were used to "brush" inoculate plants of the resistant variety. These, in turn, were incubated for 10 days and then examined.

As before, when the race mixture was used directly on the resistant variety, a type-2 reaction was observed on 1 out of approximately each 200 seedlings inoculated. When these pustules were increased and used to inoculate the differential series race 9 was recovered in each case.

The results obtained from infection studies with mixtures of races 9 and 5 on Wabash x American Banner were similar to the results found with mixtures of races 9 and 15.

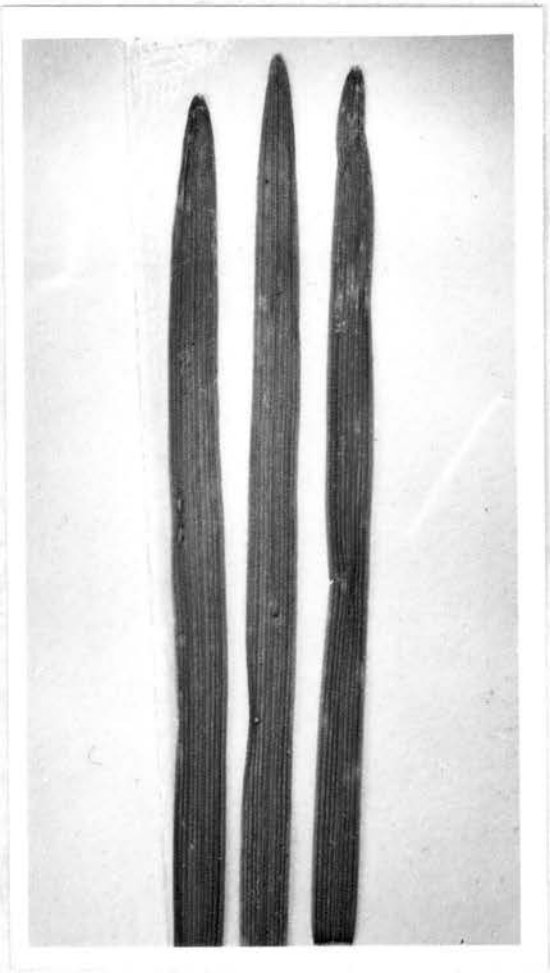

Figure 2. Reaction of the wheat variety Wabash x American Banner C.I. 12757 to races 9 and 15 of Puccinia recondita and to the mixture of these two races. Left, race 9; middle, mixture (races 9 and 15); right, race 15.

Only race 9 could be recovered from the type-2 pustules produced by the mixture of races 9 and 5 on the resistant variety. In no instance was any other race recovered from this mixture.

Control plants inoculated with race 9, race 5 or race 15 used alone showed no variation in reaction; only flecking of the primary leaf was produced.

Infection studies with mixtures of races 5 and 15 on a resistant variety (Wabash x American Banner) did not produce any evidence of variation in pathogenicity to initiate either a new or a known race of the leaf rust fungus. From over 600 seedlings inoculated with the mixture of races 5 and 15, only flecking of the primary leaf was observed.

Tests were then made with mixtures of other races of leaf rust. In these tests a different resistant variety (Chinese+Aegilops umbellulata C.I. 13483) was used. Unlike Wabash x American Banner, this variety is resistant to all of the leaf rust races now known. Mixtures of races 5 and 105B, 15 and 105B, and a mixture of six races (5, 9, 9A, 15, 105, and 105B) were used to inoculate this variety.

The results of inoculations with urediospore mixtures of races 5 and 105B and 15 and 105B were entirely negative. In each case only flecking of the primary leaf occured. There was no evidence that fusion between these races had produced a new pathogenic type capable of infecting this resistant variety.

Heavy flecking developed on all plants inoculated with the mixture of six races. A type-2 pustule developed on three of the inoculated plants. Each pustule was increased and identified on the differentials series. Race 9A was recovered from two of the pustules and a mixture of races 9A and 5 was recovered from the third. None of these cultures were able to

reinfect seedlings of the variety Chinese + Aegilops umbellulata.

To determine if there might be any antagonistic effects between races of Puccinia recondita, experiments were conducted in the greenhouse similar to those of Johnston and Huffman (9). Pure cultures of physiologic race 5 and 9 of the leaf rust fungus were used in these tests.

Twelve pots (4 in.) each containing 10 to 15 seedlings of the variety Democrat were grown in the greenhouse for ten days, after which they were inoculated with a uniform dosage of urediospores of race 9. This race causes only a fleck-type reaction on the differential variety Democrat, whereas race 5 produces a type-4 susceptible pustule on Democrat. The inoculations were made as previously described. Only primary leaves were inoculated. Four pots of seedlings inoculated with race 9 and four pots of uninoculated control seedlings were then inoculated with urediospores of race 5, two, three, and five days following the initial inoculation with race 9. Observations of the inoculated seedlings were made after ten days of incubation.

The results of tests did not indicate any effects of local antagonism between races of the leaf rust fungus. Heavy flecking and chlorosis, caused by the infection of race 9, together with the susceptible pustules of race 5 developed on the plants that were inoculated with race 5 five days after the initial race 9 inoculation. The plants inoculated with race 9 developed the normal susceptible reaction to race 5 but only light flecking and no chlorosis developed from the race 9 inoculation. The susceptible type pustules of race 5 developed on all of the plants inoculated with this race (Fig. 3).

There was no indication of a decrease in the total number of pustules of race 5 that developed when plants were first inoculated with race 9

compared with the number that developed on control plants not previously inoculated with race 9. The pustules of race 5 that developed on the seedlings previously inoculated with race 9 were so far as could be determined, the same size as those produced on plants inoculated only with race 5.

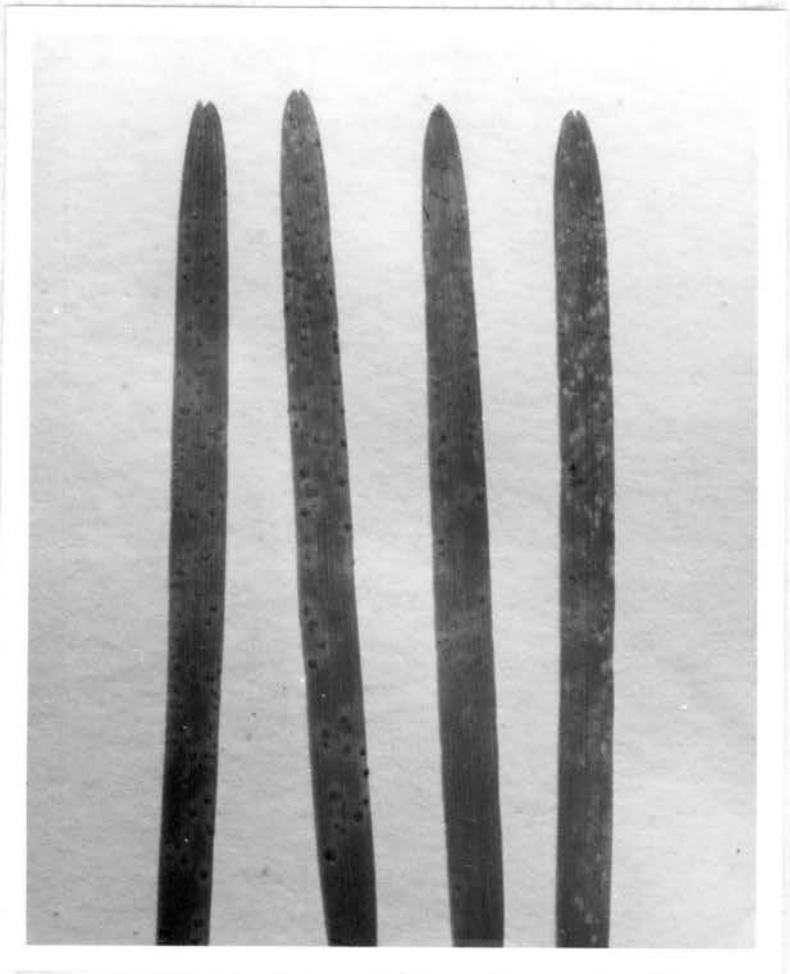

Figure 3. Response of primary leaves of the wheat variety Democrat to infection by certain races of Puccinia recondita. Left, inoculated only with race 5; next 3 leaves to the right inoculated with race 9, two, three and five days respectively, prior to inoculation with race 5.

DISCUSSION

Fusion between germ tubes from urediospores of Puccinia graminis have been observed both on artifical media and on the surfaces of wheat leaves (19). The evidence presented in these studies indicates that fusion between hyphae or germ tubes from urediospores of different races of Puccinia recondita occurs on artifical media.

The formation of fusion bodies at the end of hyphal branches of the germ tubes followed by the fusing of germ tubes from another race with these bodies, may be one method by which the nuclei from different sources are brought together to form new combinations. This process has been demonstrated in the wheat stem rust fungus, Puccinia graminis (19).

The development of Puccinia recondita race 35 from an inoculation of a mixture of races 9 and 15 on the wheat variety Wabash x American Banner indicates that an exchange of nuclei may have taken place. Although all possible means of keeping each race pure and the seedlings clean were followed, the possibility of contamination can never be completely ruled out. It seems, however, if the development of race 35 was due to contamination, that this race would have occured more frequently; at least more than once from some 3000 seedlings inoculated with the combination of races 9 and 15. If, on the other hand, the development of race 35 from the mixture of races 9 and 15 was due to an exchange of nuclei in the vegetative hyphae, this phenomenon must occur only rarely. It might be equally plausible to suggest that a mutation had taken place when such a magnitude of spores were involved.

The sporulation of race 9, following inoculation with a mixture of races 9 and 15 on Wabash x American Banner, suggests that a synergistic reaction may have taken place since race 9, when inoculated alone produces

only a slight flecking on this variety. The same effect was observed when races 9 and 5 were used to inoculate Wabash x American Banner, but when races 5 and 15 were used no such effect was noted.

According to Hussain (7), when wheat leaf rust races 9 and 15 were mixed in equal proportions and carried through four uredial generations on the varieties Triumph and Comanche which are susceptible to both races, race 9 composed over 90 percent of the mixture. It has also been shown that urediospores of race 9 have the ability to germinate more rapidly than certain other races, particularly at low temperatures (5).

If it is assumed that race 15 produced or broke down a substance needed by race 9 at some stage of the infection process, coupled with the fact that race 9 is able to germinate much faster than most races, it is possible that when urediospores of these two races germinate in proximity only race 9 will be able to sporulate on the resistant variety.

The results of inoculations with urediospore mixtures of races 5 and 105B, and 15 and 105B on the resistant variety Chinese + Aegilops umbellulata did not indicate that hyphal fusions, if they occured, had resulted in the production of races virulent on this variety. Neither was there any evidence of a synergistic reaction here.

The sporulation of races 9A and 5, from infection studies with a mixture of six different races of Puccinia recondita on Chinese + Aegilops umbellulata also suggested a synergistic reaction between races of the leaf rust fungus.

Although there is some evidence of antagonism and/or cross protection between rust organisms of the same genera (9), there was no indication in these studies of local antagonism between races 9 and 5 of the leaf rust fungus.

SUMMARY

1. Numerous fusions between hyphal branches of the germ tubes of different races of Puccinia recondita were observed on artifical media. After 16 hours of incubation, fusion bodies that had formed on the end of some germ tubes were observed fusing with hyphae from a different race.

2. From a mixture of urediospores of races 9 and 15 inoculated on the resistant wheat variety Wabash x American Banner, race 35 of the leaf rust fungus was recovered once from some 3000 inoculated seedlings.

3. It was observed that race 9 sporulated frequently when mixtures of races 9 and 15 and 9 and 5 were inoculated on the resistant variety Wabash x American Banner. When used alone, race 9 never sporulated on this variety.

4. No sporulation occured when a mixture of 5 and 15 was used to inoculate the variety Wabash x American Banner. Similar results were obtained when mixtures of races 5 and 105B and 15 and 105B were used to inoculate the variety Chinese + Aegilops umbellulata.

5. Further evidence of a synergistic reaction between certain races of leaf rust was obtained when a mixture of six different races was inoculated on the resistant variety Chinese + Aegilops umbellulata. From a mixture of races 5, 9, 9A, 15, 105 and 105B, two pustules of race 9A and one pustule which was a mixture of races 5 and 9A were produced.

6. Greenhouse tests gave no indication of local antagonism between races 9 and 5 of wheat leaf rust.

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