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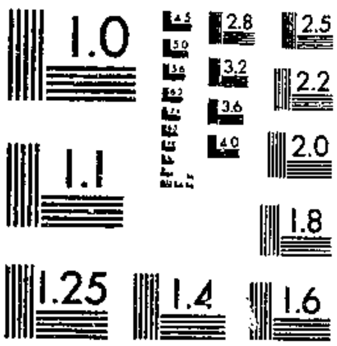

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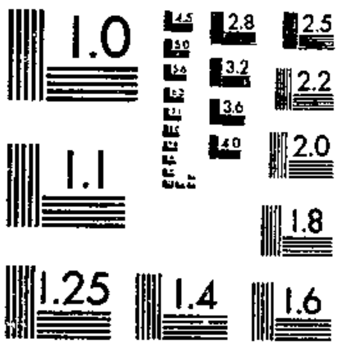

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Inheritance in Rice of Reaction to Helminthosporium oryzae and Cercospora oryzae[1]

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CONTENTS

INTRODUCTION

Certain diseases of rice (*Oryza sativa* L.) are of great economic importance and have been the object of considerable research. Among the principal diseases are those caused by *Helminthosporium oryzae* B. de H. and *Cercospora oryzae* Miy. The fungus *H. oryzae* causes seedling blight, a leaf spot, and attacks the neck of the culm and branches of the panicle, the glumes, and the kernels of rice. *H. oryzae* overwinters in the field, cannot be controlled by seed treatment, and is pathogenic on other grasses. The only satisfactory control appears to be through the breeding of resistant varieties. The fungus, *C. oryzae,* causes a leaf spot on rice. This disease is rather generally distributed throughout the rice-growing regions of Arkansas, Louisiana, and Texas. In the rice-breeding program in Arkansas, some promising cercospora-resistant and moderately resistant medium-grain selections of desirable plant type have been isolated from the cross Kameji, resistant, × Supreme Blue Rose, susceptible. The average yield of two resistant selections from this cross in 1938 was 46.9 bushels; of seven moderately resistant selections, 64.4 bushels; of seven susceptible selections, 40.7 bushels; and of Supreme Blue Rose, 44.5 bushels per acre. A wide range in reaction both to *H. oryzae*

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and *C. oryzae* has been observed among different varieties of rice. All varieties grown extensively in Arkansas are susceptible. Crosses between rice varieties differing in disease reaction were made and the present bulletin reports the results of studies on the inheritance of reaction to the two diseases in certain of the crosses.

LITERATURE REVIEW

Wei (*20*),[3] who reviewed the literature on *Helminthosporium oryzae*, stated that the disease was first noted by Von Thuemen in 1889, and that Van Breda de Haan of Java named the causal fungus in 1900. Ito and Kuribayashi (*5*) found the perfect stage in culture but not under natural conditions, and proposed the name *Ophiobolus miyabeanus*. Drechsler (*3*) suggested putting this fungus in the new genus *Cochliobolus* instead of *Ophiobolus*.

Ocfemia (*10*) studied specimens of *Helminthosporium oryzae* from Louisiana, the Philippines, Java, and Japan and observed slight physiological differences, but concluded that they were all strains of *H. oryzae*.

The symptoms have been described fully by several investigators. Tullis (*17, p. 81*) stated:

> Except for minor differences, the manifestations of the disease as it occurs in the United States seem to be the same as elsewhere in the world. The lesions produced by the fungus are usually narrowly elliptical spots with grayish centers and brown margins. Various gradations are found from narrowly elliptical lesions in some varieties to circular spots in others.

Ocfemia (*11*) reported that although infections of coleoptile, mesocotyl, and seedling roots were more abundant and the lesions developed faster at high than at low soil temperatures, the infections at higher temperatures were less harmful and were finally outgrown by the plant.

Ocfemia (*10*) reported that, in the Philippines, from 10 to 58 percent of the plants were killed by *H. oryzae*. Many of the remaining plants were stunted and weakened so that they were later attacked and killed by other fungi. Cralley and Tullis (*2*) reported *H. oryzae* to be one of the most important fungi causing seedling blight of rice in Arkansas, listing it as second in importance in their experiments. Wei (*20*) reported that seedling blight, caused by *H. oryzae*, was so severe in seedbeds in the area around Sungkiang, China, that in some cases it was necessary to reseed.

The damage caused by this fungus during the growth of the rice plant from the seedling stage to maturity cannot be estimated accurately. However, the author has observed that plants severely attacked are stunted and weakened, and therefore probably do not produce normal yields.

The damage caused by *H. oryzae* during the flowering and maturing stages of the rice plants is a little more evident. Ocfemia (*10*) observed that infected panicles show a black mass of conidia and conidiophores on the grain, in some cases completely enclosing the caryopsis. Suzuki (*15*) reported that rice kernels internally infected with this fungus showed a general visible discoloration and sometimes were shriveled. Tullis (*18*), reporting on the causes of discolored rice kernels in 13 varieties grown in Arkansas, Louisiana, and Texas in

[3] Italic numbers in parentheses refer to Literature Cited, p. 17.

2 years, found 0 to 88 discolored kernels per 50-gram sample of rough rice. *H. oryzae* was the cause of 15.5 percent of the discoloration.

Nishikado (*9*) studied the temperature tolerance of *H. oryzae* and recommended treating the seed with hot water. Cralley and Tullis (*2*) concluded that none of the treatments they tried could be recommended for control of seedling blight in Arkansas. Ito (*4*), Lin (*7*), Suzuki (*15*), and Wei (*20*) reported that mycelia and conidia of *H. oryzae* remained viable for 1 to 3 years under field conditions.

A number of investigators have reported varietal differences in reaction to *H. oryzae.* Ocfemia (*10*), Tullis (*17*), and Suzuki (*16*) reported various degrees of resistance among rice varieties to *H. oryzae* and suggested that the best means of control would be to develop resistant varieties. Lin (*7*) tested 500 strains of rice for reaction to *H. oryzae* in the seedling stage, and also studied the mature plant reaction of 30 of these strains. He concluded that mature plant reaction did not coincide closely with the reaction in the seedling stage. He found 3 varieties very resistant to *H. oryzae.*

Wei (*20*) listed 23 grasses susceptible to *H. oryzae.* Many of these grow in rice fields in the United States.

The literature on the mode of inheritance of reaction to disease-causing organisms in rice is limited. Kato, according to Jones (*6, p. 452*), reported a single factor difference for reaction to "*Leptosphaeria* (Catt.) and *Melanomma oryzae*" with resistance dominant. The work of Kato is summarized by Ando (*1*). Sasaki (*14*), according to Jones (*6*), reported a single factor difference for reaction to *Piricularia oryzae* Br. et Cav. with resistance dominant. Nakatomi, according to Jones (*6*), studied the inheritance of reaction to *P. oryzae* and reported segregation in a ratio of nine resistant to seven susceptible. Ramiah and Ramaswami (*12*), in studies on the reaction to *P. oryzae*, found the mode of inheritance to be simple in one case and more complex in another. They obtained disease-free selections that yielded better than the susceptible parent. Nagai and Hara (*8*) studied the inheritance of reaction to *Helminthosporium oryzae* and in the F_2 generation obtained a ratio of three healthy plants to one diseased.

Tullis (*19*) discussed the causal fungus and described the symptoms of the disease caused by *Cercospora oryzae.* Ryker (*18*) discussed possibilities of developing strains of rice resistant to this fungus.

INHERITANCE OF REACTION TO HELMINTHOSPORIUM ORYZAE

Material and Methods

In 1934, 21 varieties of rice reported to be resistant to diseases were grown in single rows. Observations were made on their reaction to natural infections caused by leaf-spotting fungi. Several of these varieties appeared to be resistant to *Helminthosporium oryzae.*

In 1934, the cross Mubo Aikoku × Supreme Blue Rose (C. I.[4] 5793) was made to study the inheritance of reaction to *H. oryzae*, the former variety being moderately resistant and the latter susceptible to this fungus.

Supreme Blue Rose is a vigorous-growing, high-yielding, late-maturing, medium-grain variety with normal green or straw color in

[4] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

the apex of the lemma and palea and is susceptible to both *H. oryzae* and *Cercospora oryzae*. It is an important commercial variety according to Jones (*6*), who reports that 50 percent of the rice acreage in the United States was sown to various strains of Blue Rose in 1934. Mubo Aikoku is an early-maturing, short-grain variety with red pigment in the apex of the lemma and palea, and it is moderately resistant to *H. oryzae*.

The F_1 plants of the cross Mubo Aikoku × Supreme Blue Rose were grown in the greenhouse during the winter of 1934–35. The grain did not mature early enough for sowing in the field in 1935, but it was sown in 1936. The F_2 plants were grown in rows 12 inches apart with the plants spaced about 4 inches apart in the row. Several rows of each of the parent varieties were grown for comparison.

The entire area on which the F_2 population and parent varieties were grown in the field was enclosed in a muslin and cheesecloth tent about the time the earliest plants began to head. The plants were inoculated with *H. oryzae* by spraying with a suspension of conidia of cultures grown on corn-meal agar and by placing naturally infected leaves from susceptible varieties in the enclosure. The inoculum was applied in the evening, and the tent was moistened and kept moist during the day following inoculation. Data on time of heading and color of apex of lemma and palea were recorded at about 7-day intervals during this period by tagging the plants that had headed. A small F_2 population also was grown in the greenhouse during the winter of 1935–36.

Lines in the F_3 and later generations were sown in the field in 8-foot rows spaced 1 foot apart. The seeds were not space planted but were sown thin enough so that the plants could be examined separately. Parent varieties were sown at frequent intervals for comparison.

The F_3 lines from the F_2 population grown in the field in 1936 were inoculated in tents in the field in 1937 in a manner similar to that used in 1936, the only difference being that inoculation was started about 2 weeks earlier and the inoculum used was conidia produced from cultures grown on oat hulls.

Preliminary studies on the reaction of rice seedlings to *H. oryzae* also were made in the greenhouse during the winters of 1935–36 and 1936–37. The following method of inoculation was found most satisfactory. The seedlings were grown by sowing 20 or 25 seeds in pint or quart paper cups. When the seedlings were 6 to 8 inches tall they were inoculated by spraying with a suspension of conidia of cultures grown on oat hulls. The plants were placed in a moist chamber at a temperature of 29° to 30° C. for 24 to 48 hours. They were then placed on greenhouse benches, and disease readings were made usually after 3 to 5 days.

The seedling reaction to *H. oryzae* of F_3, F_4, and F_5 lines was likewise studied in the greenhouse in the winter of 1937–38. The plants were grown on Crowley silt loam in pint paper cups, and each line was grown in duplicate in the greenhouse. The same method was followed as was used in the greenhouse in 1936–37. If there was sufficient seed, each of the F_3 lines was divided into four parts. All of the lines studied in the greenhouse were sown in the field at Stuttgart, Ark., in 1938. The lines in which there was sufficient seed for four parts also were sown in the field at Beaumont, Tex., in 1938.

The lines grown in the field in Arkansas in 1938 were sown in 8-foot rows spaced 9 inches apart with frequent rows of the parent varieties for comparison. Seed of the composite of several very susceptible varieties were sown in the alleys. The lines sown in Texas were alternated with rows of the susceptible composite. In Arkansas, straw from susceptible varieties grown in 1937 was applied to the land at the first irrigation.

Five arbitrary classes, numbered 1 to 5, were used to record the reaction to *H. oryzae*. Plants with lesions less than 1 mm. in length that did not have grayish centers were placed in class 1. In classes 2, 3, and 4 the lesions were about 1.5, 2.0, and 3.0 mm. in length, with grayish centers. In class 5 the lesions were large and not sharply delimited. There was an increasing number of lesions from classes 1 to 5, so that in class 5 the lesions often merged to form large blotches.

RESULTS

The seedling reaction of a number of rice varieties to *Helminthosporium oryzae*, inoculated as described herein, was observed during the winter of 1936–37. The varieties tested and their reaction are given in table 1.

TABLE 1.—*Reaction of seedlings of rice varieties to Helminthosporium oryzae, artificially inoculated and grown in the greenhouse at different temperatures during the winter of 1936–37*

Variety	C. I. No.	Reaction rating in different series at temperature of—						Average
		20° C.		24° C.	28° C.			
		Series 1	Series 2	Series 1	Series 1	Series 2	Series 3	
Mubo Aikoku	6346	1	1–2	1	......	1	1	1.2
Akaho	7358	......	1–2	......	......	1–2	1–2	1.5
Onishiki	6526	......	......	......	......	1–2	......	1.5
Gin Bozu	6355	2	2	1	......	1–2	1	1.6
Do	6873	2	......	1	......	2	......	1.7
Kinai	6508	......	......	......	......	1–3	......	2.0
Meshibu	5581	1	2	1	......	3–4	1	2.2
Selection from Storm Proof × Spain Jap	......	......	......	......	1–3	3	......	2.3
Zenith	7787	4	4–5	2	......	2	1–2	3.0
Nira	2702	......	3–4	......	......	3	2	3.0
Carolina Gold	1645	......	......	......	......	4	......	4.0
Shoemed	3625	4	......	3–4	......	5	......	4.3
Supreme Blue Rose	5703	......	5	......	5	5	5	5.0
Early Blue Rose	7785	......	......	......	......	5	......	5.0
Early Prolific	5883	......	5	......	......	5	5	5.0

Of the varieties tested, Mubo Aikoku was the most resistant. This was in agreement with the preliminary field observations made on adult plants.

The first seven varieties listed in table 1 are of the short-grain, narrow-leaf type. The selection from Storm Proof × Spain Jap is the progeny of a cross in which the male parent was of the short-grain type. The other seven varieties had wider leaves and were rank in growth. The difference between the first eight and last seven varieties in degree of infection is probably related to the size of the intercellular spaces, which are reported by Tullis (*17*) to be smaller in the short-grain varieties.

An F_2 population of the cross Mubo Aikoku × Supreme Blue Rose was grown in the field at Stuttgart, Ark., in 1936, and the plants inoculated with conidia of *H. oryzae*. Some infection was obtained but not enough to differentiate clearly between resistant and susceptible plants. The inheritance of time of heading and of anthocyan pigment in the apex of the lemma and palea also was studied.

One-hundred and sixty-seven F_3 lines from this cross were grown in the field at Stuttgart in 1937. Seventy-seven of these lines were inoculated with conidia of *H. oryzae* and classified according to reaction to that fungus. The results are given in table 2.

TABLE 2.—*Reaction to Helminthosporium oryzae of F_3 lines from the cross Mubo Aikoku (class 2) × Supreme Blue Rose (class 4) grown in the field in 1937*

Item	Plants or lines in reaction class—				Average reaction
	2	3	4	Total	
	Number	*Number*	*Number*	*Number*	
Individual plants	210	474	683	1,367	3.25
Average F_3 lines	1	40	36	77	3.45

A definite genic analysis of the mode of inheritance of reaction to *Helminthosporium oryzae* is not attempted, because of the absence of a distinct difference between resistance and susceptibility. Rather, there was a regular gradation from moderately resistant to very susceptible. To set up arbitrary classes in material of this nature would seem to make genic analysis unreliable. All the observations indicated, however, that resistance was recessive and that there was more than one factor difference between the resistant and susceptible parents.

Preliminary studies with a number of varieties appeared to indicate a rather close relationship between reaction in the seedling stage in the greenhouse and mature plant reaction in the field. The progenies of the cross Mubo Aikoku × Supreme Blue Rose were used to determine further this relationship. The reaction of progenies of the same cross also was studied in the greenhouse. Most of the material was F_4 lines from the F_3 progeny reported in table 2. The F_3 lines that were grown in the field in 1937 were grown in the greenhouse and artificially inoculated in 1937–38 to check the reaction to *H. oryzae* under greenhouse conditions and to determine the possibility of eliminating susceptible lines by inoculating the seedlings in the greenhouse.

The correlation between greenhouse and field reaction for the material used was highly significant in F_3 lines but less significant in F_4 lines selected from the F_3 lines.

The results obtained with F_3 lines in 1937 in the field, and in 1937–38 in the greenhouse, are given in table 3. The correlation coefficient between reaction to *H. oryzae* in the field and in the greenhouse was +0.52. This value may be considered significant, as the value of P is less than 0.01.

TABLE 3.—*Reaction to Helminthosporium oryzae of F_3 lines from the cross Mubo Aikoku × Supreme Blue Rose grown in the field in 1937 and in the greenhouse in 1937–38* [1]

Reaction class in field	Number of lines in greenhouse in reaction class—			
	1.5–1.9	2.0–2.4	2.5–3.0	Total
2.0–2.4		1		1
2.5–2.9	1	2		3
3.0–3.4		3	4	7
3.5–3.9		5	7	12
4.0			3	3
Total	1	11	14	26

[1] $r_{xy}=+0.52$. P less than 0.01.

The results obtained with F_4 lines in 1937–38 in the greenhouse, and in 1938 in the field, are given in table 4. The correlation coefficient was +0.23. This value is rather low, but it may be considered statistically significant, as the value of P is less than 0.01.

TABLE 4.—*Reaction to Helminthosporium oryzae of F_4 lines from the cross Mubo Aikoku × Supreme Blue Rose grown in the greenhouse in 1937–38 and in the field in 1938* [1]

Reaction class in greenhouse	Lines in field in reaction class—					
	2.0 [2]	2.5 [2]	3.0 [3]	3.5 [3]	4.0 [3]	Total
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Resistant:						
1.0	1		3	2	2	8
1.5	5	4	10		7	26
2.0	9	6	21	11	11	58
Susceptible:						
2.5	6	6	32	23	39	106
3.0	[3] 2	[3] 5	15	13	26	61
Total	23	21	81	49	85	259

[1] $r_{xy}=+0.23$. P less than 0.01. [2] Resistant. [3] Susceptible.

Table 5 is made up from the data presented in table 4 in order to point out the possibilities of eliminating susceptible lines on the basis of reaction to *H. oryzae* of seedlings grown in the greenhouse.

The results, on the basis of data shown in tables 4 and 5, strongly indicate that it is possible to eliminate some of the susceptible lines on the basis of seedling reaction to *Helminthosporium oryzae*. Thus, if all lines were grown in the greenhouse and inoculated with *H. oryzae* approximately a third of them would be saved as resistant (classes 1.0–2.0), and of those, approximately 27 percent would be found to be resistant (classes 2.0–2.5) in the field; whereas, if the lines were selected at random for sowing in the field, approximately 17 percent would be found to be resistant (classes 2.0–2.5). This difference, when space is limited, appears to be sufficient to justify the labor and expense involved in testing the seedlings in the greenhouse. About 1,000 lines can be grown in 100 square feet of greenhouse bench. If the greenhouse sowing is early enough, the resistant plants probably can be grown to maturity and seed obtained in time to sow in the field in the same summer. This procedure would save 1 year in the breeding program.

TABLE 5.—*Relation between reaction to Helminthosporium oryzae in the greenhouse and in the field of F_4 lines from the cross Mubo Aikoku × Supreme Blue Rose*

Reaction class in greenhouse	Resistant (reaction 2.0–2.5) in field	All resistant (reaction 2.0–2.5) in field	All susceptible (reaction 3–4) in field
	Percent	*Percent*	*Percent*
1.0–2.0	27.17		
2.5–3.0	11.38		
1.0–3.0	16.99		
1.0–2.0		56.82	31.16
2.5–3.0		43.18	68.84

The data on the mode of inheritance of time of heading and red pigment in the F_2 population are given in table 6. From seeding to heading Mubo Aikoku and the early F_2 plants required from 90 to 107 days and Supreme Blue Rose and the late F_2 plants from 108 to 118 days. All plants classed as early and grown in the F_3 generation bred true for earliness. All plants classed as late and grown in the F_3 generation bred true for lateness or segregated for time of heading.

The results show that there is one main factor for time of heading with lateness dominant and one main factor for glume apex color with red dominant. The 9 : 3 : 3 : 1 ratio in the F_2 generation was confirmed by the breeding behavior of F_3 lines. The chi square (χ^2) value was 16.93 and the P value was between 0.05 and 0.02. The factors for earliness and red pigment were inherited independently as indicated by the χ^2 test for independence and association. The value of χ^2 was 0.77 and the value of P was between 0.90 and 0.80. These factors for earliness and red pigment also appeared to be independent of reaction to *Helminthosporium oryzae.*

TABLE 6.—*Time of heading and pigmentation for the F_2 population of the cross Mubo Aikoku × Supreme Blue Rose*

Heading and color class	Plants			χ^2	P lies between
	Observed	Calculated			
		3 : 1 ratio	9 : 3 : 3 : 1 ratio		
	Number	*Number*	*Number*		
Late	746	756.75		0.61	0.50–0.30
Early	263	252.25			
Red	742	756.75			
Green	267	252.25		1.15	.30–.20
Late, red	554		567.5625		
Late, green	192		189.1875		
Early, red	188		189.1875		
Early, green	75		63.0625	2.66	.50–.30

INHERITANCE OF REACTION TO CERCOSPORA ORYZAE[5]

Material and Methods

The following crosses were used in studies on the inheritance in rice of reaction to *Cercospora oryzae* and on other characters: Akaho × Supreme Blue Rose, Meshibu × Supreme Blue Rose, Gin Bozu (C. I. 6355) × Zenith, Early Prolific × Onishiki, Gin Bozu (C. I. 6873) × Carolina Gold, and Meshibu × Zenith. Supreme Blue Rose, Zenith, and Early Prolific are medium-grain varieties and Carolina Gold is a long-grain variety; all are susceptible to *C. oryzae*. Akaho, Meshibu, Gin Bozu (C. I. 6355), and Gin Bozu (C. I. 6873) are short-grain varieties, resistant to *C. oryzae*.

Akaho has short culms and compact panicles, whereas Supreme Blue Rose has taller culms and more open panicles. The growth type of Supreme Blue Rose is more desirable than that of Akaho, so these characters in the segregating populations were observed in order to determine the possibilities of obtaining a resistant selection possessing the more desirable type of growth.

This material was sown and handled in the field in the same manner as reported in the studies with *Helminthosporium oryzae*. However, no attempt was made to inoculate the plants artificially with *Cercospora oryzae*. The amount of inoculum that occurred naturally each year was sufficient to cause infections severe enough for differential readings.

In the segregating generations there was a very wide range in type of reaction to *C. oryzae* from plants that were immune to those that were completely susceptible, that is, with a reduction in leaf area of 50 percent or more. This made it very difficult to classify the plants accurately. However, they were placed in three arbitrary classes designated as resistant, intermediate, and susceptible. The resistant class was recorded as class 1, intermediate as class 2, and susceptible as class 3. Only plants that appeared to be free of diseases were placed in class 1. Plants that had up to about 10 percent of the leaf area reduced were placed in class 2. Plants that were reduced more than 10 percent in leaf area were placed in class 3. The readings were further complicated by the occurrence of a physiological spotting that is very similar in effect to the cercospora leaf spot. Because of physiological spotting some plants were classed as intermediate, which in breeding tests proved to be resistant. Also, some susceptible plants were classed as intermediate, apparently because they had partly escaped infection.

Results

The segregations for reaction to *Cercospora oryzae* and other characters in the F_2 generation of the cross Akaho × Supreme Blue Rose are given in tables 7 and 9. These results indicate that there was one main dominant factor for susceptibility. The resistant class was deficient in number. The value of χ^2 was 16.90 for a 1 : 2 : 1 ratio, and the value was 16.39 for a 3 : 1 ratio. The value of P was less than 0.01 in both cases. It is possible that some resistant plants were classed as intermediate because of the physiological spotting.

[5] While this bulletin was in process of publication a paper entitled "Inheritance of resistance to *Cercospora oryzae* in rice," by T. C. Ryker and N. E. Jordan, appeared in Phytopathology 30 (12): 1041-1047, December 1940.

TABLE 7.—*Reaction to Cercospora oryzae, plant height, and panicle length of Supreme Blue Rose, Akaho, and the F_2 population of Akaho × Supreme Blue Rose*

Variety	Plants in reaction class			Plant height		Panicle length	
	1	2	3	Inches	Standard deviation	Millimeters	Standard deviation
	Number	*Number*	*Number*				
Supreme Blue Rose			All	49.9±0.30	3.35±0.21	208.1±2.25	25.13±1.59
Akaho	All			32.9± .48	3.38± .34	137.9±2.20	15.39±1.59
Akaho × Supreme Blue Rose F_2	233	616	323	41.3± .16	5.32± .11	175.4± .81	26.92± .55

TABLE 8.—*Reaction to Cercospora oryzae of F_3 lines of the cross Akaho × Supreme Blue Rose*

Reaction classes of F_2 plants	F_3 lines				
	All class 1	Segregating, classes 1 and 2	Segregating, classes 1, 2, and 3	Segregating, classes 2 and 3	All class 3
	Number	*Number*	*Number*	*Number*	*Number*
1. Resistant	10	6	3		
2. Intermediate	8	7	14	3	
3. Susceptible			10	4	11
Total	18	13	27	7	11

TABLE 9.—*Plant height and reaction to Cercospora oryzae of an F_2 population from the cross Akaho × Supreme Blue Rose and height classification of parent varieties*

Plant height classes (inches)	F_2 plants in reaction class—				Akaho	Supreme Blue Rose
	1	2	3	Total		
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
24		2		2	1	
31	16	54	34	104	34	
38	106	269	151	526	14	1
45	71	240	111	422		36
52	40	51	27	118		88
Total	233	616	323	1,172	49	125

A number of F_3 lines were grown to determine the breeding behavior of the F_2 plants. The results for the F_3 lines are given in table 8. Eighteen lines bred true for resistance, 40 segregated, and 11 bred true for susceptibility to *Cercospora oryzae*. The value of χ^2, calculated on the basis of a 1 : 2 : 1 ratio, was 3.17. The value of P was between 0.10 and 0.05. This confirmed the assumption that there was one main factor difference between the two parents for reaction to *C. oryzae*.

In height (table 7) the F_2 population was intermediate between the parents and significantly more variable than either parent. Likewise, panicle length was intermediate and somewhat more variable than either parent. Apparently each of these characters was controlled by several factors. The distribution of the F_2 population for plant height and panicle length in relation to reaction to *C. oryzae* is shown in tables 9 and 10. The χ^2 test was used to determine whether there was any association between the characters studied. The results are given in table 11. Resistance to *C. oryzae* appeared to be associated with plant height. The high value of χ^2 was due largely to an excess number of plants in the tall-resistant class. This apparent association was between resistance and tallness, the latter a character from the susceptible parent. The data did not indicate any association between reaction to *C. oryzae* and panicle length, but did indicate that plant height and panicle length were associated. This would be expected, since a factor for elongation of the internode would probably affect the internodes of both the culm and panicle.

TABLE 10.—*Panicle length and reaction to Cercospora oryzae of F_2 population from the cross Akaho × Supreme Blue Rose and panicle length classification of parent varieties*

Panicle length classes (millimeters)	F_2 plants in reaction class—				Akaho	Supreme Blue Rose
	1	2	3	Total		
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
123	13	42	22	77	24	
150	68	187	96	351	23	3
177	78	221	109	408	2	26
204	56	127	62	245		56
231	18	35	29	82		29
258		3	5	8		11
285		1		1		
Total	233	616	323	1,172	49	125

TABLE 11.—*Tests of independence or association among the characters, reaction to Cercospora oryzae, plant height, and panicle length for Akaho, Supreme Blue Rose, and Akaho × Supreme Blue Rose, F_2*

Variety	Reaction to *Cercospora oryzae* and—				Plant height and panicle length	
	Plant height		Panicle length			
	χ^2	P	χ^2	P	χ^2	P
Akaho					1.37	0.30–0.20
Supreme Blue Rose					15.60	.01– .00
Akaho × Supreme Blue Rose, F_2	21.79	0.01–0.00	12.53	0.30–0.20	380.12	.01– .00

In a comparison between plant height and panicle length in F_2 plants and F_3 lines the correlation coefficient for plant height was 0.87 and for panicle length 0.73, and P was less than 0.01 in both cases.

One-hundred and thirty-seven F_4 lines, progeny of the cross Akaho × Supreme Blue Rose, were grown in 1938. The lines were from F_3 plants resistant to *Cercospora oryzae* and approached the Supreme Blue Rose parent in plant height and panicle length. Insofar as possible only plants that had grains of medium length were used. This character had not received as much attention, however, so fewer of the lines had this characteristic as compared with the other desired characters. The results obtained are given in table 12. Seventy-six lines were resistant to *C. oryzae* and had the desired plant height and panicle length. Only two of these were of medium-grain type, but they indicate that it is possible to get resistance to *C. oryzae* combined with desirable morphological characters.

The cross Meshibu × Supreme Blue Rose was handled in the same manner as the cross Akaho × Supreme Blue Rose. Meshibu is an early variety and Supreme Blue Rose is late. The F_2 and later generations segregated for time of heading, and this character was observed to determine if it was associated with reaction to *Cercospora oryzae*. The F_2 population based on time of heading was divided into two classes. The first comprised all plants earlier than Supreme Blue Rose, and the second plants that were as late as Supreme Blue Rose. There were no F_2 plants earlier than Meshibu and none later than Supreme Blue Rose.

TABLE 12.—*Plant height, panicle length, grain type, and reaction to Cercospora oryzae of F_4 lines from the cross Akaho × Supreme Blue Rose*

Plant height	Panicle length	Grain type	Lines	
			Resistant	Segregating
			Number	*Number*
Tall	Long	Medium	2	
Do.	do.	Intermediate	12	
Do.	do.	Segregating	50	9
Do.	do.	Short	12	1
Intermediate	do.	Intermediate	1	
Do.	do.	Segregating	12	
Do.	Segregating	do.	1	
Segregating	Long	Medium	1	
Do.	do.	Segregating	13	4
Do.	Segregating	Medium		1
Do.	do.	Intermediate	1	
Do.	do.	Segregating	15	2
Total			120	17

The distribution of the F_2 population of the cross Meshibu × Supreme Blue Rose for reaction to *C. oryzae* in 1936 is given in table 13. The results indicate a duplicate factor difference, with susceptibility dominant. The value of χ^2 for a 15:1 ratio is 1.25; the value of P was between 0.30 and 0.20. The χ^2 test was used to determine if there was any association between reaction to *C. oryzae* and time of heading. The value of χ^2 was 20.71 and P was less than 0.01. This indicates some association between the two characters. However, the high value of χ^2 was due to an excess number in the late-resistant class and a deficient number in the late-susceptible class. This indicates that the high value of χ^2 was probably caused by late plants escaping infection.

TABLE 13.—*Reaction to Cercospora oryzae and time of heading, Meshibu × Supreme Blue Rose, F_2, 1936*

Time of heading	Plants in reaction class—			
	1	2	3	Total
	Number	*Number*	*Number*	*Number*
Early and intermediate	26	107	342	475
Late	20	47	77	144
Total	46	154	419	619

One hundred and forty-three F_3 lines were grown in 1937, and the reaction to *C. oryzae* for individual plants in each line was determined. Each class was given a numerical rating, and the average for each line was computed. The results are given in table 14.

TABLE 14.—*Reaction to Cercospora oryzae of F_2 plants in 1936 and F_3 lines in 1937 progeny of the cross Meshibu × Supreme Blue Rose*

F_2 plants in reaction class—				Average reaction of F_3 lines
1. Resistant	2. Intermediate	3. Susceptible	Total	
Number	*Number*	*Number*	*Number*	
14	14	3	31	1.1
3	7	2	12	1.4
4	7	8	19	1.7
3	7	2	12	2.0
4	6	6	16	2.3
4	3	13	20	2.6
----------	7	26	33	2.9
32	51	60	143	--------

The results obtained in F_3 indicate that errors were made in classifying the F_2 plants. Plants that should have been placed in the intermediate class undoubtedly escaped infection and were placed in the resistant class, and resistant plants were probably placed in the intermediate or susceptible classes because of the physiological spotting. When the breeding behavior in F_3 lines is taken as the indication of the genotype of the F_2 plants it appears that there is only one factor for reaction to *C. oryzae*. There were 31 resistant lines, 79 segregating, and 33 susceptible. On the basis of a 1 : 2 : 1 ratio, χ^2 is 1.63 and the value of P lies between 0.50 and 0.30. The correlation coefficient for reaction to *C. oryzae* in the F_2 and F_3 was +0.56. This is a statistically significant value, as P is less than 0.01. The correlation coefficient between number of days from seeding to average date of heading and average classification of reaction to *C. oryzae* was −0.25 and the value of P is less than 0.01. This apparent correlation between resistance and late maturity is probably due to late plants escaping infection and to the presence of the physiological spotting.

One hundred and sixty-two F_4 lines in all maturity groups from the cross Meshibu × Supreme Blue Rose were grown in 1938. These were from F_3 lines that appeared to be breeding true for resistance to *C. oryzae*. There were 133 resistant lines, 26 segregating, and 3 susceptible.

The progeny of the other hybrids listed earlier in this section also were used in the study of the inheritance of reaction to *C. oryzae*. All crosses were studied in the F_2 and F_3 generations and Gin Bozu (C. I. 6355) × Zenith and Meshibu × Zenith were also studied in F_4. The results for the F_2 populations are given in table 15 and for the F_3 lines in table 16.

TABLE 15.—*Reaction to Cercospora oryzae of the F_2 populations from various crosses*

Cross: Parent varieties	Cross: No.	Year grown	Plants: Resistant	Plants: Susceptible	Plants: Total	Ratio	χ^2	P
			Number	*Number*	*Number*			
Gin Bozu × Zenith	358A4	1938	408	115	523	3 : 1	2.52	0.20-0.10
Early Prolific × Onishiki	352A1	1937	627	255	882	3 : 1	7.20	Less than .01
Do	352A2	1937	152	60	212	3 : 1	1.23	.30- .20
Do	352A1	1938	236	81	317	3 : 1	.05	.90- .80
Total			1,015	396	1,411	3 : 1	7.07	Less than .01
Gin Bozu × Carolina Gold	353A3	1938	82	20	102	3 : 1	1.58	.30- .20
Meshibu × Zenith	355A5	1937	105	76	181	9 : 7	.23	.70- .50
Do	355A6	1937	272	219	491	9 : 7	.00	.98- .95
Do	355A6	1938	110	41	151	3 : 1	.37	.70- .50

TABLE 16.—*Reaction to Cercospora oryzae of F_3 lines from various crosses grown at Stuttgart, Ark.*

Cross: Parent varieties	Cross: No.	Year grown	Lines—Resistant	Lines—Segregating	Lines—Susceptible	Ratio	χ^2	P
			Number	*Number*	*Number*			
Gin Bozu × Zenith	358A	1937	10	37	14	1:2:1	4.22	0.20-0.10
Do	358A4	1938	23	27	11	1:2:1	5.52	.02- .01
Total			33	64	25	1:2:1	1.34	.70- .50
Early Prolific × Onishiki	352A2	1938	28	32	17	1:2:1	5.22	.10- .05
Gin Bozu × Carolina Gold	353A3	1938	34	49	16	1:2:1	6.56	.05- .02
Meshibu × Zenith	355A	1937	28	39	17	1:2:1	3.31	.20- .10
Do	355A6	1938	19	41	12	1:2:1	2.75	.30- .20
Total			47	80	29	1:2:1	3.69	.20- .10

The results obtained with these crosses differed from those obtained with the two already discussed. In the first two crosses susceptibility to *Cercospora oryzae* was dominant, whereas in these crosses resistance was dominant.

In the F_2 population of the cross Gin Bozu (C. I. 6355) × Zenith there were 408 resistant to 115 susceptible plants. Calculated on the basis of 3 resistant to 1 susceptible, the value of χ^2 is 2.52 and P lies between 0.20–0.10. These results indicate that resistance to *C. oryzae* is conditioned by one main factor. Breeding tests with F_3 lines should give 1 resistant, 2 segregating, and 1 susceptible, if this is true. The results gave 33 lines breeding true for resistance, 64 segregating, and 25 breeding true for susceptibility. Calculated on the basis of a 1 : 2 : 1 ratio, the values of χ^2 and P were 1.34 and 0.50, respectively.

Similar results were obtained in three F_2 populations of the cross Early Prolific × Onishiki. Two of these populations conformed to the ratio of 3 resistant plants to 1 susceptible. The other also indicated a single factor difference, but the results were not statistically significant. A number of F_3 lines from this cross also were grown, and they gave a ratio of 1 resistant to 2 segregating to 1 susceptible plant.

A small F_2 population and a number of F_3 lines from the cross Gin Bozu (C. I. 6873) × Carolina Gold were grown. The results obtained, as shown in tables 15 and 16, also indicated that there was one main factor for reaction to *C. oryzae* with resistance dominant.

The results obtained with the cross Meshibu × Zenith, as given in tables 15 and 16, indicate that a more complicated condition prevailed in this cross. In this case, F_2 populations were grown from two F_1 plants. One of these, 355A6, was divided and grown part in 1937 and part in 1938. Number 355A5 was grown only in 1937. The results obtained with both populations in 1937 indicated complementary factors for resistance. If resistance was due to complementary factors, the results to be expected in F_3 would be 1 resistant to 8 segregating to 7 susceptible lines. Computing χ^2 on the basis of the results obtained gives a value of 56.67 for the 1 : 8 : 7 ratio. As the value of P approaches zero, the results obtained cannot be considered as a chance variation from the 1 : 8 : 7 ratio. All F_3 lines grown conformed to the 1 : 2 : 1 ratio for a one factor difference.

F_4 lines from the crosses Meshibu × Zenith and Gin Bozu (C. I. 6355) × Zenith were grown. Ninety-one lines from the cross Meshibu × Zenith were grown and 66 appeared to be breeding true for resistance, 24 segregated, and 1 was susceptible in reaction to *C. oryzae*. Of the 72 lines from the cross Gin Bozu × Zenith, 66 appeared to breed true for resistance and 6 segregated for reaction to *C. oryzae*.

Because of the nature of the disease caused by *C. oryzae* in Arkansas, it is difficult to classify the plants accurately in hybrid populations. Under the conditions of these experiments, two disturbing elements made a detailed classification somewhat doubtful. The first was physiological spotting, which caused some plants resistant to *C. oryzae* to be classed as intermediate and intermediate type plants to be classed as susceptible. The second difficulty was that some plants that were genotypically intermediate or susceptible escaped infection and were classed as resistant.

These difficulties in classification naturally make a genic analysis of the results less valuable. Yet the results appear to be conclusive enough to point out one fact at least. Susceptibility to *C. oryzae* seemed to be dominant in both crosses in which Supreme Blue Rose was the susceptible parent and recessive in the other four crosses studied. This can be explained by assuming that there is in rice an allelomorphic series of at least three genes for reaction to *C. oryzae*. On the basis of this assumption, Supreme Blue Rose carries a gene dominant to the gene in the resistant varieties, but the latter is dominant to the gene in Zenith, Early Prolific, and Carolina Gold for reaction to this fungus. This appears to be the case when the two crosses, Meshibu × Supreme Blue Rose and Meshibu × Zenith, are compared. From general observations of plants and lines studied in these experiments it appears that there may be involved a number of modifying factors and possibly physiologic races. Additional work needs to be done on the question of the allelomorphic series, modifying factors, and physiologic races.

The fact that the gene or genes for reaction to *C. oryzae* are not closely linked with the genes for the other characters studied is of great importance. All the resistant varieties used in these studies had one or more undesirable characters, such as short grain, short straw, compact panicles, too early maturity, and low yielding capacity.

Most short-grain varieties have short culms and narrow leaves, whereas medium- and long-grain varieties usually are tall and have relatively wide leaves. Tullis (*17*) reports that the intercellular spaces are relatively smaller and less numerous in the short-grain types than in the other two types. Although most resistant varieties are of the short-grain type, resistance does not appear to be due to morphological and anatomical characters. Shoemed, Nira, and Fortuna are highly resistant to *C. oryzae*, and have wide leaves and are rank in growth. Shoemed and Fortuna are reported by Tullis (*17*) to have large intercellular spaces. Also, many selections, obtained in these studies, that are highly resistant to this fungus have tall culms and wide leaves. It appears, therefore, that resistance is due to physiological differences and these differences are controlled by genetic factors.

SUMMARY

Data on the inheritance of reaction to *Helminthosporium oryzae*, *Cercospora oryzae*, time of heading, color of lemma and palea apex, and the relationship of reaction to *H. oryzae* between seedlings and mature plants are presented.

The results indicate that reaction to *H. oryzae* was controlled by several genetic factors and that, in the particular crosses studied, resistance was recessive. Under the conditions of these experiments, there was a fairly close relationship between reaction to *H. oryzae* on seedlings grown in the greenhouse and that on mature plants grown in the field.

Time of heading and lemma and palea apex color were monogenic characters inherited independently, and both were apparently independent of the factors for reaction to *H. oryzae*.

Difficulty was encountered in classifying plants for reaction to *C. oryzae*. However, by carrying the studies through the second, third, and fourth generations it was possible to determine the main genetic factors for reaction to this fungus. Supreme Blue Rose, a susceptible variety, has at least one factor for reaction to *C. oryzae* dominant to the factor for reaction to *C. oryzae* in the resistant varieties used. The factor for reaction to *C. oryzae* in the resistant varieties is dominant to the factor for susceptibility to *C. oryzae* in the Zenith, Early Prolific, and Carolina Gold varieties. The results indicate that probably a number of modifying factors are involved.

The factor for reaction to *C. oryzae* was not closely linked with factors for the other characters studied. Selections resistant to this fungus were obtained that had the desired grain type, plant height, panicle length, time of maturity, and apparently high yielding ability.

Differences in reaction to *C. oryzae* appear to be due to physiological rather than morphological or anatomical differences in rice varieties, and these physiological differences are inherited.

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