Inheritance of Resistance to *Pyricularia oryzae* in Rice Cultivars Grown in the United States

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ABSTRACT

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Inheritance studies were conducted with U.S. rice cultivars to identify and characterize genes for resistance to local pathotypes of *Pyricularia oryzae*. Three new recessive resistance (*Pi-*) genes were identified: *pi-n* in Brazos (resistance to race IB-54 of *P. oryzae*), *pi-g* in Gulfrose (IG-1), and *pi-d* in Lebonnet (IB-1). Brazos also had the *Pi-k*^{s} gene (IB-54), independent of the *pi-n* gene. The *Pi-z* gene (IC-17, IG-1, and IH-1) was identified in Gulfrose and Vista with Vista also having independently inherited *Pi-k*^{s}. Lebonnet and most related cultivars have the *Pi-k*^{h} gene (IB-45, IB-54, IG-1, and probably IH-1), which is closely linked to the recessive *pi-d* gene (3.3% crossover value). An unnamed dominant *Pi-* gene (IH-1), independent of *Pi-z*, was identified in PI 331581 (dwarf Bluebelle). Another unnamed *Pi-* gene, independent of *Pi-k*^{h}, which confers resistance to race IB-49, which is virulent on all U.S. commercial rice cultivars, was identified in the international blast differential cultivar Usen.

Additional key words: discriminatory resistance, specific resistance, true resistance, vertical resistance.

Early work by Atkins and Johnston (2) on inheritance of pathotype-specific resistance to rice blast, caused by *Pyricularia oryzae* Cav., indicated single independent genes conferring resistance to then-designated U.S. races 1 and 6 in the cultivars Northrose (also Nato) and Gulfrose (also Zenith), respectively. They named the resistance genes Pi_1 (in Northrose) and Pi_6 (in Gulfrose). U.S. race 1 is now known as international race IB-54, and race 6 may be either IG-1 or ID-13, depending upon the reaction of the international differential Usen (15,16). Most isolates of *P. oryzae* from Nato since the early 1960s have been identified as race IG-1 (20; J. G. Atkins and M. A. Marchetti, *unpublished data*). A more recent work by Eroutor et al (4) showed that resistance to races IB-54 and IG-1 was controlled by a single dominant gene in the cultivar Lebonnet. On the basis of these two studies, we know of at least three different major genes for pathotype-specific blast resistance in U.S. rice cultivars.

The most comprehensive and systematic studies of pathotype-specific blast resistance have been conducted in Japan by Kiyosawa. He has identified and named some 13 *Pi-* genes in Japanese and exotic rice cultivars, including several American cultivars, using Japanese and Philippine isolates of *P. oryzae*. He discovered the *Pi-z* gene in Zenith and also found Zenith to have the *Pi-a* gene, which is common in Japanese cultivars (9). He found the *Pi-k*^{s} gene in Lacrosse and Caloro (10), the *Pi-a* gene in Bluebonnet (11), and the *Pi-k*^{h}, *Pi-i*, and *Pi-a* genes in Dawn (13,14). *Pi-k*^{h} and *Pi-k*^{s} are allelic.

It is important to identify and characterize *Pi-* genes against pathotypes of *P. oryzae*. Such information is essential to the success of any of a number of strategies for blast management being proposed by rice pathologists and breeders (5–8)—e.g., gene rotation, pyramiding, multilines, or use with sources of rate-reducing resistance. In breeding for resistance to rice blast in the southern United States, we are emphasizing utilization of *Pi-* genes in combination with rate-reducing resistance and pyramiding of *Pi-* genes.

Work is under way to characterize the *Pi-* genes in U.S. rice cultivars and to relate them, to the extent possible, to those already identified and named by Kiyosawa (9–11,13,14). Here we report on *Pi-* genes found in Lebonnet, Vista, Brazos, Gulfrose, and some related cultivars.

MATERIALS AND METHODS

The crosses and parental reactions to seven pathotypes of *P. oryzae* used in this study are summarized in Table 1. Although there have been differences of opinion regarding the pathogenic stability of isolates of *P. oryzae* (15,22), we have had little difficulty in maintaining pathogenic stability among isolates collected from rice fields in the southern United States (20). Isolates 429 and 793 have maintained their pathogenic and cultural characteristics since their collection in 1959 and 1967, respectively; the year of isolation for the other five isolates is indicated by the first two digits of the respective isolate numbers (Table 1). Inheritance studies were conducted in the greenhouse during March–May and September–November to avoid extremes in greenhouse

temperatures. F_2 plants were space-planted in galvanized iron flats measuring 25 × 35 × 10 cm, four rows per flat, 20 seeds per row. Total F_2 populations tested varied between 150 and 840 plants. Seed for F_3 lines was harvested from F_2 plants that had been direct-seeded on 30-cm centers in the field. F_3 lines were planted in single rows in flats, five lines per flat, 12–20 seeds per line.

When plants were in the two- to three-leaf stage, they were fertilized with ammonium sulfate (21% N) at 4 g per flat. Plants were inoculated at the three- to four-leaf stage with 20 ml per flat of aqueous spore suspensions containing 10^4–10^5 spores per milliliter. Spores were harvested from 8- to 12-day-old cultures grown in 125-ml flasks on 2% rice polish agar (15) at 26–28 C under continuous cool-white fluorescent illumination (4,000 lux). Inoculated plants were incubated 16–18 hr in dew chambers (21) at 24–25 C, then moved to the greenhouse. Plants were evaluated for disease reaction 6–8 days after inoculation on a 0–9 scale: 0 = no symptoms; 1 = small, pinpoint, brown lesions (type 1 lesion); 2 = larger, pinhead, brown lesions, few with ashen centers (type 2 lesion), mixed with type 1 lesions; 3 = small, round to slightly elongated, necrotic, ashen lesions with brown margins 1–2 mm in diameter (type 3 lesion), mixed with type 1 and 2 lesions; 4 = as in 3, with the addition of a few spindle-shaped, "eyespot" lesions with brown margins, 4–8 mm long, that support sporulation (type 4 lesion); 5 = about 10% type 4 lesions 0.5–1 cm long, mixed with type 1, 2, and 3 lesions; 6 = between 5 and 7; 7 = 25–50% type 4 lesions, some not completely delineated with brown margins, mixed with type 1, 2, and 3 lesions; 8 = more than 50% type 4 lesions, some longer than 1 cm, many without brown margins, appearing water-soaked basally, frequently coalescing, usually with some type 1, 2, and 3 lesions; 9 = plants killed.

The production of susceptible-type eyespot lesions (rating of 4 or greater) indicates the absence of *Pi-* gene resistance; 0–2 ratings indicate *Pi-* gene resistance. A rating of 3 is uncertain. In our experience with cultivar-pathotype combinations whose reactions have been observed over many years, especially favorable test conditions (as indicated by overall test results) tend to increase susceptibility—i.e., cultivars that usually show ratings of 2 to a particular pathotype may show more susceptible ratings of 3. Conversely, under less favorable conditions, usually associated with several days of daytime greenhouse temperatures of 35 C or above, cultivar-pathotype combinations that usually produce ratings of 4 may be rated 3 or lower. Included in the inoculations were the parent lines and a set of international differentials (3,17) to assess test conditions by familiar rice-line disease reactions and to verify the pathogenic character of test isolates. When inheritance of resistance was clearly bimodal, the environmental sensitivity of class 3 was considered in hypothesizing beyond a simple 3:1 ratio.

In two instances, F_2 ratios more closely fit 13 resistant:3 susceptible than the 3:1 indicative of single dominate-gene resistance, thus indicating the presence of an independently inherited, recessive resistance gene. To verify the existence of the recessive gene, F_3 lines from 20–30 susceptible F_2 plants were checked for segregation for resistance by inoculating with the relevant isolate of *P. oryzae*. Segregation in the F_3 would indicate that the susceptible parent F_2 was heterozygous for the recessive resistance gene.

TABLE 1. Disease reactions of isolates of *Pyricularia oryzae* on parental combinations used in studies of inheritance of blast resistance in greenhouse studies at Beaumont, TX, 1977–1985

	Reactions to pathotypes of *P. oryzae*[a]						
Isolate:	81L19	75L5	793	429	75T38	74T3	74L2
Cross {♀/♂} Pathotype:[b]	IB-1	IB-45	IB-49	IB-54	IC-17	IG-1	IH-1
Labelle/Usen	R/S[c]	R/S	S/R	R/R	S/R	R/R	R/R
Lebonnet/Vista	R/S	R/S	S/S	R/R	S/R	R/R	R/R
Lebonnet/Gulfrose	R/S	R/S	S/S	R/S	S/R	R/R	R/R
Brazos/Gulfrose	S/S	S/S	S/S	R/S	S/R	S/R	S/R
Gulfrose/PI 331581[d]	S/S	S/S	S/S	S/S	R/S	R/S	R/R[d]
Brazos/Caloro	S/S	S/S	S/S	R/R	S/S	S/S	S/S
Vista/CI 9888[e]	S/S	S/S	S/S	R/S	R/S	R/S	R/S

[a] Based on results from routine greenhouse inoculations with single isolates conducted during 1963–85.

[b] Race designations according to Ling and Ou (17), based on reactions of international rice blast differentials (3).

[c] Underscores indicate pathotype-cross combinations used in study; R = resistant, S = susceptible.

[d] PI 331581 = Bluebelle*6/Taichung Native 1—essentially Bluebelle with semidwarf gene from Taichung Native 1. PI 331581 resistance to IH-1 frequently manifested as pinhead necrotic or ashen-centered (type 2) lesions.

[e] CI 9888 = Rexoro/red rice/ /Magnolia selection/3/Lacrosse/Magnolia.

RESULTS

Data from the Brazos/Gulfrose F_2 indicated that Brazos carries both a dominant and recessive gene conferring resistance to race IB-54 of *P. oryzae*, each acting independently (Table 2). The presence of the recessive gene, tentatively designated *pi-n* (for the Nova parent of Brazos, since the *b* symbol has been used [12]), was verified when 19 of 30 F_3 lines from susceptible F_2 plants segregated at about 1 resistant:3 susceptible to IB-54. Results from the Brazos/Caloro cross indicate that the dominant resistance gene in Brazos is *Pi-k*^{s}, the gene identified in Caloro by Kiyosawa (10) (Table 2).

Segregation of the Brazos/Gulfrose F_2 indicated that Gulfrose possesses both a dominant and recessive gene, each conferring resistance to race IG-1 independently (Table 2). We did not attempt to verify the presence of the recessive in the F_3, but additional evidence for the recessive *Pi-* gene is presented later. The gene analysis of the F_3 did not bear out the F_2 findings with the 7 resistant:8 segregating:1 susceptible ratio expected from the 13 resistant:3 susceptible ratio of the F_2, but it did indicate that genes conferring resistances in the respective parents are not linked (Table 3). Since Zenith is a parent of Gulfrose and their reactions to all local pathotypes of *P. oryzae* are identical (1; *unpublished data*), we concluded that the dominant *Pi-* gene in Gulfrose is *Pi-z*.

The Lebonnet/Vista cross was made for varietal improvement to combine the blast resistances of Lebonnet and Vista, which together would produce major-gene resistance to all pathotypes except IB-49 of *P. oryzae* found in the United States and multiple resistance to several common pathotypes, notably IG-1 and IH-1. The F_2 population was grown in a winter nursery in Puerto Rico and underwent some selection for plant type and earliness of maturity. Consequently, we have only data for F_3 lines from seed of panicles collected in Puerto Rico. Inoculations of F_3 lines with races IB-45 and IC-17, against which Lebonnet and Vista have complementary resistances, respectively, showed that both resistances were conferred by single, dominant, independent genes (Table 4). Blast resistance in Lebonnet was transferred from its male grandparent, Dawn (Fig. 1). Dawn possesses *Pi-k*^{h}, *Pi-i*, and *Pi-a* resistance genes, and possibly others (13,14). Since cultivars known to possess the *Pi-a* (Aichi Asahi) and *Pi-i* (Ishikari Shiroke) genes are susceptible to race IB-45 (15; *unpublished data*), we concluded that resistance to IB-45 was conferred by *Pi-k*^{h}.

F_2 plants of Lebonnet/Gulfrose segregated 3 resistant:1 susceptible when inoculated with race IB-54, but they segregated with more susceptible than resistant plants when inoculated with IB-1, though not fitting a 1:3 ratio ($P = 0.05$) (Table 2). Lebonnet/Gulfrose F_1 plants were not available, but F_1 plants of the cross Labelle/RU7502023, also resistant/susceptible (R/S) to both IB-1 and IB-54, were susceptible to IB-1, which is evidence for a recessive resistance gene. Lebonnet and Labelle are closely related (Fig. 1) and have identical resistances to blast (Table 1). The Labelle/Usen (R/S to IB-1) F_2 population segregated 1 resistant: 3 susceptible when inoculated with IB-1. Therefore, we concluded that resistance of Lebonnet and related cultivars (Dawn and Labelle) to IB-1 was conferred by a recessive gene, tentatively designated *pi-d*, for Dawn, the probable donor in the resistant cultivars (Fig. 1).

Linkage analysis of Lebonnet/Gulfrose F_3 lines inoculated with IB-54 and IB-1 indicated close linkage between the *Pi-k*^{h} and *pi-d*

genes, with an estimated crossover value of 3.3% (Table 5). F_4 lines were recovered from F_3 plants in the nonparental classes that were resistant to IB-1 and susceptible to IB-54, and vice versa.

A second set of 100 Lebonnet/Gulfrose F_3 lines segregated 1 resistant:2 segregating:1 susceptible when inoculated with either race IB-1 or IB-54 (Table 6). They segregated 35 resistant:26 segregating:3 susceptible when inoculated with IG-1, as was expected with a dominant resistance gene (*Pi-k*^{h}) from Lebonnet and the dominant (*Pi-z*) and hypothesized recessive (*pi-g*, for Gulfrose) genes from Gulfrose conferring resistance to IG-1, all acting independently. Of 17 F_3 lines of Lebonnet/Gulfrose from F_2 plants rated susceptible to IG-1, 8 segregated for resistance to IG-1.

F_2 data from Vista/CI 9888 indicate that resistances to races IB-54, IC-17, IG-1, and IH-1 in Vista are conferred by single dominant genes (Table 2). According to F_3 data, resistance to IB-54 segregates independently from resistance to IC-17 (Table 7), and resistances to IC-17, IG-1, and IH-1 probably are allelic (Tables 8 and 9). There were a few nonparental segregants recorded in lines inoculated with IC-17, IG-1, and IH-1, but they can be explained either by outcrossing in the F_1 or errors in classification. Given the parentage of Vista (Rexoro/Zenith/ /Lacrosse/Magnolia), probably the *Pi-k*^{s} gene from Lacrosse (10) confers resistance to race IB-54, and *Pi-z* from Zenith (9) confers resistance to IC-17, IG-1, and IH-1.

F_2 plants of the cross Gulfrose/PI 331581 (R/R to IH-1) segregated 15 resistant:1 susceptible to race IH-1 (Table 2), indicating that resistance genes in Gulfrose (*Pi-z*) and PI 331581 are nonallelic and not linked. The *Pi-* gene in PI 331581 confers resistance only to race IH-1.

DISCUSSION

It is obvious from some of the F_2 ratios presented in Table 2 that not all disease reactions fit neatly into resistant-susceptible dichotomies. In fact, many major-gene-controlled reactions probably were modified by minor genes that contribute to slow-blasting or dilatory blast resistance. The existence of substantial levels of dilatory blast resistance in U.S. rice cultivars has been demonstrated in several studies at Beaumont (18,19). Therefore, we feel justified in making judgments about the intermediate class 3 reactions, in those tests where there were intermediate reactions, to favor a likely simple inheritance ratio.

We report here the existence of three recessive *Pi-* genes. There have been reports of recessive blast resistance from India (23) and Taiwan (25). The instance from India involved rice cultivar CI 5309, one of the original U.S. blast differentials (16) and also one of the major blast-resistance donors in Dawn, which in turn is the blast-resistance donor in all subsequent Texas long-grain cultivars, including Labelle and Lebonnet (Fig. 1) (24). The gene that we are calling *pi-d* is different from that reported in CI 5309; CI 5309 is susceptible to race IB-1, the pathotype rendered avirulent to Lebonnet and Dawn by *pi-d*. According to routine screening tests,

TABLE 2. Segregation of blast resistance in F_2 progeny from selected rice crosses inoculated with different pathotypes of *Pyricularia oryzae* in greenhouse studies in Beaumont, TX, 1977–1985

Cross {♀/♂}	Test pathotype[a]	Parent reactions[b]	Number of plants[c] R	M	S	Ratio Observed	Expected	χ^2	P
Brazos/Gulfrose	IB-54	R/S	141		32	13.2:3	13:3	0.01	>0.90
	IG-1	S/R	278		57	14.6:3	13:3	0.66	>0.40
	IH-1	S/R	135		43	3.1:1	3:1	0.06	>0.75
Gulfrose/PI 331581	IH-1	R/R	115	257[d]	32	11.6:1	15:1	1.93	>0.15
Brazos/Caloro	IB-54	R/R	221		0	1:0	1:0	···	1.0
Lebonnet/Gulfrose	IG-1	R/R	790		45	52.7:3	61:3	0.93	>0.30
						17.6:1	15:1	1.06	>0.30
	IB-1	R/S	151	17	252	1:1.8	1:3	26.9	<0.001
	IB-54	R/S	180		61	3:1	3:1	0.02	>0.90
Labelle/Usen	IB-1	R/S	53	42	181[e]	1:2.7	1:3	0.43	>0.50
	IB-45	R/S	192	31	55	3:1	3:1	0.01	>0.90
	IB-49	S/R	347		116	3:1	3:1	0.01	>0.90
	IC-17	S/R	344		114	3:1	3:1	0.01	>0.90
Vista/CI 9888	IB-54	R/S	324		127	2.6:1	3:1	2.14	>0.10
	IC-17	R/S	334		108	3.1:1	3:1	0.08	>0.75
	IG-1	R/S	343		113	3:1	3:1	0.01	>0.90
	IH-1	R/S	336		116	2.9:1	3:1	0.11	>0.70

[a] International race designations according to Ling and Ou (17).
[b] R = resistant and S = susceptible to test pathotype, ♀/♂.
[c] R = resistant; M = class 3, uncertain; and S = susceptible.
[d] Underscore indicates R and M were considered R for χ^2 test. Reactions of PI 331581 to IH-1 ranged from 1 to 3.
[e] Underscores indicate M class was split between R and S for χ^2 test.

TABLE 3. Contingency table for segregation of 266 F_3 rice lines from cross Brazos/Gulfrose inoculated with races IB-54 and IG-1 of *Pyricularia oryzae*[a]

IB-54	No. of F_3 lines IG-1 Resistant	Segregating	Susceptible	IB-54[b] total
Resistant	31 (30)	29 (29)	7 (7)	67
Segregating	68 (66)	67 (64)	12 (16)	147
Susceptible	21 (24)	20 (23)	11 (6)	52
IG-1 total[b]	120	116	30	266

[a] Expected values (shown in parentheses) based on frequencies of resistant, segregating, and susceptible lines to each pathotype and assumption of no linkages among resistance genes.
[b] Independent inheritance: $\chi^2 = 6.17$, df = 4, $P > 0.10$.

TABLE 4. Inheritance and linkage analysis of genes conferring resistance to race IC-17 (*Pi-z*) of *Pyricularia oryzae* in Vista rice and race IB-45 (*Pi-k*^{h}) in Lebonnet in 121 F_3 lines from cross Lebonnet/Vista, Beaumont, TX

IC-17	No. of F_3 lines IB-45 Resistant	Segregating	Susceptible	IC-17 total[a]
Resistant	8	18	6	32
Segregating	16	24	22	62
Susceptible	4	14	9	27
IB-45 total[a]	28	56	37	121

[a] IC-17 χ^2 1:2:1 = 0.49, $P > 0.75$; IB-45 χ^2 1:2:1 = 2.01, $P > 0.25$. Independent inheritance (no linkage between *Pi-z* and *Pi-k*^{h}): $\chi^2 = 7.48$, $P > 0.25$.

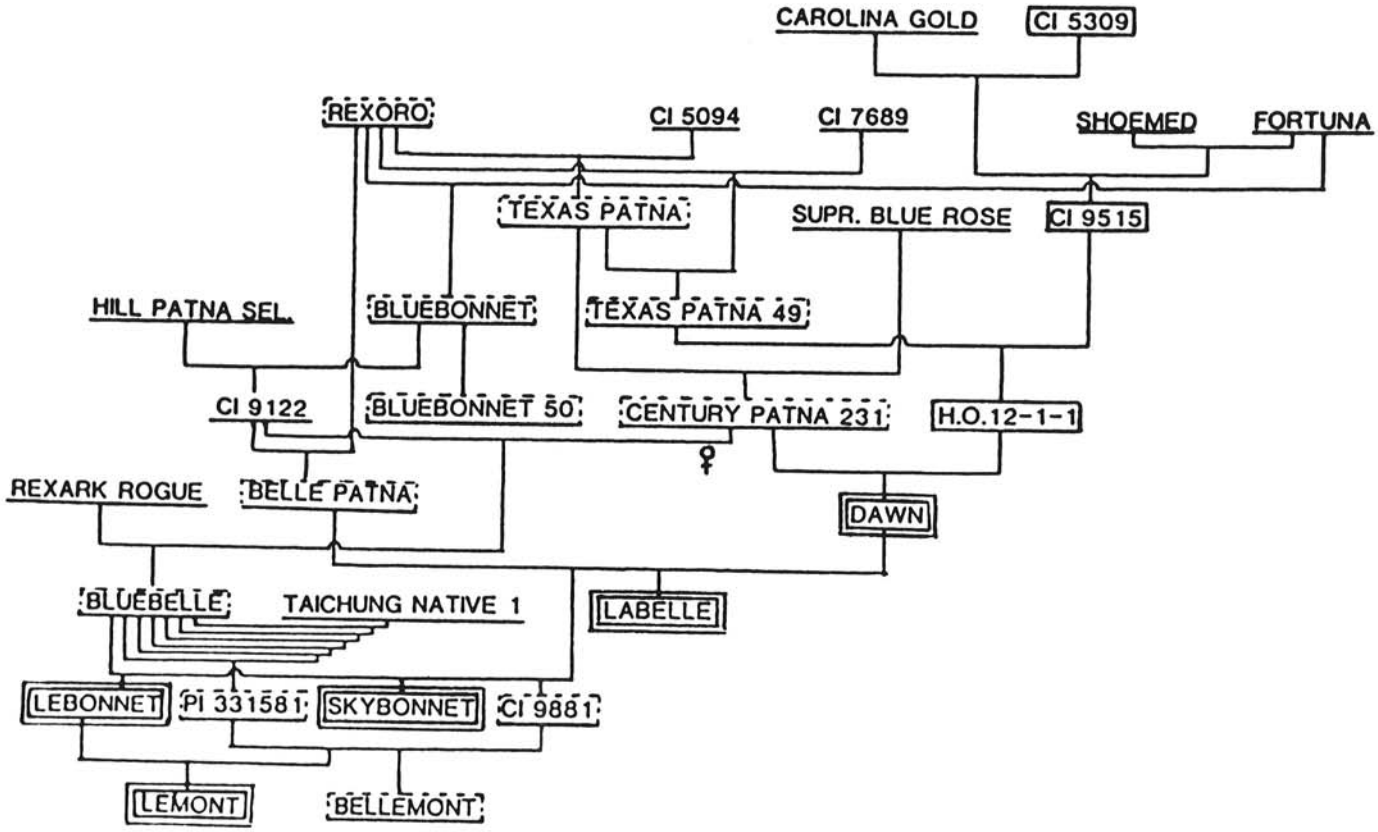

Fig. 1. Genealogy chart of Texas long-grain rice cultivars. All cultivars shown are susceptible to races IB-49 and IC-17 of *Pyricularia oryzae*. Cultivars in broken-line boxes are resistant only to race IH-1, whereas cultivars in solid-line boxes are resistant to races IB-45, IB-54, IG-1, and IH-1. Cultivars in double boxes are resistant to race IB-1, in addition to the above pathotypes. The indicated resistance of H.O.12-1-1 is assumed to be like that of CI 9515 but could be like that of Dawn; line is no longer available for testing. Except where indicated, left parent is female in each cross. Adapted from Lemont genealogy chart (23).

TABLE 5. Linkage analysis for dominant and recessive genes conferring resistance of Lebonnet rice to races IB-54 and IB-1, respectively, of *Pyricularia oryzae* in 147 F_3 lines from cross Lebonnet/Gulfrose, Beaumont, TX

Reaction class		No. of F_3 lines		
			Expected	
IB-54	IB-1	Actual[a]	Allelic	Independent
Resistant	Resistant	26	37	9
Resistant	Segregating	3	0	18
Resistant	Susceptible	0	0	9
Segregating	Resistant	2	0	18
Segregating	Segregating	79	73	37
Segregating	Susceptible	1	0	18
Susceptible	Resistant	0	0	9
Susceptible	Segregating	0	0	18
Susceptible	Susceptible	36	37	9

[a] F_4 plants were recovered that were resistant to IB-1 and susceptible to IB-54, and vice versa, from nonparental F_3 lines. Estimated crossover = 3.3%.

TABLE 6. Inheritance of resistance to races IB-1, IB-54, and IG-1 of *Pyricularia oryzae* in 100 F_3 rice lines from cross Lebonnet/Gulfrose and linkage analysis of genes controlling resistance to IG-1 in Lebonnet and Gulfrose, Beaumont, TX

Pathotype	No. of F_3 lines			Expected ratio	χ^2	P
	Resistant	Segregating	Susceptible			
IB-1	23	57	20	1:2:1	2.14	>0.25
IB-54	28	54	18	1:2:1	2.64	>0.25
IG-1	52	42	6	35:26:3[a]	0.38	>0.75

[a] Dominant gene in Lebonnet and dominant and recessive gene in Gulfrose, all independently inherited, are hypothesized (see also Table 2).

Table 7. Inheritance and linkage analysis of genes conferring resistance of Vista rice to races IB-54 (*Pi-k*^{s}) and IC-17 (*Pi-z*) of *Pyricularia oryzae* in 200 F_3 lines from cross Vista/CI 9888, Beaumont, TX

IB-54	No. of F_3 lines			
	IC-17			IB-54 total[a]
	Resistant	Segregating	Susceptible	
Resistant	13	26	9	48
Segregating	21	62	20	103
Susceptible	13	26	10	49
IC-17 total[a]	47	114	39	200

[a] IB-54 χ^2 1:2:1 = 0.19, $P > 0.90$; IC-17 χ^2 1:2:1 = 4.56, $P > 0.10$. Independent inheritance (no linkage between *Pi-k*^{s} and *Pi-z*): $\chi^2 = 1.33$, $P > 0.75$.

TABLE 8. Inheritance and linkage analysis of genes conferring resistance of Vista rice to races IG-1 and IC-17 of *Pyricularia oryzae* in 200 F_3 lines from cross Vista/CI 9888, Beaumont, TX

IG-1	No. of F_3 lines			
	IC-17			IG-1 total[a]
	Resistant	Segregating	Susceptible	
Resistant	47	1[b]	0	48
Segregating	0	112	2[b]	114
Susceptible	0	1[c]	37	38
IC-17 total[a]	47	114	39	200

[a] IG-1 χ^2 1:2:1 = 4.92, $P > 0.05$; IC-17 χ^2 1:2:1 = 4.56, $P > 0.10$. Independent inheritance: $\chi^2 = 370$, $P < 0.001$.

[b] Outcrossing or error in classification possible.

[c] Error in classification possible. Outcrossing not likely since there are no known rice lines that are resistant to IC-17 and susceptible to IG-1.

neither the maternal parent of Dawn, Century Patna 231, nor the paternal grandparents, Texas Patna 49 and CI 9515 (Fig. 1), are resistant to race IB-1, which raises a question as to the source of the *pi-d* gene. Either Dawn or its paternal parent, H.O.12 (no longer available), has an unknown parent, or *pi-d* is a spontaneous mutation. Given the close linkage between *pi-d* and *Pi-k*^{h}, which came from CI 5309, we believe that mutation is the more likely explanation.

The presence of the two other recessive *Pi-* genes, *pi-n* in Brazos and *pi-g* in Gulfrose, was not verifiable in the F_1, as was the *pi-d* gene, because each was masked by the effects of dominant *Pi-* genes. However, segregating F_3 lines from susceptible F_2 plants bore out the hypothesized recessive resistance genes indicated by 13:3 ratios in the F_2 from the Brazos/Gulfrose crosses. Masking of *pi-g* by the *Pi-z* gene probably explains why Atkins and Johnston did not detect the recessive *pi-g* in their study (2).

Based on our results we can make certain inferences about the virulence genes in the test isolates of *P. oryzae* (Table 10), as well as about resistance genes in the test cultivars and similarly reacting, related cultivars (Table 11), in a manner similar to that of Kiyosawa (9,12). Although resistance does not necessarily prove the interaction of known resistance-avirulence genes, susceptibility in the presence of known resistance genes does prove the absence of the complementary avirulence genes. For example, if cultivar *a* with the *pi-k*^{s} gene is susceptible to isolate *a*, then we can conclude that isolate *a* does not possess the *Av-ks* gene. On the other hand, if cultivar *a* is resistant to isolate *b*, it may or may not be the *Pi-k*^{s} gene that provides the resistance; some unidentified resistance gene may be operating. There is a question as to whether this concept applies in the case of the recessive *Pi-* genes. Padmanabhan et al (23) referred to the recessive resistance gene in CI 5309 as an inhibitory gene. In any case, the three recessive genes that we found were pathotype-specific and therefore were treated similarly to the dominant *Pi-* genes in Table 11.

Future research will include additional verification of the recessive *Pi-* genes by test-cross procedures and their further characterization against other pathotypes of *P. oryzae*, as well as the identification of the *Pi-* genes in Usen (which is resistant to a pathotype that is virulent on all U.S. rice cultivars) and in PI 331581 and related cultivars. From the breeding standpoint, we have encountered no problems with combining any of the *Pi-* genes dealt with in these studies, except perhaps the recombination of *Pi-d* with *Pi-* genes that are allelic to *Pi-k*^{h}.

TABLE 9. Inheritance and linkage analysis of genes conferring resistance of Vista rice to races of IG-1 and IH-1 of *Pyricularia oryzae* in 160 F_3 lines from cross Vista/CI 9888, Beaumont, TX

	No. of F_3 lines			
	IH-17			IG-1
IG-1	Resistant	Segregating	Susceptible	total[a]
Resistant	29	4[b]	0	33
Segregating	0	85	4[b]	89
Susceptible	0	0	38	38
IH-1 total[a]	29	89	42	160

[a] IG-1 χ^2 1:2:1 = 2.34, $P > 0.25$; IH-1 χ^2 1:2:1 = 4.12, $P > 0.10$. Independent inheritance: $\chi^2 = 235$, $P < 0.001$.
[b] Possible errors in classification or outcrossing of F_1 with lines resistant to IG-1 only.

TABLE 10. Summary of hypothesized virulence genes in seven U.S. pathotypes of *Pyricularia oryzae* based on reactions of rice cultivars in inheritance studies conducted at Beaumont, TX, 1977–1985

	Resistance genes in rice cultivars							
Pathotype[a]	*pi-d*	*pi-g*	*Pi-k*^{h}	*Pi-k*^{s}	*pi-n*	*Pi-r*^{b}	*Pi-u*^{b}	*Pi-z*
IB-1		*Av-g* +[c]	*Av-kh* +[d]	*Av-ks* +[d]	*Av-n* +	*Av-r* +	*Av-u* +	*Av-z* +
IB-45	*Av-d* +	*Av-g* +		*Av-ks* +	*Av-n* +	*Av-r* +	*Av-u* +	*Av-z* +
IB-49	*Av-d* +	*Av-g* +	*Av-kh* +	*Av-ks* +	*Av-n* +	*Av-r* +		*Av-z* +
IB-54		*Av-g* +				*Av-r* +		*Av-z* +
IC-17	*Av-d* +	*Av-g* +	*Av-kh* +	*Av-ks* +	*Av-n* +	*Av-r* +		
IG-1	*Av-d* +[e]			*Av-ks* +	*Av-n* +	*Av-r* +		
IH-1	?[f]			*Av-ks* +	*Av-n* +			

[a] Pathotype designations according to nomenclature of Ling and Ou (17).
[b] *Pi-r* and *Pi-u* genes are named to simplify this table only, pending further studies. They are different from all other resistance genes shown here.
[c] *Av-g* + is virulence gene corresponding to avirulence gene *Av-g*, according to nomenclature of Kiyosawa (9).
[d] *Av-kh* + and *Av-ks* +, named according to *Pi-* genes they attack, have not been demonstrated to be allelic in pathogen, as the corresponding *Pi-* genes have been in the host; therefore *h* and *s* are not shown as superscripts.
[e] Probably IG-1 has *Av-d* + gene, otherwise Lebonnet/CI 9888 F_2 lines should have segregated 13 resistant:3 susceptible to IG-1 instead of 3:1 (4).
[f] No relevant data.

TABLE 11. Summary of *Pi-* genes for resistance in rice cultivars to pathotypes of *Pyricularia oryzae* identified in inheritance studies conducted at Beaumont, TX, 1977–1985

	Test pathotype[a]							
Cultivar	IB-1	IB-45	IB-49	IB-54	IC-17	IC-1	IH-1	Cultivars with identical reactions to test pathotype[b]
Lebonnet	*pi-d*[c]	*Pi-k*^{h}	S[d]	*Pi-k*^{h}	S	*Pi-k*^{h}	*Pi-k*^{h}	Dawn, Labelle, Lemont, Skybonnet
Vista	S	S	S	*Pi-k*^{s}	*Pi-z*	*Pi-z*	*Pi-z*	Saturn
Gulfrose	S	S	S	S	*Pi-z*	*Pi-z*, *pi-g*	*Pi-z*	Zenith
Brazos	S	S	S	*Pi-k*^{s}, *pi-n*	S	S	S	Caloro, Lacrosse, Nato, M-101
PI 331581	S	S	S	S	S	S	*Pi-r*[e]	Belle Patna, Bluebelle, Bellemont
Usen	S	S	*Pi-u*[e]	*Pi-u*	*Pi-u*	*Pi-u*	*Pi-u*	

[a] Pathotype designations according to nomenclature of Ling and Ou (17).
[b] Based on repeated greenhouse inoculations over 5–15 yr.
[c] *Pi-* gene conferring resistance to pathology of *P. oryzae* listed above.
[d] S = Susceptible to pathotype listed above.
[e] Named to simplify this table only, pending further studies to determine whether they are among genes already named by Kiyosawa (12). *Pi-r* gene is different from any identified in this study and is independent of *Pi-z* gene. *Pi-u* may represent more than one gene—i.e., resistance to race IB-49 and resistance to any or all other avirulent test pathotypes may be conferred by different genes.

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