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Inheritance of Resistance to Races of Blast Disease in Rice.

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ABSTRACT

Studies on inheritance of resistance to race 6 of rice blast (Piricularia oryzae Cav.) were investigated. Material from the cross involving parent strains 1709 and CI 9418 was tested for reaction to race 6 in F_1, F_2 and F_3 generations. Selected F_3 lines of known reaction to race 6 were also tested with races 8 and 16.

Before testing the hybrid material, preliminary tests were conducted on 16 varieties and strains of known reaction to races 1 and 6. The techniques of inoculation of rice seedlings and evaluation of infection for six lesion types were standardized. All tests were carried out in the green house, under high humidity chambers during the spring and fall of 1962.

The preliminary tests showed reasonably good agreement with those reported by previous workers, indicating that the techniques used in the present study were reliable.

The strain 1709 was found to be resistant to races 6, 8 and 16 but susceptible to race 1, while CI 9418 was found to be susceptible to all four races.

The reaction of the four F_1 plants to race 6 was similar to the resistant parent, indicating that resistance is dominant to susceptibility in this cross. The behavior of 66 F_2 plants showed a good

fit to ratios of 3 resistant:1susceptible and 9 resistant:7 susceptible. However, the fit was closer to the 3:1 ratio, suggesting that the parents 1709 and CI 9418 differed by only one pair of genes. Segregation of 135 F_3 families into a ratio of 1 homozygous resistant:2 segregating:1 homozygous susceptible confirmed the assumption that resistance to race 6 is conditioned by a single dominant gene in strain 1709. This gene has been provisionally designated as "Pi_1".

Presence of one or more modifier genes apparently caused the occurrence of a few susceptible plants in apparently homozygous resistant lines and a few resistant plants in apparently homozygous susceptible lines.

A reasonably close agreement in the reaction of 50 to 53 F_3 lines to races 6, 8 and 16 suggested that basically one major dominant gene governs the reaction to these three races. But the reaction of each race seems to be influenced by a different set of modifier genes.

Due to the complex pedigree of the strain 1709, the exact source of resistance could not be determined.

The results of the present studies revealed that simple and inexpensive green house tests can be used advantageously to isolate resistant lines in early segregating generations.

The strain 1709, besides being resistant to at least three races of blast, possesses several important agronomic characters. It should, therefore, prove to be a useful parent in future blast breeding programs.

INTRODUCTION

Although the blast disease of rice has been known for centuries, it was in 1891 that the Italian mycologist Cavara first described the causative fungus and named it *Piricularia oryzae*. For more than half a century the disease has been of great concern to rice breeders and plant pathologists in many rice growing countries of the world.

The development and severity of blast disease on rice are greatly influenced by rainfall, temperature, humidity, stage of plant growth, soil type, irrigation and cultural practices. In recent times many rice growing countries are using large quantities of fertilizers for high rice production. It is now well established that large applications of nitrogenous fertilizers aggravate the possibilities for serious outbreaks of blast. The disease is less common in certain years but is a continual threat to rice culture because of its destructiveness when it becomes epiphytotic. In spite of the fact that several fungicides are known to combat the disease, prophylactic measures often fail due to the suddeness of the development of the disease and the inability to apply them at the proper time. Consequently, substitution of resistant varieties for susceptible ones offers the best means of avoiding heavy losses due to blast. Therefore, considerable effort has been directed towards control of this internationally important disease of rice by breeding resistant varieties.

One important complicating factor of blast disease that was recognised rather recently is the occurrence of physiologic races of _Piricularia oryzae_ Cav. Rice breeders in most countries are experiencing the failure of new varieties to maintain their resistance every year in all localities. Varieties resistant in one locality or year often become susceptible in another. This differential behavior of varieties has been attributed to the existence of physiologic races of the pathogen. The first positive evidence of the existence of physiologic races of _P. oryzae_ was obtained in the United States in 1953. Since then, varietal reaction to the different races of blast fungus has been studied extensively in this country.

Considerable progress has been made in breeding for blast resistance in different rice growing countries and numerous publications pertaining to varietal resistance to blast have appeared. However, relatively few publications have been reported on the inheritance of resistance to blast in general, and practically none on the inheritance of resistance to individual races. A knowledge of the inheritance of resistance to individual blast races is basic to a well planned breeding program which will enable the breeder to incorporate more efficiently the genes for resistance to many races in a variety.

The present studies were carried out mainly to provide information on the inheritance of resistance to blast race 6, which is the most common race present in the United States. Attempts were also made to find out whether the same gene or genes controlling race 6 also govern the resistance to races 8 and 16.

F_1 seeds of the cross 1709 X CI 9418 were obtained from the Rice Experiment Station, Crowley. The 1709 parent was known to be resistant to blast under field conditions at the Rice Experiment Station while the CI 9418 parent was known to be susceptible. F_1 and F_2 plants were raised in the green house and the F_2 and F_3 seeds were harvested in 1961, spring and summer, respectively. The seedling reaction of F_1, F_2, and F_3 lines to race 6, and of seleted F_3 lines to races 8 and 16, were carried out in the green house during the fall of 1962.

REVIEW OF LITERATURE

The Literature Review in this dissertation has been presented in the following order:

1. Studies on breeding and testing varieties for resistance to the blast disease in rice.

2. Inheritance of resistance to blast disease.

3. Studies on physiologic specialization of *Piricularia oryzae*.

4. Sources of resistance to blast.

1. Studies on Breeding and Testing Varieties for Resistance to the Blast Disease in Rice.

Testing and breeding of rice varieties for blast disease resistance has been intensively carried out in Japan, U.S.A., India, Taiwan, and Ceylon.

Fulton (12) was one of the earliest investigators who obtained varietal differences in rice for reaction to blast disease. He found that Honduras was least susceptible to blast, while red rice was highly susceptible.

By repeated inoculation studies of about 430 rice varieties Nishikado (43) observed that 34 varieties were comparatively resistant to blast disease. However, none were entirely immune.

Thomas (66) carried out experiments to determine the relative resistance of a large number of varieties. He found two varieties, namely Co. 4 and GEB 24, to be highly resistant, while Korangusamba was highly susceptible. Subsequently, these varieties formed the parental material for effecting crosses by Ramiah and Ramaswamy (55). They isolated pure breeding, disease-free selections, which yielded 10 to 50 percent more than the susceptible variety Korangusamba.

Crawley and Adair (9) conducted varietal tests to determine whether the common commercial varieties and hybrid selections differ in their reaction to blast. They observed significant differences in the varietal reactions. Early Prolific was very susceptible while Zenith and Arkansas Fortuna were resistant. Two high yielding hybrid selections, Arkrose and Prelude, were moderately resistant.

Iwatsaki (25) obtained ten highly resistant and productive varieties with desirable characters, such as stiffness of straw, plant type, and grain quality, by using Fatuba and Shinji in his breeding work.

Using distantly related parents, _indica_ and _japonica_ types, Shigemura (60) successfully bred a variety that showed stronger resistance to blast than the parents Fatuba and Kanto 51. The hybrid variety was back-crossed three times to the _japonica_ parent to restore fertility and to obtain _japonica_ characteristics.

Saito (56) tested a series of 83 varieties from Japan, China and India under late sown irrigated and upland conditions. He found that Chinese semiglutinous and Japanese upland varieties were highly susceptible, while Japanese irrigated and Taiwan upland varieties were moderately susceptible. However, Indian varieties, Chinese nonglutinous and Taiwan irrigated varieties were highly resistant.

Although certain old Japanese varieties are resistant to blast, rice breeders in Japan have used introduced varieties of the indica type as a source of blast disease resistance.

Koyama (28) crossed two Chinese blast resistant varieties, Reishiko and To, with two commercial Japanese varieties, Norin 10 and Ginbozu. He obtained Kanto 51 and Kanto 52, from Ginbozu X To, and Kanto 53 and Kanto 54 from Norin 10 X Reishiko. All four of these hybrid varieties had higher resistance to blast than other rice varieties in Japan.

Hashioka (15) conducted studies on the annual and local variation of the varietal resistance of rice to the blast disease. He grouped the varieties into the following four classes based on the order of resistance of leaves, panicles and nodes of culms.

1. A resistant group consisting of Taichung No. 114 Kaohsium No. 10.

2. A moderately resistant group, No. 103, Taichung No. 65, Taipei No. 6.

3. A moderately susceptible group, Hsin Chu Ailoku No. 1, Tainang No. 22.

4. A susceptible group, Kameno-O.

Mello-Sampayo, *et al.* (36) tested varieties from *Oryza glaberrima*, *O. minuta* and local cultivated varieties of Spain and Portugal for blast resistance. They reported, that most varieties were susceptible, but a few displayed less infection than others. Del Prado (10) studied comparative susceptibility of several varieties to *P. oryzae*, and he found 5 ML 77-1-3 to be moderately resistant.

Narasinga Rao (41) reported a high degree of blast resistance in strains 6522 and 6517, which were isolated from a cross between Co. 4 and a short duration variety Co. 13.

Li (32) tested a series of rice varieties belonging to the Penglai type for blast resistance. Pai-mi-fen, Kug-fu 1, Kao-hsiung 27 and Kao-hsuing 22 were found to be the most resistant varieties.

Reviewing the work done in India, Padmanabhan (49, 50) mentioned that out of 500 varieties tested, 14 were selected for resistance to blast disease. From among these, five of the early maturing varieties were in field trials at various localities in India.

A pureline selection, M. 42, isolated from a local indigenous variety named Molakolukulu, has been reported to be tolerant to blast, especially under late planted conditions. (Narasinga Rao, *et al.* (42).

Ramachandrarao, *et al.* (54) discussed the performance of blast resistant strains isolated from the cross BCP 1 X Co. 4. They found strains 5390 to be superior over the rest of the strains with regard to blast resistance and yield.

Varietal differences in susceptibility to blast were obtained in France by Bernaux (5). Three varieties, namely Americano 1600, Senatore Novelli and Adelaide Chiappelli, were found resistant. In general tetraploid species, such as *Oryza latifolia*, were found less susceptible than the diploid species.

Ou (45) reviewing the diseases of rice in Taiwan reported that, in general, "Ponlai" rice was more susceptible to the blast disease than the native varieties. He tested more than 1000 varieties by artificial inoculation techniques and by field tests. Over 170 varieties showed a high degree of resistance. Bai-Kitow which was almost immune in three locations in the North and central Taiwan became quite susceptible in the South. The resistance of rice varieties to blast also varied from year to year.

About 21 low land rice varieties were tested by artificial inoculation for resistance to blast by Gallardo (13) in the Philippines. Inomay, AC 440, DR 260, and Malaman were found useful in breeding for resistance, since they showed only very slight infection when inoculated at seedling, tillering or boot leaf stage. Nine other varieties showed moderate resistance.

Peiris, *et al.* (53) determined varietal resistance to *Piricularia oryzae* by raising highland nursery beds and predisposing the rice plants to the disease. According to their assessments, SR 26 B, Murungakayan 302 and 304 and V I 28061 were very resistant, while Bengawan 27, Tjahja 27, and Segadis 3443 showed exceptionally high resistance. About 46 other varieties showed extreme susceptibility.

Discussing the disease resistance of the variety groups of rice native to the different latitudinal regions in Asis, Hashioka (16) stated that the Japanese lowland rice group was highly susceptible to leaf blast, as compared with the resistance of the Tropical insular and Continental groups. However, he observed that this tendency was not so distinct in the case of neck and node-blast. Evidently the varietal groups differed in their reaction to the leaf, neck and node-blast depending upon the latitude.

Ou _et al_. (47) effected 34 cross combinations from 29 parent varieties belonging to four rice groups in Taiwan. They employed pedigree, bulk and back-cross methods in their selection which was made from fields where blast disease was severe. Ten highly resistant and nine moderately resistant homozygous lines were obtained from three Ponlai varieties.

In Ceylon yield tests of blast resistant varieties were conducted and information on their degree of resistance was obtained by Fernando _et al_. (11). Three of the improved varieties, namely H. 4 (Murungakayan 302 X Mas), H 105 (C. 104 X Murungakayan), and H 501 (GEB 24 X Vellai Illankalyan) were especially recommended to farmers because of their good response to heavy fertilization, combined with superior blast resistance.

Reviewing the work on varietal resistance of rice to blast disease, Marks _et al_. (34) reported 23 resistant or highly resistant rice varieties, out of a total collection of 126 indigenous types, in Ceylon.

Chang (7) reviewed the rice breeding program and its recent developments in Taiwan, with reference to breeding for blast resistance. He reported that the response of rice to blast in the latter part of the growing season, differed from that in the seedling stage. The following four varieties were tested and found to be resistant: (1) Chia-nung 242, (2) Taichung 178, (3) Taichung 179, (4) Kaohsiung-yu 71.

Padmanabhan _et al_. (51) studied the reaction of 470 types from the world genetic stocks in India by artificial infection with blast at the seedling stage and subsequent testing for field reaction. From the final tests in the field BJ 1, Co. 4, S 67, SM 6, and SM 9 were found to be resistant while 16 other varieties were moderately resistant. They, however, observed that certain varieties were resistant at one stage of growth and susceptible at another. It was suggested that it would be preferable to select varieties which are resistant at all stages of growth.

In Japan according to IRC working party report (21) Shigemura and Kitamura obtained the highly resistant varieties Pi No. 1 and Pi No. 2 by repeatedly back-crossing Senbon Asahi to Tadukan. Subsequently Kitamura bred varieties Pi No. 3 and Pi No. 4 which are highly resistant to blast with all the characteristics of the recurrent _japonica_ parent, by back-crossing Norin 8 five and four times, respectively, to Tadukan.

The reactions of three populations viz. T 4, B and PT of wild rice _Oryza sativa f. spontanea_, to blast disease were investigated by Narise (40). He observed that the T. 4 population collected from Samalkota (Andhra Pradesh, India) was found to be highly resistant, while the B. and PT populations collected from Chinsura (West Bengal, India) and Puttalam (Ceylon), respectively, were highly susceptible. However, by partitioning the components of variance, he concluded, "That plants in wild population are highly heterozygous with respect to disease susceptibility and the inter population variability is very high".

Takaos (64) reported the incidence of blast on six varieties grown in Hungary. Among the six varieties, Allolio early and line 45 were found to be highly resistant.

Leaf and neck reactions of 27 rice varieties of Ponlai rice (japonica type) and seven varieties of native rice (indica type) were listed by Chang (8). Taichung 176, 178, 179, 180 and Tee-Geo-Woo-Tsin were resistant to leaf reaction while, Taichung 178 and 179 and Bei-Ne-Fen and Kaohsiung Tali-Chinyu were resistant to neck reaction. He further observed that resistant lines showed little variation in their reaction to blast at different levels of manuring, while the less resistant lines exhibited larger variation.

Wang et al. (69) published the reaction of 50 newly selected hybrid lines of Ponglai (Horai) type of rice under natural blast infection. A few of the lines were found sufficiently resistant for further use in the breeding program.

In a world collection of varieties tested for reaction to the blast fungus, Simon (61) observed certain varieties to be resistant with good agronomic characters and quality of rice. The native selection Pallagi 73 was one among them.

Ou (46) discussed the different aspects of rice blast and tested the reaction of about 1700 rice varieties and hybrid progenies to the blast fungus. The results indicated that resistant varieties are of equal number from North and North-east regions and a greater number are susceptible in the central region of Thailand. He observed that the floating types are mostly intermediate in reaction. In sample tests of F_5 and F_6 generations, resistant plants selected in F_5 did not segregate in F_6 population consisting of 450 plants, but remained resistant. The very susceptible plants selected in F_5 remained susceptible in F_6. However, individual plants which showed intermediate reaction segregated into more resistant and more susceptible types.

Samad (57) reported the release of two blast resistant strains, Co. 29 and Co. 30 isolated from Co. 13 X Co. 4 and GEB 24 X Co. 4, respectively.

Templeton et al. (65) tested 67 varieties and lines during 1960 in the green house and in the field. They noticed considerable differences among the varieties in their reaction to blast. From among the 11 commercial varieties tested, Gulfrose, Zenith and Lacrosse are the only resistant varieties, while the remaining varieties were susceptible. It was concluded that seedling reaction is fairly closely correlated to neck-rot reaction of mature plants.

Katasuya (26) tested the reaction of 92 strains of 20 species of the genus _Oryza_, three inter-specific hybrids of _Oryza_, two strains of _Zizania latifolia_ and a strain of _Chikusichloa aquatic_ with two isolates, namely P 2 and 54.04, of _P. oryzae._ He observed that strains of _O. sativa f. spontanea_, _O. perennis_, _O. barthii_, _O. stapfii_ and _O. breviligulata_ exhibited either resistance or susceptibility or a moderate resistance. However, _Zizania latifolia_ and _Chikusichloa aquatic_ behaved differently, the former being resistant and the later susceptible. He could not establish any relationship with regard to susceptibility, locality and chromosome number.

Since 1942 considerable efforts were made in Japan to improve the local _japonica_ type of varieties which are highly susceptible to blast. They have often utilized Chinese varieties in the hybridization program for evolving suitable commercial varieties which are highly resistant to blast. As a result of such efforts, Ito (24) obtained Kanto 53 by crossing Norin 10 and Reishiko (resistant Chinese variety). Although Kanto 53 was highly resistant to blast, it did not possess other desirable characters, such as lodging resistance and high yield. By further hybridization of Kanto 53 with Norin 29, a leading commercial variety Kosubue was obtained, which proved extremely popular in the Kanto-tosan region in Japan.

Atkins _et al_. (4) have tested for several years, a large number of United States varieties to blast in field grown nurseries and also in the green house by artificial inoculation. Due to the prevelance of different physiologic races, they have adopted the process of screening varieties in the green house for individual races and those that are resistant to several races are then tested in the field. They emphasized that varietal reaction based on field observation alone would be incorrect for two reasons: 1. A variety though really susceptible may seem resistant due to the fact that it escapes the disease. 2. Presence or absence of a particular physiologic race within the area, may cause aparent inconsistencies in the behavior of the varieties.

They found that several U. S. varieties were resistant to one or the other of the ten existing races, while none were resistant to all.

The Working Party on Rice Production and Protection (22) at its ninth session at New Delhi, recommended the establishment of uniform blast nurseries as a prerequisite in breeding for blast resistance. The committee also recommended the use of the upland nursery technique, to assess the varietal resistance to blast and repeat such tests for three to four consecutive years.

On the recommendation of the Working Party on Rice Breeding in 1955 (23) cooperative blast resistant trials were undertaken by Japan, U.S.A., India, Philippines, Egypt, Taiwan and Thailand. Results from such tests indicated that reaction of varieties in Japan differed from those in other countries which "seems to arise from a lower working standard of resistance in Japan". The differential behavior of the *japonica* rice indicated the existence of physiologic races of the blast fungus. It was also reported that well-known resistant or susceptible varieties of one country remained consistantly resistant or susceptible in all other countries.

2. Inheritance of Resistance to Blast Disease.

Studies on the inheritance of disease resistance in crop plants have been a fruitful field for the application of genetic principles to plant breeding. Such studies are voluminous in crops like wheat, barley and other crops.

Although fairly good progress has been made with regard to varietal testing and breeding for blast resistance in rice, relatively meager information has been reported on the inheritance of blast resistance. A review of the inheritance studies on blast resistance will serve to show the diversity of results obtained thus far.

The earliest investigation on the inheritance of resistance to blast disease was carried out by Sasaki in 1922 (59). He observed blast resistance as controlled by a single dominant gene in several crosses, giving a ratio of 1:2:1, of resistant, segregating and susceptible plants in the F_3 generation.

Nakatomi (39)reported complementary dominant genes governing blast resistance giving ratios of 9:3:4 and 9:7 in two different sets of crosses. His results were based on the survival of plants in the F_3 generation.

Ramiah *et al*. (55) studied the inheritance of blast reaction in two sets of crosses, namely:

1. GEB 24 X Korangusamba

2. Co. 4 X Korangusamba

They found the F_1 plants to be intermediate in the first cross, while they were resistant in the second cross. From the segregation data in F_2 generation they considered that resistance might be a simple recessive to susceptibility in the first cross while the inheritance in the second cross was more complicated. Although the susceptible parent Korangusamba was common to both the crosses, the inheritance was found different in the two cases.

According to Nagai (38) Nakamori made some interesting studies with regard to varietal reaction to blast at high and low altitudes. He observed that most varieties behaved resistant at one location but susceptible at the other, while only a few were of the same type of reaction at both the locations. To study the inheritance of resistance in those varieties, he effected crosses between varieties of the two types. He obtained segregates which were either resistant or susceptible at both locations. He also recovered the parental types. From this behavior he postulated two dominant genes, each of which gave resistance at one location but inactive at the other location. The F_3 data confirmed the expected ratio of 9:3:3:1 on the basis of two independent genes, in which nine were resistant or segregating at both locations; three were resistant or segregating at low altitude but susceptible at high altitude; three resistant or segregating at high altitude but susceptible at low altitude; one susceptible at both the altitudes.

Hashioka (14) studied the reaction of several varieties to leaf blast, neck blast and nodal blast in Taiwan. He effected several crosses between resistant and susceptible varieties and observed that at least two dominant genes were responsible for resistance to blast disease, in those crosses.

Studying the resistance of leaf blast in crosses between resistant foreign varieties and susceptible Japanese varieties, Okado and Maeda according to Nagai (38) observed that the F_1 was intermediate. They postulated three dominant genes, R_1, R_2, and R_3, with additive effects for resistance. The degree of resistance increased progressively with the simultaneous presence of these dominant genes.

Oka _et al_. (44) used biometrical methods for genic analysis of the resistance of blast disease in their studies. F_2, F_3 families and an F_3 bulk population of a cross Pei-Ku X Taichung 65, which were phylogenetically distant varieties, were employed, and the degree of infection was measured on a single plant basis by a series of index numbers. The number of effective factors governing resistance was calculated as one, by Mather's partitioning method. The mode of frequency distribution was such that the gene for susceptibility appeared to be dominant over resistance. They also observed linkage between the resistance gene and the "Gametic-Development genes", thus disturbing the segregation ratio.

Bhapkar *et al*. (6) studied the inheritance of blast disease resistance in the following three crosses: (1) EK 70 X Bavadya; (2) H 566 X Zinya 31; (3) T 3 X K 540. From the behavior of the F_1 and F_2 progenies, they assumed resistance as dominant over susceptibility and that the dominance was governed by one or two major genes.

Ou *et al*. (57), without citing experimental evidence, stated as following in their report on rice breeding for blast disease resistance: "The resistance seems to be governed by one pair (or more) of genes which is not completely dominant. The resistant gene (or genes) in the highly resistant native variety is found to be in link with that of other desirable characters".

Ou (46), summarizing varietal resistance to blast in Thailand, reported the nature of resistance from an F_2 segregating population. His studies involved the following cross combinations between resistant (R), moderately resistant (M), and susceptible (S) groups: R X R; R X M; R X S; M X M; M X S; S X S. The results of such crosses showed that in general the F_2 progeny of R X R were all resistant; of R X M, mostly in between R and M; of R X S, varying from resistant to susceptible and mostly intermediate groups; of M X M also varying from resistant to susceptible beyond the range of the parental varieties; of M X S mostly between the parental ranges; of S X S, all susceptible. Finally, he concluded that the resistance to blast is governed by several pairs of genes.

In Japan results of gene analysis in the hybrid varieties Pi 1; Pi 2; Pi 3; Pi 4; showed that the blast resistance is controlled by a single dominant gene "Pi". However, in varieties Kanto 51, Kanto 55 and Imochi Shirazu, resistance is controlled by one major gene other than "Pi". New varieties which have both the major gene and the "Pi" have also been isolated (21).

Simon (61) observed resistance as generally recessive in crosses between Dunghan Shali (susceptible parent) and Agostano and line 45.

Six resistant, six intermediate and seven susceptible rice varieties from the U. S., Japan, and Taiwan were crossed by Hsieh *et al*. (18), in order to study the inheritance of resistance of rice seedlings to *Piricularia oryzae*. Artificial inoculations were made and the F_2 plants were classified into resistant and susceptible based on six lesion types. They concluded that in a majority of crosses the F_2 showed monogenic segregation, resistance being dominant over susceptibility. However, in a few crosses 9:7 and 9:3:4 ratios were obtained indicating that at least two dominant genes are involved in governing the resistance of blast disease. The F_2 data, however, were not confirmed by a study of F_3 lines. More over their inoculum was composed of a number of isolates collected from various regions of Taiwan. If the inoculum consists of more than one race of the fungus, obviously the results will be complicated.

3. <u>Studies on Physiologic Specialization of Piricularia oryzae</u>.

In breeding rice varieties for resistance to blast, consideration should be given to the possible existence of physiologic races. A knowledge of distinct pathogenic races, by establishing differential test varieties, will serve as an important tool in screening and breeding resistant varieties. The nature and distributation of physiologic races of a crop disease is also important and should be known well before a thorough breeding program can be initiated.

Using different cultural characteristics, Sasaki (58) distinguished three strains, A, B, and C, of the blast fungus. However, he recognised only two races A and B by their pathogenicity to different rice varieties.

Subsequently, Hemmi *et al*. (14) reported physiologic specialization of *Piricularia oryzae* with 23 cultures obtained from different sources. They observed variations in general cultural characters, temperature relations, and their pathogenicity.

Tochinai *et al*. (67) made an extensive study of a large number of cultures from various sources. These cultures, developed from single spore isolates, grown on four types of culture media, were found to differ in their cultural characters. They finally recognised nine distinct "physiologic forms" based on their cultural behavior. However, no differential rice varieties were used to recognize their pathogenicity.

Isolates collected by Todayosi (63) from Korea, Formosa and Tiba prefecture (Japan) and cultured on nutrient media, showed differential behavior from which the author distinguished several "types" of blast fungus. From infection studies of these types on rice varieties, differential behavior of the isolates was observed. This points out the possibility of the existence of physiologic specialization in the pathogen.

Aoki, according to Padwick (52), distinguished "different types" of the blast fungus from a study of 23 cultural strains. His studies included formation of aerial hyphae, degree of sporulation, color of the submerged mycelium in one percent potato-sucrose-agar and growth of submerged mycelium in synthetic media.

A distinct variation in pathogenicity of the different culture strains was recognized by Abe (1). In his studies strains no. XIII and IX showed strongest pathogenicity, while strain no. V was weakest. When 16 rice varieties were inoculated with three cultural strains, namely V, IX and VIII, all the varieties succumbed to strain no. IX while pathogenicities of the strains no. V and VIII were weak and indistinguishable. He did not, however, differentiate them as specific pathogenic races.

Cultural characteristics of 21 different cultural strains of the blast fungus were determined by Inoue (20) by their ability to decompose cellulose. The fungus strains were grown on synthetic agar plates containing colloidal cellulose. Strains no. 3, 9, 10, 12, 15, 20, 21, 29, and 34 showed most active ability to decompose cellulose while no. 17, 25, and 32 were inert. The rest of the strains were intermediate between these two groups. The active ability to decompose cellulose was positively correlated with virulent pathogenicity of the strains on rice plants.

Although several workers in Japan distinguished cultural types of blast with distinct pathogenicity, Hashioka (14) could not get any evidence for the presence of physiologic races on the basis of differential pathogenicity to selected rice varieties. He reported as follows from his extensive field experiments:

"Also in the present experiments which are largest in scale among the field trials, on the blast disease, ever reported up to the present, presence of the races of the fungus distinctly different in pathogenicity had not been found."

The first positive evidence of the existence of physiologic races of *P. oryzae* under natural conditions in the field, followed by experimental evidence from green house tests, was obtained by Latterell et al. (30). They distinguished two physiologic races from a collection of seven isolates based on their differential pathogenicity to Zenith and Caloro rice varieties. These two races are now well established as race 1 and race 6. Zenith is highly resistant to race 6 but susceptible to race 1, while Caloro is highly resistant to race 1 but susceptible to race 6.

The possibility of the existence of physiologic races of blast in Ceylon was suggested by Peiris *et al.* (53), although no experimental evidence was obtained.

Venkatarayan (68) also expressed the possibility of occurrence of physiologic races of the blast fungus in India but failed to cite any experimental evidence. Subsequently, Padmanabhan (48) attempted to get evidence of races of blast. The tests were conducted with four different isolates obtained from Delhi, Coimbatore, Cuttack and Wynad. But no evidence of races distinctly different in pathogenicity was obtained. Recently Kulkarni et al. (29) reported three races of blast in Bombay Province.

From a series of experiments conducted in Taiwan from 1956 to 1958, a great deal of difference in blast resistance with respect to variety, locality and year, was obtained by Chang (7) and Ou et al. (47). They suggested the presence of physiological races as causing this variation. Although this can only be regarded as circumstancial evidence, Chang (8) obtained the first positive evidence of physiologic specialization in Taiwan under field conditions. Chainung 242, which was fairly resistant in five different locations, was found highly susceptible in Taitung center. It was further reported that "a preliminary study of six monoconidial isolates on 16 differential varieties of rice has suggested the division of five different pathogenic races. It is expected that more pathogenic races would be added to the list."

Very recently, Hung et al. (19) confirmed the findings of Chang (loc cit.) by inoculation tests with seven isolates on 16 standard rice varieties. They indicated the possibility of the occurrence of five distinct blast races in Taiwan.

In Japan physiologic specialization of the blast fungus has been emphasized since 1954. A cooperative blast resistant scheme sponsored by FAO was organized at the National Institute of Agricultural Sciences, Hiratsuka and other centers (Morinaga, 37). Results from these studies indicated the presence of physiologic races of blast in Japan. The races so far known were classified into the following three groups.

1. T group - Pathogenic to Tadukan and Pi no. 1.
2. C group - Pathogenic to Chokoto Reishiko and Yakeiko, which were introduced from China.
3. N group - Pathogenic only to Japanese varieties.

These groups were further subdivided into several subgroups (21).

Later reports from Japan, indicated that studies were carried out with two races, namely P 2 and 54 04 (Katasuya, 26). But it is not clear whether these two races belong to any of the three main groups listed above.

Latterell _et al_. (31) reported 15 physiologic races of _P. oryzae_, characterized by their ability to infect ten differential rice varieties. A total of 165 isolates were collected from various rice growing countries and tested against ten differential varieties. From the results obtained, they concluded that "isolates of similar pathogenicity were found from widely separated rice growing areas of the world." Further, more than one race was found to be present in several countries. Races 1, 2, 4, 7, and 8 were reported to occur in the U.S.

Atkins (3) confirmed the findings of Latterall _et al_. (loc cit). He identified one additional race, 16, from collections made in

1959-1960. It was reported that at least ten races are now known to occur in the U.S. Table I shows the nature of reaction of the ten differential test varieties to the ten physiologic races prevalent in the U.S. The distribution of the known races of blast in the U.S. is presented in Table 2.

Table I. Nature of Reaction of Differential Varieties to Different Races

Differential Varieties	Races of P. oryzae Present in U.S.A.									
	1	2	3	4	5	6	7	8	10	16
1. Zenith	S	R	R	R	R	R	S	R	R	R
2. Lacrosse	R	S	R	R	R	S	S	S	R	S
3. Caloro	R	S	S	S	R	S	S	S	R	S
4. CI. 8970(P)	R	R	S	R	R	S	S	S	R	S
5. CI. 8970(S)	S	R	S	R	S	S	S	S	R	S
6. CI. 5309	R	R	R	R	R	R	S	S	R	R
7. PI. 180061	S	R	R	R	R	R	S	S	R	S
8. PI. 201902	R	R	R	R	R	R	R	R	R	S
9. PI. 231128	R	R	R	R	R	R	R	R	R	-
10. PI. 231129	R	R	R	R	R	R	R	R	R	-

R = resistant
S = susceptible

Table 2. Distribution of Races of P. *oryzae* in the U. S.

Name of the State	Races									
	1	2	3	4	5	6	7	8	10	16
Arkansas		x	x		x	x				x
Louisiana	x	x	x	x	x	x	x	x	x	x
Texas			x			x		x		x
Mississippi										x
Florida	x									

4. Sources of Resistance to Blast.

One of the earliest reports of varietal tests in Japan, by Nakatomi (39), indicated that varieties from India, Philippines and Java were highly resistant. Since then, rice breeders in Japan have turned to introduced *indica* varieties as an important source of blast resistance to improve the susceptible *japonica* varieties.

Testing the reaction of certain species of the genus *Oryza* to blast infection, Kawamura (27) observed *Oryza sativa* L. and *O. cubensis* as susceptible and *O. latifolia* and *O. minuta* as resistant. He even crossed the susceptible *O. sativa* with *O. minuta* and found the F_1 progeny to be resistant like the resistant parent, thus indicating the possibility of introducing blast resistance from wild species.

Very recently Katasuya (26) reported studies on the reaction to blast of 92 strains belonging to 20 species of the genus *Oryza*. His results confirmed some of the reactions obtained by Kawamura (*loc cit*.). It was observed that some strains of *O. sativa f. spontanea*, *O. perennis* and other wild species were also found to be resistant to blast. Evidently some of the wild species which are somewhat closely related to the cultivated rice *O. sativa* appear to be important sources of blast resistance. The necessity of utilizing the resistance from wild parents will arise only when we exhaust all possible sources from cultivated varieties.

Genecological studies carried out by Matsuo (35), using a large number of cultivated rice varieties, revealed varietal differences in degree of infection to blast. He found varieties of plant type "A" (from Japan, Korea, Hopei and Africa) were susceptible, while varieties of plant type "B" (from Java, Sumatra, Philippines, Europe and America) and "C" (from India, Indochina and Formosa) were resistant. Resistance to these three groups was in the order of "C" type, "B" type, and "A" type.

Koyama (28) reported four introduced Japonica varieties, namely Reishiko, To, Chinkeishu and Yakei non-glutinous, as important sources of blast resistance. These resistant varieties were successfully used in transferring genes for resistance to susceptible commercial japonica varieties (Ito, 24).

In India, Padmanabhan et al. (51) listed Co. 4 from Madras, S. 67 from Mysore and Bhogjira 1 from West Bengal as resistant varieties. The blast resistant strains Co. 25, Co. 26, Co. 29 and Co. 30 from Madras State and strains 5352, 5392, 6517, 6522 from Andhra Pradesh, developed through hybridization and intensive selection, have derived their resistance from Co. 4, which is an outstanding resistant variety in South India.

Fernando et al. (11) reported six varieties which were recently bred in Ceylon, as resistant, while varieties that have been under cultivation for more than 15 years are highly susceptible, with the exception of Periavellai. Another variety, Murungakayan 302, was reported as a popular variety with high blast resistance. By using Murungakayan 302 as a resistant parent in a cross with Mas, a leading commercial variety, H. 4, was bred with high resistance to blast.

Stevenson _et al_. (62) listed three important sources for blast disease resistance in U. S. rice varieties. They are (1) P.E.I. 13056 (CI. 1344) from Formosa in 1905. (2) P.E.I. 31169 (CI. 1779) from Philippines in 1911. (3) Selections from commercial varieties.

For several years Atkins _et al_. (4) have been screening rice varieties by green house testing, confirmed by field grown nurseries, in order to discover new germ plasm for breeding blast resistant varieties. They observed that none of the varieties from the U.S. have resistance to all of the ten races so far known to occur in this country. However, several of the promising experimental varieties were found resistant to nine of the ten races, while others are resistant to eight races. Zenith, Nira, Gulfrose, Improved Blue Rose and Mo. R 500 were important sources of blast resistance among the U.S. varieties. Zenith has shown resistance to 13 out of 16 races so far discovered but is susceptible to three races, namely 1, 7 and 13. The rest of the varieties are resistant to more than 6 races. Thus sources of resistance to individual races were found in old and new U. S. varieties.

The results obtained from the cooperative blast resistant trials sponsored by F A O in various rice growing countries have indicated fruitful results. The well-known resistant varieties like Bengawan of Indonesia, S. 67 of India, Ramnad Str. 3 of the Philippines and Chainongyo 280 of Taiwan have proved their resistance all over the world (23).

Another line of promising field of disease resistance is irradiation breeding.

Lin *et al*. (33) established resistant lines from irradiated seeds of Taichung 65, a highly susceptible variety in Japan. They considered that blast resistance in their material was obtained "by induced polygenic mutations caused by irradiation".

MATERIALS AND METHODS

Six F_1 seeds of the cross 1709 X CI 9418 were supplied by Mr. N. E. Jodon, Agronomist, Rice Experiment Station, Crowley, Louisiana. The F_1 seeds were sown on February 16, 1961 in the green house at Baton Rouge and F_2 seeds were harvested on July 8, 1961. The F_2 seeds were planted in the green house at the Rice Experiment Station on July 28, 1961 and the pots were subsequently moved to Baton Rouge, where the plants were grown to maturity. F_3 seeds were harvested from individual F_2 plants on December 5, 1961.

The resistant parent, 1709, is a homozygous selection from the cross Rexoro-Red X 250 Magnolia. Rexoro-Red in turn, is a selection from a natural cross between local red rice and Rexoro. Rexoro was selected in 1926 from Marong-Paroc, a variety originally introduced from the Philippines in 1911. On the other hand, 250 Magnolia is a selection from the cross Lacrosse X Magnolia. The strain 1709 is an early maturing (100 days), fine grain type, with gold hulls and short awns.

The susceptible parent, CI 9418, is a selection from the following multiple cross.

		4-11-1-8	Blue Rose X Rexoro	
CI 9418	X			
		Rexoro X C 252 (Early segregate)	Rexoro X C 252 selection	Iola-Blue Rose X Shoemed-Fortuna

It matures in 120 days and is awnless with straw hull color.

Four F_1 plants of the cross 1709 X CI 9418 were maintained through vegetative propagation since July 1961 in the green house for testing their reaction to blast.

Before testing the hybrid material, the technique of inoculation of plants and evaluation for lesion types were standardized by conducting preliminary tests on 16 varieties and strains of known reaction. The two parents were also included in these preliminary tests. The reactions of the varieties and strains to races 1 and 6 were established and the lesion types were determined. The 16 varieties and strains used in this study were: Colusa, Caloro, Blue-Bonnet, Fortuna, Rexoro, Mo. R 500, Gulf Rose, Zenith, Nira, PI 180061, PI 201902, Blue Rose selection, Strain 1709, Strain I, Strain 5088 and CI 9418. Seeds of all varieties were obtained from the Rice Experiment Station, Crowley.

Four F_1 plants, 66 F_2 plants and 135 F_3 lines were tested for reaction to race 6 in three series. In each series of testing, the two parents were always included for comparison.

The reaction of the parents and the varieties Zenith and Nira to races 8 and 16 was also determined.

In a separate test the nature of reaction of Lacrosse to race 6 was also determined along with the resistant parent 1709 in an attempt to determine the source of the resistance present in the 1709 parent.

Finally several F_3 families whose reaction to race 6 had been determined were tested separately with races 8 and 16 to secure information as to whether the same gene or different genes are involved in governing resistance in 1709 to these three races.

Isolates of races 1, 6, 8, and 16 were supplied by Dr. John G. Atkins, Plant Pathologist, Rice-Pasture Experiment Station, Beaumont, Texas. The original isolates were transferred to tubes and petri dishes containing a 4% rice polish-agar medium. The culture medium for growing the blast fungus was prepared by mixing 40 grams of rice polish in 1000 ml. of distilled water. The mixture was cooked for 30 to 60 minutes at boiling temperature, and then strained through double cheese cloth. Finally the volume was brought back to 1000 ml. To this 16 grams of agar were added and dissolved by boiling. The culture medium was poured into test-tubes, plugged and then sterilized along with empty petri dishes in an autoclave at 17 lbs. pressure and 120°C. for 30 minutes.

Transfers from original isolates were made to slanted tubes and petri dishes containing the medium. The cultures were allowed to grow at room temperatures for 9-10 days before they were used for inoculating the rice seedlings. The cultures in the tubes were utilized as a source for further transfers, while the petri dishes were used for inoculating the seedlings. Sporulation of the fungus was periodically checked by mounting slides and examining under the microscope.

Three isolates of race 6 designated (59 T IE, D 136, D 73) and one isolate of each of races 1 (59 L 13), 8 (62 F 1) and 16 (61 L 4) were cultured. Since the sporulation was poor in isolates 59 T IE and D 136 of race 6, only D 73 was finally used in testing the hybrid material.

The rice seedlings were grown in galvanized iron flats (16" x 20") containing a mixture of river silt and sand. About 20 seedlings of each variety or F_3 line involved were sown in either one or two rows, thus sowing 5-10 lines in each flat. At any one planting time, a maximum of 58 lines and with the two parents were sown in 6 flats. The seedlings were top-dressed with a complete fertilizer 4-5 days before they were ready for inoculation. The seedlings were inoculated with spores of Piricularia oryzae when they had reached the second leaf stage. Prior to inoculation water was sprayed on the plants and the leaves were rubbed with wet fingers to remove the waxy surface. This was found to help in retaining the inoculum in a fine mist on the leaves. When the seedlings were sprayed without rubbing, free moisture formed on the leaves in large droplets.

In order to increase the effectiveness of the inoculations, the wetting and adhesive agents suggested by Anderson and Henry (2) were used. Two and a half grams of gelatin (adhesive agent) and 0.5 grams of sodium oleate (wetting agent) were dissolved in 1000 ml. of distilled water and kept as a stock solution.

The spores were harvested from the rice polish-agar plates by adding a few drops of the sodium oleate-gelatin solution and scraping the upper surface with a bent flat needle. Sufficient of the sodium oleate-gelatin solution was added and the mixture was stirred for 30 seconds in a waring blender to produce a uniform conidial suspension. Spore concentration in the resulting suspension was determined before inoculating the plants by examining a drop or two under the microscope.

Two or three petri dish cultures were used for every 100 ml. of sodium oleate-gelatin solution. One hundred ml. of this conidial suspension was sprayed on every two flats of seedlings. The seedlings were inoculated with a sprayer attached to a compressor or with a hand sprayer. The inoculated seedlings were placed inside a chamber for at least 24 hours, where the humidity was maintained at 100%. To ensure against escapes, the inoculation was repeated a second, and occasionally a third time 24-48 hours after the first inoculation.

The humidity chamber consisted of a plastic cover supported by a wooden frame over a deep wooden bench in the green house. The bottom of the bench was also provided with a plastic sheet to allow standing water to a depth of 2 inches. Under normal temperature conditions no special equipment for raising the humidity was used, since the required humidity was achieved by closing the chamber air-tight. The plants were kept covered with free moisture throughout the period inside the chamber by spraying with water at frequent intervals.

Flats of inoculated seedlings were usually left inside the humidity chamber for 8-10 days, after which they were moved to an open bench.

In scoring the reaction of the seedlings to the blast infection, the lesion types were considered as criteria. Six lesion types were recognized and adopted in the present study. These lesion classes were numbered 0, 1, 2, 3, 4 and 5 and are described in Table 3.

Lesion types 0, 1, 2, and 3 are considered as representing resistant reaction,while lesion types 4 and 5 are considered as indicating susceptible reaction.

Table 3. Descriptions of the Six Lesion Types Which Were Adopted in Classifying Plants of the Varieties and Hybrid Populations.

Lesion Type	Degree of Infection	Description of Infection
Type 0	Immune	No visible sign of infection.
Type 1	Highly resistant	Light brownish pinpoint flecks on the leaves.
Type 2	Resistant	Brownish specks darker in color and larger in number.
Type 3	Moderately resistant	Small brownish lesions with grey center, not developing further.
Type 4	Susceptible	Elliptical dark brown lesions with enlarging greyish white center, tending to coalesce.
Type 5	Highly susceptible	Large lesions, rapidly extending and frequently causing early death of the entire leaf.

RESULTS

1. Preliminary tests with 16 varieties and strains of known reaction to races 1 and 6.

The first experiment was carried out to evolve suitable techniques for obtaining reliable results from infection of blast desease on rice seedlings. Sixteen varieties and strains with known reactions to races 1 and 6 were included in these preliminary tests.

In the first test, carried out during April, 1962, seedlings in flats were inoculated in the 3rd leaf stage and kept in the high humidity chamber for 12 hours. An electrically operated atomizer was used to maintain high humidity inside the chamber. Only moderate infection developed and several plants escaped infection. Also, a part of the young seedlings were damaged by steam from the atomizer. Because of these complications the first test was not considered successful and readings on reaction of the varieties to blast were not taken.

In the second test, conducted in May, 1962, the seedlings were inoculated in the second leaf stage. Two inoculations were made with a 24 hour interval between. In this test the atomizer was not used. Instead, 1-2 inches of standing water was kept in the bottom of the chamber and it was closed air tight to obtain 100% humidity. A thin film of free moisture was thus obtained on the leaves for about 12 hours to enable the spores to germinate and establish infection.

Undue rise in temperature, particularly during bright sunny days, was prevented by frequently opening the chamber and spraying water on the seedlings. The flats were kept in the chamber for more than four days.

Heavy infection was obtained this time; however, a few escapes were observed 10 days after the 2nd inoculation. Hence, the seedlings were inoculated a 3rd time in the 3rd leaf stage and kept inside the chamber. A satisfactory infection was observed following the 3rd inoculation and the seedlings were classified one week afterward. The final reactions noted in this test are presented in tables 4 and 5 for races 1 and 6, respectively. In both of these tables plants, classified under lesion types 0 to 3 were considered as resistant while plants with lesion types 4 and 5 were considered as susceptible.

Data presented in table 4 show that the reactions of 13 out of the 16 varieties and strains to race 1 were identical with their previously known reactions. Results with the other three varieties, namely Fortuna, Nira and strain 1, were not in full agreement with their previously reported reactions. Fortuna and Nira had been reported to be susceptible and strain 1 to be resistant to race 1. However, in the test conducted here both resistant and susceptible plants occurred in each of these varieties. Thus, the classification of these three was inconclusive and uncertain.

It may also be seen from table 4 that a single resistant plant occurred in each of the susceptible varieties Rexoro and strain 1709. These, resistant plants were considered as representing mechanical mixtures.

Considering the varietal reaction to race 6, it may be seen from table 5, that 13 out of 16 varieties and strains tested showed reactions which are in complete agreement with that previously reported. In this series, again, there were three exceptions, namely Bluebonnet, Fortuna and strain 1. All three had been reported to be susceptible but were found to contain both resistant and susceptible seedlings in the present studies. Their reaction was inconclusive. The single resistant plant observed in Caloro and in CI 9418 are considered here, also, as mechanical mixtures.

From these results it may be concluded that, over all, the techniques used in the present studies are reasonably reliable. In 26 of the 32 cases tested, the present results were in complete agreement with those reported by other workers. In the 6 exceptions, both resistant and susceptible plants were found in varieties involved. Four of the six cases involved the varieties Fortuna and strain 1. In no case did a variety or strain react in the present studies in a completely contradict manner to that reported by other workers. Consequently, it is felt that the disagreement with previously reported results is not of a serious nature.

It may also be mentioned that occasionally resistant type of lesions 1, 2, and 3 were observed along with susceptible lesion types 4 and 5 on the same leaf blade. Such plants were classified on the basis of the highest lesion type and were designated susceptible. In some cases secondary infection developed on new leaves a week after inoculation, especially in susceptible plants.

Table 4. A Comparison of the Present and Previously Known Reactions of 16 Varieties and Strains to Race 1 of *Piricularia oryzae*.

Variety or Strain	Lesion Types: Resistant 0	1	2	3	Susceptible 4	5	Present Reaction	Previously Reported Reaction*
Colusa	17			1			R	R
Caloro	19						R	R
Mo. R-500			6	10			R	R
PI 201902	18						R	R
Blue Rose Selection	16	1					R	R
Bluebonnet					9	9	S	S
Rexoro			1		9	8	S	S
Gulfrose					4	13	S	S
Zenith					6	14	S	S
PI 180061					13	8	S	S
Strain 1709				1	12	4	S	S
Strain CI 9418					13	7	S	S
Strain 5088					6	13	S	S
Fortuna			3	5	7	3	I	S
Nira		3	3	3	7		I	S
Strain 1		4	11	5	2		I	R

R = Resistant
S = Susceptible
I = Inconclusive reaction
Strain 1 = Rec 13 X long grain dwarf

*Based on unpublished paper by J. G. Atkins and N. E. Jodon entitled "Aspects of Breeding Rice for Resistance to Diseases, Particularly Blast (*Piricularia oryzae*)."

Table 5. A Comparison of the Present and Previously Known Reactions of 16 Varieties and Strains to Race 6.

Variety or Strain	Lesion Types: Resistant 0	1	2	3	Susceptible 4	5	Present Reaction	Previously Known Reaction*
Mo. R 500	17						R	R
Gulfrose	13	3					R	R
Zenith		20					R	R
Nira		17	3	1			R	R
PI 180061	12	1	6				R	R
PI 201902		17	3				R	R
Blue Rose Selection	3	3	9	5			R	R
Strain 1709		12	4				R	R
Strain 5088	15	4	2				R	R
Colusa					11	9	S	S
Caloro				1		17	S	S
Rexoro					10	8	S	S
Strain CI 9418				1	10	7	S	S
Bluebonnet			8	4	4		I	S
Fortuna			6	4	8		I	S
Strain 1				5	9	5	I	S

R = Resistant
S = Susceptible
I = Inconclusive
Strain 1 - Rec 13 X long grain dwarf

*Based on unpublished paper by J. G. Atkins and N. E. Jodon entitled "Aspects of Breeding Rice for Resistance to Diseases, Particularly Blast (*Piricularia oryzae*)."

2. Reaction of the Parent Strains 1709 and CI 9418 to Races 1, 6, 8, and 16.

The varieties and strains listed earlier in tables 4 and 5 included the parents of the hybrids used in studies of inheritance of reaction to several races of blast. These parent strains are 1709 and CI 9418. It may be seen from table 4 that both of the parents were susceptible to race 1. Consequently, inheritance of resistance to this race could not be investigated. On the contrary, the parents differed for reaction to race 6, as observed in table 5. The data show that strain 1709 is resistant while CI 9418 is susceptible.

In a later experiment, the reactions of the parent strains 1709 and CI 9418 to races 8 and 16 were determined, in addition to the races 1 and 6 already tested. The reaction of the parent strains to races 1, 6, 8 and 16 are presented in table 6.

It may be seen from table 6 that strain 1709 was resistant to races 6, 8, and 16 but susceptible to race 1. The other parent, CI 9418, showed susceptibility uniformly to all 4 races. Thus, it is seen that the two parents differed in their reaction to three out of the four races tested. In all cases, 1709 was resistant and CI 9418 was susceptible. This evidence provides a basis for studying inheritance of reaction to the three races 6, 8, and 16 in the cross of 1709 with CI 9418.

In order to investigate the possible source of the blast resistance present in strain 1709, the reactions of three other varieties known to be resistant to blast, namely Zenith, Nira, and Lacrosse, were determined in this study.

The results furnished in table 6 show that Zenith was resistant to races 6 and 8, but susceptible to race 1, like 1709. It however, differed appreciably from 1709 with respect to its reaction to race 16. On Zenith, the infection was more severe than on 1709 but did not approach any of the susceptible lesion types. If the reactions of 1709 and CI 9418 are considered as resistant and susceptible, respectively, then Zenith appears to be moderately resistant to race 16.

Like 1709 and Zenith, Nira was resistant to races 6 and 8, but it differed from 1709 in its reaction to race 16. Because of its reaction similar to Zenith, Nira was classified as moderately resistant. Its reaction to race 1 was inconclusive due to the occurrence of both susceptible and resistant plants.

Lacrosse was tested only for reaction to race 6. It did not show either typical resistant or susceptible lesions. Dark brownish flecks developed on the 4th day after inoculation, which quickly enlarged, resulting in slight discoloration of the leaves. The reaction of Lacrosse also was, therefore, regarded as moderately resistant.

The reaction of Zenith, Nira and Lacrosse to these races gave a possible clue to the source of resistance of the 1709 strain. This will be dealt with in detail under discussion.

Table 6. Reaction of 1709, CI 9418, Zenith, Nira and Lacrosse to Different Races of Blast.

Variety or Strain	Reaction to Race 1	6	8	16
Strain 1709	S	R	R	R
Strain CI 9418	S	S	S	S
Zenith	S	R	R	MR
Nira	I	R	R	MR
Lacrosse	-	MR		

R = Resistant
S = Susceptible
I = Inconclusive reaction
MR = Moderately resistant

3. Reaction of F_1, F_2, and F_3 Populations from the Cross 1709 X CI 9418 to Race 6.

The hybrid material of the cross 1709 X CI 9418 was tested in the F_1, F_2, and F_3 generations. The first material to be tested consisted of 56 F_3 lines, which were inoculated with race 6 on June 14, 1962. Surprisingly, no infection developed despite the earlier success with the technique on varieties. A microscopic examination of mounts from the cultures of the fungus revealed the presence of very few spores. Sporulation in later cultures of the fungus was found to be extremely poor, although there was abundant growth of mycelium. It was found, subsequently, that high temperature in June inhibited sporulation of the fungus. Due to high room temperatures in June, July and August the inoculation tests were suspended and were resumed in October after making certain that conditions were favorable for sporulation.

The F_1, F_2, and F_3 populations were tested for their reaction to race 6 during the months of October and November. Symptoms of blast developed on seedlings of the parents and the hybrid populations in about five days after inoculation and the final classification for lesion types was made in about 10 days. The accuracy of classification was measured mainly by the reaction of the parent strains 1709 and CI 9418.

The observed reactions of the parents, four F_1 and 66 F_2 plants are furnished in table 7.

It may be seen from this table that the resistant parent strain, 1709, showed infection of lesion type 1 in a majority of the plants. A few plants with lesion types 2 and 3 also occurred. The plants of the susceptible parent, CI 9418, showed lesion types 4 and 5, but a majority of the plants had the former lesion type. The few plants that showed lesion type 5 were not, however, completely killed. The single plant that had lesion type 3 (resistant class) is questionable. This plant was assumed to be a mechanical mixture. It should also be mentioned that CI 9418 showed not only leaf blade infection but also infection on ligule, leaf sheath and leaf margin. Therefore, in classifying the hybrid plants these features were also taken into account.

The reaction of the four F_1 plants was similar to the resistant parent 1709, showing lesion type 1. This indicates that the blast resistance of parent strain 1709 is dominant to susceptibility in this cross.

A total of 66 F_2 plants were tested. The F_2 data presented in table 7 show a continuous segregation covering the complete range of the parents, i.e., lesion types 1 to 5. However, despite the continuous nature of the F_2 it did not show a normal distribution. There was a tendency for the F_2 to form a bimodal distribution, with modes in the 1 and 4 lesion classes. Based on the performance of the parents, the F_2 plants were divided into two main classes. One of them included the lesion types 1, 2, and 3, corresponding with the reaction of the 1709 parent and was designated as resistant. The second class included plants of lesion types 4 and 5, corresponding with the reaction of the CI 9418 parent and was designated as susceptible.

A perusal of the F_2 data shows a ratio of 47 resistant to 19 susceptible plants. The ratio shows a good fit to 3 resistant: 1 susceptible, with a probability of 0.70-0.50. The number of resistant and susceptible plants also shows a good fit to a ratio of 9:7, with a probability of 0.30. Since the F_2 data fit both 3:1 and 9:7 ratios, it was not possible to determine from it whether one or two genes were involved. However, the closer fit to a 3:1 ratio suggested that the parents differed by only one pair of genes.

Comparable to F_2 data, the reactions of the F_3 families were also separated into 2 classes. Plants with lesion types 0, 1, 2, and 3 were classed as resistant and plants with lesion types 4 and 5 as susceptible. A perusal of the data presented in table 8 shows that the 135 families can be brought under the following five groups.

1. Twenty-nine families in which all plants were resistant.
2. Three families in which all plants were resistant except a single plant in each.
3. Thirty eight families in which all plants were susceptible.
4. Two families in which all plants were susceptible except for one or two resistant plants.
5. Sixty three families in which several plants are resistant and several plants are susceptible.

The first and second groups were similar in behavior. These two groups of families were combined and considered as homozygous resistant. The third and fourth groups, having only or almost entirely susceptible plants, were combined and considered as homozygous susceptible. The fifth group, having several resistant and several susceptible plants, were considered as heterozygous. This led to the conclusion that 32 families were homozygous resistant, 63 families were segregating and 40 families were homozygous susceptible. This ratio of 32:63:40 is a good fit to a ratio of 1 homozygous resistant: 2 segregating: 1 homozygous susceptible with a probability of 0.50-0.30. Though the homozygous susceptible class is slightly in excess and homozygous resistant and heterozygous classes are slightly deficient, the deviation is probably due to chance. Thus the reaction of F_3 families confirmed the assumption that a single gene for resistance to race 6 is involved in this cross.

As pointed out earlier, three F_3 families, 90, 91, and 124, which were considered to be homozygous resistant, contained one susceptible plant each. Since extreme care was used in harvesting and threshing the F_2 plants, it is not probable that these susceptible plants resulted from mechanical mixture. The most probable explanation for them is the presence of modifying genes from the susceptible CI 9418 parent. It is assumed that these susceptible plants were homozygous for the major gene for resistance from 1709 but showed a susceptible reaction because of the presence of minor genes, derived from CI 9418, which modified the effect of the major gene.

Similarly modifying genes probably account for the occurrence of one or two resistant plants in families 36 and 64, which were assumed to be homozygous susceptible for the major gene.

The assumption of modifying genes will also account for the fact that in five families, 20, 22, 24, 113 and 130, the number of susceptible plants exceeded the number resistant. Some of the susceptible plants in these families probably contained the major gene for resistance but were influenced in their reaction by modifiers also present.

From the above results it may be concluded that the resistance to race 6 in parent 1709 is governed by a single dominant major gene with a modifier gene or genes influencing the resistance.

It may also be pointed out that plants more susceptible than the susceptible parent were observed in the F_2 and F_3 populations. The data presented in table 7 show that four F_2 plants with lesion type 5 were completely killed while the three plants of the susceptible parent with lesion type 5 were not killed. In conformity with the F_2 observations, several homozygous susceptible F_3 families were observed in which all plants were killed. In families 73, 74 and 88, all plants with lesion type 5 were killed. These observations are indicative of a possible gene interaction involving modifier genes contributed by the resistant parent.

Table 7. Reaction of Parents F_1 and F_2 Population to Race 6.

Population	Number of Plants With Lesion Types 0	1	2	3	4	5	Diseased Class R* (0+1+2+3)	S** (4+5)	Total
1709		11	3	2			16		16
CI 9418				1	14	3	1	17	18
F_1		4					4		4
F_2		25	9	13	15	4	47***	19***	66

* = Resistant
** = Susceptible
*** = Probability 3:1 - 0.70 - 0.50
9:7 - 0.30

Table 8. Reaction of Parents and 135 F_3 Families From the Cross 1709 X CI 9418 to Race 6.

Parents and F_3 Lines	Number of Plants With Lesion Types						Disease Classes		Genotype
	0	1	2	3	4	5	R (0+1+2+3)	S (4+5)	
1709		11	3	2			16		
CI 9418				1	14	3	1	17	
6		19					19		HR
13		20	2				22		HR
19		19	1				20		HR
25		21	1	1			23		HR
26		15	4	2			21		HR
29		16	4				20		HR
31		18		1			19		HR
33		9	12	1			22		HR
34		18	4				22		HR
39		8	5				13		HR
57		17	3	1			21		HR
60		14	6				20		HR
90		17		3		1	20	1	HR
91		18			1		18	1	HR
93		15		6			21		HR
95		16		4			20		HR
97		15	2	3			20		HR
99		20		1			21		HR
102		16		1			17		HR
109		20					20		HR
111		15		4			19		HR
112		10	1	5			16		HR
114		12	2	5			19		HR
115		13	2	6			21		HR
119		17		4			21		HR
123		10	9	2			21		HR
124		13	1	6	1		20	1	HR
133		14	1	2			17		HR
137		8		5			13		HR
142		10	5	4			19		HR
143		17		2			19		HR
144		6	9	3			18		HR
2		14			5	1	14	6	H
4		14			3	1	14	4	H
7		12	5		5		17	5	H
9		15	1		4	1	16	5	H
10		10	2	1	4	2	13	6	H
15		15			2	3	15	5	H
16		15			5		15	5	H

Table 8. (Continued)

Parents and F_3 Lines	Number of Plants With Lesion Types 0	1	2	3	4	5	Disease Classes R (0+1+2+3)	S (4+5)	Genotype
21		16			3	2	16	5	H
27		13			7	1	13	8	H
28		14	1		5		15	5	H
30		13				7	13	7	H
32		14			5	3	14	8	H
35		2	5	5	6	2	12	8	H
40		14	1	1	4	2	16	6	H
41		17			3	2	17	5	H
42		15		1	3	2	16	5	H
43		7	2	1	5	3	10	8	H
48		10	1		4		11	4	H
50		12	3		3	2	15	5	H
52		15			3	4	15	7	H
61		10	6		4	1	16	5	H
68		7	3	5	4	1	15	5	H
69		9	3		1	7	12	8	H
70		3	4	7	2	4	14	7	H
71		5	6	2	3	1	13	4	H
72		11	2	2	2	5	15	7	H
76		5		8	2	2	13	4	H
77		8		3	2	6	11	8	H
79		5		3	4	1	8	5	H
80		14	1	3	1	3	18	4	H
81		8				3	8	3	H
82		11	1	4	5	2	16	7	H
83		12	2	2	3	3	16	6	H
86		17			2	4	17	6	H
92		10			3	4	10	7	H
96		13	1	1	2	5	15	7	H
98		6	6		2	8	12	10	H
101		10		3	5	1	13	6	H
103		10	3		5	3	13	8	H
105		12		3	2	3	15	5	H
106		8		4	2	4	12	6	H
108		11		1	4	4	12	8	H
117		15		1	2	2	16	4	H
120		7		1	1	5	8	6	H
121		7	1	4		4	12	4	H
122		9	2	7	1	3	18	4	H
126		11	1	3	3	1	15	4	H
127		1	13		2	2	14	4	H
128		13		2	5		15	5	H

Table 8. (Continued)

Parents and F_3 Lines	Number of Plants With Lesion Types						Disease Classes		Genotype
							R	S	
	0	1	2	3	4	5	(0+1+2+3)	(4+5)	
129		9	2	2	4		13	4	H
131		11	1		4		12	4	H
132		10	1		4	2	11	6	H
135		3	1	3	4	2	7	6	H
139			6	4	2	2	10	4	H
141		1	5	7	2	2	13	4	H
146		12	2	2	4	1	16	5	H
20		10			7	5	10	12	H
22		6	2		5	5	8	10	H
24		8		1	3	9	9	12	H
55		6	3	2	8	3	11	11	H
104		10			4	6	10	10	H
113		7		3	11	1	10	12	H
130		1	4	4	10		9	10	H
1					8	11		19	HS
5					11	10		21	HS
8					12	8		20	HS
14					14	8		22	HS
17					6	13		19	HS
18					9	11		20	HS
23					10	10		20	HS
36				1	12	9	1	21	HS
38					9	6		15	HS
44					20	1		21	HS
45					9	12		21	HS
47					8	12		20	HS
49					5	16		21	HS
51					12	9		21	HS
56					10	4		14	HS
62					12	6		18	HS
63					6	13		19	HS
64		2			7	9	2	16	HS
67					1	20		21	HS
73						19		19	HS
74						21		21	HS
75					4	17		21	HS
78					11	9		20	HS
84					1	20		21	HS
85					7	11		18	HS
87					19			19	HS
88						22		22	HS
89					5	14		19	HS

Table 8. (Continued)

Parents and F_3 Lines	Number of Plants With Lesion Types						Disease Classes R	S	Genotype
	0	1	2	3	4	5	(0+1+2+3)	(4+5)	
94					2	13		15	HS
100					3	16		19	HS
107					10	10		20	HS
110					5	16		21	HS
116					2	18		20	HS
118					10	9		19	HS
125					20			20	HS
134					15	4		19	HS
136					17	3		20	HS
138					12	6		18	HS
140					10	6		16	HS
145					12	4		16	HS

HR = Homozygous resistant
HS = Homozygous susceptible
H = Heterozygous
R = Resistant
S = Susceptible

4. <u>Reaction of Selected F_3 Lines to Races 8 and 16.</u>

After testing with race 6 there was sufficient seed of some F_3 families for further tests. Since the parent strains 1709 and CI 9418 differed also for their reaction to races 8 and 16 (table 6), lines of known reaction to race 6 were tested for these races.

Seedlings from 14 F_3 families homozygous resistant to race 6, 18 segregating families, and 18 homozygous susceptible F_3 families and the two parents were inoculated with race 8. The data showing the reaction of the 50 F_3 lines to race 8 in comparison with their reaction to race 6 are presented in table 9.

It is evident from this table, that the reaction of the parents to race 8 is in agreement with their reaction to race 6. The 1709 parent was resistant to both races while CI 9418 was susceptible to both.

The first group of 14 F_3 families, which were homozygous resistant to race 6, contained only plants which were resistant to race 8 with the exception of two families, 29 and 102, which had one susceptible plant in each. Consequently, these 14 F_3 families were considered also to be homozygous for resistance to race 8.

The second group of 18 families that segregated for reaction to race 6 also underwent segregation for reaction to race 8, showing approximately 3/4 resistant and 1/4 susceptible as expected if the parents differed by one gene pair. However, in this group, family 70 is an exception. In this family there were 6 resistant and 7 susceptible plants.

In the third group of 18 families that were homozygous susceptible to race 6, fifteen families showed all susceptible plants. In two additional families, namely 8 and 107, all plants were susceptible except for a single resistant plant in each. Thus, 17 of the 18 families which were homozygous for susceptibility to race 6 could also be considered definitely homozygous for susceptibility to race 8. In the other family, 23, there were 14 susceptible and four resistant plants out of a total of 18. The proper classification of this family for reaction to race 8 is uncertain. It would not normally be considered to be segregating because of the predominance of susceptible plants.

Thus, it seems in general that the reaction of the 50 individual F_3 families was the same to both races. These results therefore indicate that a single gene in 1709 conditions resistance to both races 6 and 8.

The occurrence of a few susceptible plants in apparently homozygous resistant lines and a few resistant plants in apparently homozygous susceptible lines can, as was suggested for reaction to race 6, be explained best by assuming the presence of minor genes which modify the expression of the major pair of genes. If we assume the presence of modifier genes, it is probable that the susceptible plants in a homozygous resistant line were homozygous for the major gene but showed susceptible reaction due to the presence of minor genes from the CI 9418 parent. Similarly, modifier genes from 1709 would also account for the occurrence of resistant plants in a homozygous susceptible family.

The two families, 29 and 102, which had one plant in each that was susceptible to race 8 were both completely resistant to race 6. Further more, families 8, 23 and 107, with a few plants in each showing resistance to race 8, had been completely susceptible to race 6. Thus, it appears probable that the set of modifiers which seemed to influence reaction of the major gene to race 8 was different from the set that influenced reaction of the same major gene pair to race 6.

The same set of 50 selected F_3 lines tested for reaction to race 8, plus three more, were also tested with race 16. The data are presented in table 10. The results show that out of 15 families that were homozygous resistant for race 6, ten families had all resistant plants for race 16. Four of the other five families, namely 9, 95, 97, and 102 had two or three susceptible plants each. These families would be normally classified as segregating. However, there is a possibility that a part or all of these four families were homozygous resistant for a major gene, with the susceptible plants caused by modifiers. The other family, 93, showed a somewhat peculiar behavior. There were 13 susceptible and five resistant plants. The genotype of this line is, therefore, difficult to determine.

In the second group of 21 families, which had been classified as segregating for race 6, both resistant and susceptible plants occurred. However, line 16, though, it could be segregating, had only one resistant plant. As per the classification used for races 6 and 8, this would be considered as homozygous resistant.

Out of the 17 families which had been classified as homozygous susceptible to race 6, 12 families contained all susceptible plants, which indicates that they were also homozygous susceptible to race 16. Five families, 20, 38, 44, 63, and 88, had only one or two resistant plants and were also regarded as homozygous susceptible. Thus 16 out of the 17 families showed similar reaction for races 6 and 16. One family, 87, which had 11 susceptible and 6 resistant plants could not be regarded as homozygous susceptible due to the occurrence of large number of resistant plants. Its behavior does not fit in to any class that would normally be classified as homozygous susceptible or segregating. Thus the reaction of this line is uncertain.

Considering the reaction of all of the 53 families together, it may be observed that 46 of the families showed reasonably close agreement in reaction to races 6 and 16. The lack of agreement in the other seven families cannot be accounted for in any logical manner by assuming a different major gene for reaction to race 16. Therefore the results can best be explained by assuming that resistance to race 16 is governed by the same major gene as that for race 6, but the reaction to race 16 seems to have been influenced more strongly by modifiers.

It may be concluded from these results that, basically, one major dominant gene governs the reaction to races 6, 8 and 16. But the reaction of each race is influenced by different sets of modifier genes.

Table 9. Reaction of Selected F_3 Lines to Race 8 in Comparison With Their Reaction to Race 6.

Parents or F_3 Line	Number of Plants With Lesion Types 0	1	2	3	4	5	Disease Classes R (0+1+2+3)	S (4+5)	Genotype For Race 8
	Group I. Homozygous resistant to race 6								
Strain 1709		14	2	1			17		
CI 9418					11	2		13	
6		17		1			18		HR
25		19					19		HR
26		19					19		HR
29		17			1		17	1	HR
31		19					19		HR
33		21					21		HR
34		22					22		HR
60		19		1			20		HR
91			14	2			16		HR
93			12	1			13		HR
95		4	1				5		HR
99		12	4				16		HR
102			12		1		12	1	HR
111			18				18		HR
	Group II. Segregating for reaction to race 6								
7		9	1		3		10	3	H
9		10	2	1	5	1	13	6	H
15		6	7	2	4		15	4	H
16		10	5	1	4		16	4	H
21		11	1	2	3	3	14	6	H
28		14	3	1	2	2	18	4	H
40		8	5		3	3	13	6	H
50		15		2	3	1	17	4	H
70			3	3	1	6	6	7	H
71		5	4	8	4		17	4	H
80		10	4		4		14	4	H
83			8	1	4		9	4	H
86		11	5	1		3	16	3	H
96		13	2		1	3	15	4	H
98		12			1	6	12	7	H
106		8	7		5		15	5	H
121			10	2	4	1	12	6	H
122		11	5		2	4	16	6	H

Table 9. (Continued)

Parents or F_3 Line	Number of Plants With Lesion Types						Disease Classes		Genotype for Race 8
	0	1	2	3	4	5	R (0+1+2+3)	S (4+5)	
Group III. Homozygous susceptible to race 6									
5						19		19	HS
8			1		15	2	1	17	HS
18						19		19	HS
22					7	7		14	HS
23			1	4	11	2	5	13	
36						17		17	HS
74						20		20	HS
75					12	4		16	HS
88						21		21	HS
100					1	16		17	HS
107				1		11	1	11	HS
116					12	5		17	HS

HR = Homozygous resistant
HS = Homozygous susceptible
H = Heterozygous
R = Resistant
S = Susceptible

Table 10. Reaction of Selected Homozygous and Segregating F_3 Lines to Race 16 in Comparison with Their Reaction to Race 6.

Parents or F_3 Line	Number of Plants With Lesion Types						Disease Classes		Genotype for Race 16
	0	1	2	3	4	5	R (0+1+2+3)	S (4+5)	
	Group I. Homozygous resistant to race 6								
1709			17	2			19		
CI 9418						16		16	
6		3	16				19		HR
25			14	6			20		HR
26		2	16	1			19		HR
29			22				22		HR
31			20	2			22		HR
33			15	3			18		HR
34		1	17	4			22		HR
60			12	5			17		HR
91			13	5	1	1	18	2	HR
93			1	4	4	9	5	13	
95			2	8	2		10	2	HR
97			9	8		2	17	2	HR
99		1	17				18		HR
102			4	2		3	6	3	HR
111			18	3			21		HR
	Group II. Segregating for reaction to race 6								
7		7	4	3		3	14	3	H
9		6	7	4		2	17	2	H
15			9	4		8	13	8	H
16		2	15	3		1	20	1	H
21			10	1	1	8	12	9	H
28		2	10	3	2	5	15	7	H
40		1	8	3	1	6	12	7	H
50			17	1		3	18	3	H
70			10	5		5	15	5	H
71		5	6	2	5		13	5	H
80		2	9	4		4	15	4	H
83		2	12	2	2	3	16	5	H
86		3	9	1	3	1	13	4	H
92			4	3		2	7	2	H
96		2	8	5		3	15	3	H
98			13	3	1	4	16	5	H
101			7	8	1	2	16	2	H
105			6	6	2	8	12	10	H

Table 10. (Continued)

Parents or F_3 Line	Number of Plants With Lesion Types 0	1	2	3	4	5	Disease Classes R (0+1+2+3)	S (4+5)	Genotype for Race 16
106			5	10		5	15	5	H
121		1	5	6		2	12	2	H
122			5	7	5	3	12	8	H
	Group III. Homozygous susceptible to race 6								
8						19		19	HS
18						21		21	HS
20			2			17	2	17	HS
23					1	18		19	HS
36					1	20		21	HS
38			1	1		12	2	12	HS
44				1		16	1	16	HS
45					1	17		18	HS
49						18		18	HS
51					1	10		11	HS
63				2		16	2	16	HS
74					1	20		21	HS
75						18		18	HS
87				6	5	6	6	11	
88				2	1	17	2	18	HS
100					2	17		19	HS
107					2	15		17	HS

HR = Homozygous resistant
HS = Homozygous susceptible
H = Heterozygous
R = Resistant
S = Susceptible

DISCUSSION

Studies reported in this dissertation have indicated that in the cross between strain 1709 and CI 9418, a single major dominant gene in 1709 was effective in providing resistance to races 6, 8 and 16 of _P. oryzae_. It was also evident that several modifier genes influenced the effect of the major gene.

Inheritance of blast resistance was investigated by several workers in the past (6, 14, 18, 21, 38, 39, 44, 55, 59, 61). Most of them observed that resistance to blast is governed by one, two or three pairs of dominant genes. Occasionally blast resistance was also reported to be recessive (61). Only a few workers have alloted symbols to the genes for resistance and no systematic procedure was followed in such symbolization. Okada _et al_. (Nagai 38) postulated three dominant genes with additive effects for resistance to blast disease and they designated them as R_1, R_2 and R_3. Oka _et al_. (44) observed one dominant gene which governed resistance for blast in a cross between _indica_ and _japonica_ rice varieties. The gene was assigned the symbol Bt. Japanese workers observed that resistance of certain new Japanese varieties is due to a single dominant gene which they called Pi (21). Thus there is a diversity in gene symbolization for blast resistance. The International Rice Commission in 1959 recommended a list of gene symbols for rice.

In this list, the symbol recommended for genes governing resistance to *Piricularia oryzae* is "Pi". The major gene detected in the present study in strain 1709 is, therefore, provisionally designated as Pi_1. It is not known whether the Pi_1 carried by 1709 and the Pi referred to by Japanese workers are the same or are different. This will require further investigation.

The results obtained by other workers in the past were based on studies carried out under natural infection in the field or under green house conditions involving the use of isolates of the fungus whose identity as physiologic races had not been determined. It appears therefore, that the results of the present study provide the first information on inheritance of resistance to individual races of rice blast.

The present study also provides information (1) that the inheritance of resistance to individual races of blast is probably monogenic, (2) that a single gene may govern resistance to more than one race and (3) that modifier genes have considerable influence on the expression of blast resistance to individual races.

An effective breeding program for development of blast resistant strains of rice requires information on available sources of resistant genes. Knowledge of the source of the gene "Pi_1" carried by 1709 should be of value. The pedigree of 1709 shows that it was derived through hybridization involving Rexoro, Lacrosse, Magnolia and red rice. Rexoro and Magnolia are known to be susceptible to race 6 from the studies of other workers. In the present studies

Lacrosse was moderately resistant to this race. Therefore, it seems probable that none of these varieties contributed the gene "Pi" to strain 1709. It is known from previous work that Zenith and Nira are resistant to race 6. However, the present studies have shown that Zenith and Nira, though resistant to races 6 and 8, differed appreciably from 1709 with respect to their reaction to race 16, being only moderately resistant. Thus it is unlikely that Zenith or Nira contributed the gene for resistance. The source of resistance in 1709 is thus uncertain.

Success in breeding disease resistant varieties is dependent on the production of varieties that are otherwise agronomically suitable also. In this respect, it is interesting to note that 1709, besides being resistant to at least three races of blast, possesses several desirable characteristics, such as early maturity (100 days), short plant height, long grain, easy threshing and good quality. Therefore, it is evident that 1709 should prove to be a useful parent in future blast breeding programs.

The fact that one gene governs resistance to several races is important in breeding for blast resistance. It should be relatively simple to transfer resistance to commercial varieties when it is controlled by a single dominant gene as in 1709. However, the occurrance of some susceptible plants in apparently homozygous resistant lines in these studies indicates that minor genes have considerable effect on the expression of blast resistance. The tendency for the disturbance of segregation within and among some

F_3 families may make it somewhat difficult to isolate homozygous resistant types. However, progeny testing in F_3 and subsequent generations and isolating desired homozygous types for major and minor genes should prove effective.

Although the backcross method is being increasingly employed in breeding blast resistant rice varieties in Japan, the pedigree method might be more desirable, particularly when the resistant parent is agronomically suitable and when resistance is partially influenced by modifier genes.

The results of the present studies also indicated that simple and inexpensive green house tests may be successfully used to eliminate susceptible lines in the early segregating generations. Where the resistance in the seedling stage corresponds with resistance to neck-rot the breeding problem will be further simplified.

SUMMARY

The hybrid material of the cross of strain 1709 X CI 9418 was tested for reaction to race 6 in F_1, F_2, and F_3 generations. Selected homozygous and heterozygous families whose reaction to race 6 had been determined, were also tested with races 8 and 16.

The tests were performed during the spring and fall of 1962 in the green house.

Preliminary tests with 16 varieties and strains for reaction to races 1 and 6 showed good agreement with those reported by previous workers, except for two or three varieties whose reactions were inconclusive. Thus the techniques used in the present study were reasonably reliable.

The two parent strains differed in their reaction to races 6, 8 and 16, with strain 1709 resistant and CI 9418 susceptible to all 3 races. Both parents were susceptible to race 1.

The reaction of the four F_1 plants to race 6 was similar to the reaction of the resistant parent, thus indicating that resistance is dominant to susceptibility in the cross 1709 X CI 9418.

The observed reaction of 66 F_2 plants gave a good fit to a ratio of 3 resistant:1 susceptible showing thereby that the parents were differentiated by a single gene pair. The major dominant gene found in 1709 was provisionally designated as Pi_1.

An analysis of the genotypes of 135 F_2 plants was made by progeny tests of F_3 families from each. A good fit was obtained to a ratio of 1 homozygous resistant:2 segregating:1 homozygous susceptible. This confirms the assumption that resistance is conditioned by a single dominant major gene.

The occurrence of a few susceptible plants in homozygous resistant lines and a few resistant plants in homozygous susceptible lines for reaction to race 6 provided evidence for the presence of other genes which modify the expression of the major gene pair.

Fifty to fifty three selected F_3 lines whose reactions to race 6 had been determined were also tested for their reaction to race 8 and 16. A reasonably close agreement in their reactions to both races were obtained, indicating that resistance to races 6, 8 and 16 is associated. Basically one major dominant gene appears to govern resistance to all the three races. But they seem to differ from each other by having independent sets of modifier genes.

Because of the complex pedigree of strain 1709, the exact source of resistance carried by strain 1709 could not be determined.

The occurrence of a few individual F_2 plants and a few F_3 families which are more susceptible than the susceptible parent is indicative of a probable gene interaction, especially due to the minor genes contributed by the resistant parent.

The fact that on susceptible seedlings both susceptible and resistant types of lesions usually occur on the same leaf blade denotes the possible interaction between the genotypes of the host and the pathogen.

The results of the present tests suggest that simple and inexpensive green house tests can be used advantageously to isolate resistant lines in early segregating generations.

It may be said in conclusion that strain 1709 provides a single good source of blast resistance to at least three races. It may also prove to be an important parent variety in future blast breeding programs by virtue of its several desired agronomic characters, such as early maturity, short plant height, long grain, good quality and easy threshing.

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VITA

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EXAMINATION AND THESIS REPORT

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Major Field: Agronomy (Plant Breeding)

Title of Thesis: Inheritance of Resistance to Races of Blast Disease in Rice

Approved:

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