THE INHERITANCE OF RESISTANCE OF THE ZENITH TYPE VARIETIES OF RICE TO THE BLAST FUNGUS

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Synopsis. Gene analyses of an American variety, Zenith, and its derivative, Fukei 67, were performed. These varieties were found to carry two dominant genes for resistance, $Pi-a$ and $Pi-z$. The latter gene is on a locus independent of or distant from the genes, $Pi-a$, $Pi-k$ and $Pi-ta$, and is linked with the gene, $Pi-i$.

Recently, the American variety of rice, Zenith, has been utilized in breeding for resistance to the blast fungus in Japan. Fukunishiki, a highly resistant Japanese variety of rice, has been derived from the American variety and was released in 1964 (HIRANO *et al.* 1964).

In this paper, genetic analyses of Zenith and its derivative, Fukei 67, will be described. These two varieties show identical reactions to many races and have been called Zenith type varieties by KIYOSAWA. Most of the blast fungus cultures isolated in Japan show avirulent reactions to Zenith and its derivatives, while MOGI and YANAGITA (1965) reported that some fungus strains can attack these varieties.

Review of Literature

Studies on the inheritance of resistances to the blast fungus (*Pyricularia oryzae*) in rice varieties were recently reviewed by TAKAHASHI (1965) and YAMASAKI and KIYOSAWA (1966). Here, studies using fungus strains with known pathogenicity for differential varieties are reviewed.

The first worker who genetically analyzed the resistance to the fungus strains with known pathogenicity is NIIZEKI (1960) who found a dominant gene for resistance in the variety Kanto 54 while another dominant gene in Aichi Asahi and Ayanishiki. IWATA and NARITA (1961) found that resistance to the fungus strain Naga 89 in derivatives from the varieties, Bozu and Asahi, is controlled by one dominant gene. IWATA and NARITA

(1964) confirmed their results by testing resistance of other varieties to the same fungus strain. VENKATASWAMY (1964) reported that resistance of a rice strain, 1709, to U.S. races 6, 8 and 16 was controlled by one dominant gene which was symbolized as Pi_1 .

Woo (1965) studied the inheritance of resistance in rice varieties to blast fungus strains identified in Formosa and obtained segregation ratios of 1:3, 3:1, 15:1, 9:7, 3:13, and 27:37. He symbolized tentatively the resistance gene as Pi_3 , Pi_5 , Pi_x , Cpi_3 , Cpi_5 , Cpi_x , spi_x , Ipi_5 , etc. Here Pi_3 was given to a dominant gene controlling resistance to race 3, Cpi_x dominant complementary gene to race X, spi_x recessive gene for resistance to race X, and Ipi_5 inhibitor acting against resistance to race 5. He did not test to know a difference or an identity among the genes which were designated by him. When gene symbols are determined in such a way, the following possibilities must be noted: the same symbol does not necessarily mean the same gene, because it is possible that two or more genes being included in different varieties control resistance to a single fungus race or strain; and different symbols do not necessarily mean different genes, because there is a possibility that one and the same gene controls resistance to two or more fungus races or strains.

ATKINS (1965) crossed the variety, Northrose, which is resistant to U.S. race 1 and susceptible to U.S. race 6, with the variety, Zenith, which showed the reverse reactions to the two races, and found two genes Pi_1 and Pi_6 , which control resistance to races 1 and 6 respectively, behaving independently.

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YAMASAKI and KIYOSAWA (1966) devoted extensive study to the inheritance of resistance of Japanese varieties to the fungus strains identified in Japan. They selected seven representative strains of blast fungus belonging to various races and determined genic constitutions of many varieties cultivated in Japan. At first, the Japanese paddy rice varieties were classified into five groups based on their resistance to the seven fungus strains. Some varieties belonging to three groups have three different genes controlling resistances. These three genes were *Pi-a* in some varieties in the Aichi Asahi group, *Pi-k* in Kanto 51, representative of the Kanto 51 group, and *Pi-i* in two varieties belonging to the Ishikari Shiroke group. They presumed, furthermore, genic constitutions of the seven fungus strains based on the gene-for-gene theory developed by FLOR: *Av-a*, *Av-k* and *Av-i* being avirulence genes and *Av-a*⁺, *Av-k*⁺ and *Av-i*⁺ being virulence genes, corresponding to resistance genes *Pi-a*, *Pi-k* and *Pi-i*, respectively. Linkage relationships were not found among these resistance genes. KIYOSAWA (1966 a) found the gene *Pi-i* also in Sekiyama 2 and the gene *Pi-k* in Reishiko, Chinese variety, and did not find linkage relationships among these resistance genes, two genes controlling xantha seedling, a gene controlling waxy endosperm, and two genes controlling colour of palea and lemma, except between waxy gene and one of two genes controlling colour of palea and lemma.

KIYOSAWA (1967) found two genes in a variety, Pi No. 1, which was bred from repeated crossing of Japanese varieties to a Philippine variety, Tadukan. One of the two genes was *Pi-a* and the other was symbolized by *Pi-ta*.

KIYOSAWA, MATSUMOTO and LEE (1967) found that resistance of the variety, Norin 22, which is semi-resistant only to one of the seven fungus strains used (Ken 54-04), was controlled by one major and two or more minor genes, and that resistance of the variety to a Philippine fungus strain, Ken Ph-03, was controlled by one major and one or more minor genes. The two major genes were considered to be the same or linked. It was suggested although not conclusive that resistance to Ken

54-04 used in the above experiment may be associated with the field resistance of that variety (KIYOSAWA, 1966 b, c).

Materials and Methods

The American variety, Zenith, and a line, Fukei 67 which was bred by repeatedly crossing Japanese varieties with Zenith were used for genetic analyses of resistance to blast. Varieties, Kamenoo and Shin 2, susceptible to all used fungus strains were used as partners for genetic analysis, and Norin 17 (carrying the resistance gene *Pi-a*), Kanto 51 (*Pi-k*), Fujisaka 5 (*Pi-i*) (YAMASAKI and KIYOSAWA, 1966) and Pi No. 1 (*Pi-ta*) (KIYOSAWA, 1966 d) were used as linkage testers. The seven fungus strains which were always used by the author in his previous studies were again used here. The injection method mainly and the spraying method scarcely were used.

Spore suspension was prepared by using barley grain medium or YOSHIMURA-SUZUKI's method (YOSHIMURA and SUZUKI, 1961), in which a mycelial mat formed on a potato sucrose agar plate was transferred on to a rice-straw decoction sucrose agar plate and was exposed to fluorescent lamp. In the injection method, spore suspension of a concentration of 20,000 spores/ml was injected with a hypodermic syringe into a young leaf in sheath, and in the spraying method spore suspension in a concentration of $5\sim 10 \times 10^4$ spores/ml was sprayed using spray gun with a compressor. After spraying, wooden boxes in which seedlings were grown were kept for about 24 hours in an inoculation room of 28°C temperature and over 95% humidity. Plants were usually kept in a greenhouse except for the 24 hours after spraying.

Method of evaluation of resistance is as follows; the type and the number of lesions developed on the inoculated leaf were recorded one week after inoculation. Plants in F₂ or F₃ generation were divided into three groups, "r", "m" and "s", based mainly on prevalent type of lesions formed in the case of injection method, and based on largest type of lesions formed in case of spraying method. Particularly in F₃ analysis, lines tested were divided into three groups: "r" lines including "r" plants, "m" lines including "m" plants

but not "r" plants, and "s" lines including only "s" plants. Mostly, each plant was inoculated with two different fungus strains, the first inoculation at 3.5~4.0 leaf stage (counted except of primary leaf) and the second at one week later as a rule.

Results

A) Gene analyses of Fukei 67. F_2 populations of crosses between Fukei 67 and Kamenoo were inoculated with fungus strains, Ina 168, Ina 72, Hoku 1 and Ken 54-04 (Table 1). For Ina 168 and Hoku 1, F_2 populations segregated into 3:1, indicating participation of one dominant gene for resistance. For Ina 72, other populations of the same hybrid segregated into 15:1 in one case, but in another it was close to 3:1. For Ken 54-04, a ratio of 15:1 was obtained. In this case, Kamenoo used as susceptible variety showed a weak resistance and F_2 plants showing resistance to a similar extent to Kamenoo were classified in "m" group. So, at least one of the two genes found may be in Kamenoo.

During F_2 analyses mentioned above, it was found that Fukei 67 was not pure. So, F_2 population that was confirmed to segregate plants showing the same reactions as Fukei 67 was grown in order to get F_3 lines. These F_3 lines were analyzed to confirm the results of F_2 analyses and to determine the relationship between genes controlling resistance to the different fungus strains.

At first, 35 lines were inoculated with two fungus strains, Ina 168 and Ken 54-20, with one week interval (Expt. III, Table 2). A ratio of 15:1 was obtained for the first used fungus strain, Ina 168, and a 3:1 ratio was obtained for the second, Ken 54-20. For the two fungus strains, a segregation ratio for rr:rs:ss agreed with 12:3:1. Here, "rs" means lines that show "r" reaction to the first fungus strain and "s" reaction to the second. This indicates that one of two genes controlling

resistance to Ina 168 controls also resistance to Ken 54-20.

Ninety eight lines involving 35 lines in the above experiment were inoculated with two fungus strains, Ina 72 and Hoku 1 (Expt. IV). In this experiment, resistance of F_3 lines was classified into three classes, "r", "m" and "s", for Ina 72. Here, "r" was similar to resistance of Fukei 67 to Ina 72 and Ina 168, in which brown spots were prevalent, and "m" was similar to that of Fukei 67 to P-2 b, Ken 53-33, Hoku 1, Ken 54-20 and Ken 54-04, in which *bg* type lesions were prevalent. For the fungus strain Ina 72, 98 F_3 lines segregated in a ratio of r:m:s=12:3:1.

Table 1. Analyses of F_2 populations of Fukei 67 × Kamenoo for reactions to four blast fungus strains using injection method

Expt. no.	Population	Fungus strain	No. of plants				P value
			r	m	s	Total	
I-1****	Fukei 67 (R)*	Ina 168	17			17	(3:1) 0.7~0.8
	Kamenoo (S)				15	15	
	F_2		84	23	28	145	
I-2	Fukei 67 (R)	Ina 72	7			7	(3:1) <0.01 (15:1) <0.01
	Kamenoo (S)		2		12	14	
	F_2		169	22	37	228	
I-3	Fukei 67 (R)	Hoku 1	10	2		12	(3:1) 0.3~0.5
	Kamenoo (S)				19	19	
	F_2		92	9	27	128	
II-1	Fukei 67 (R)	Ina 72	47			47	(15:1) 0.7~0.8 (3:1) 0.05~0.10
	Kamenoo (S)		1	1	43	45	
	F_2		99	35	10**	144	
II-2	Fukei 67 (M)	Hoku 1	45		4***	49	(3:1) 0.7~0.8
	Kamenoo (S)			3	46	49	
	F_2		96	6	24	126	
II-3	Fukei 67 (M)	Ken 54-04	31			31	(15:1) 0.3~0.5 (3:1) <0.01
	Kamenoo (MS)		2	19	10	31	
	F_2		59	31	9	99	

*: Resistance of the parent to fungus strain inoculated was evaluated by YAMASAKI-KIYOSAWA's method in six classes, R^b, R, MR, M, MS and S.

**: Ratio between value obtained after values underlined were summed up and the other value was compared with expected ratio using χ^2 test.

***: Since Fukei 67 was confirmed to be not pure, these plants seem to be susceptible segregants.

****: Experiments in the same Roman numeral were performed under the same environmental condition at the same time.

Table 2. Analyses of F_3 lines of Fukei 67 $\times$ Kamenoo for reactions to seven fungus strains

Expt. no.	Parent	Fungus strain	② ①	Number of lines			$P_{①}^{***}$
				r	m	s	
III	P_1 Fukei 67 (R^h , M)	① Ina 168** (Spr.)****	r m s	26(P_1)*	5	31	(15 : 1) 0.2~0.3
	P_2 Kamenoo (S, S)	② Ken 54-20 (Inj.)	Total	26	9	35	(rr:rs:ss=12:3:1) 0.3~0.5
			$P_{②}$	(3 : 1) 0.09~0.95			
IV	P_1 Fukei 67 (R, M)	① Ina 72 (Inj.)	r m s	55(P_1) 21	16	71 21	(12 : 3 : 1) 0.7~0.8
	P_2 Kamenoo (S, S)	② Hoku 1 (Inj.)	Total	76	22	98	(rr:rs:mr:ss=9:3:3:1) 0.8~0.9
			$P_{②}$	(3 : 1) 0.5~0.7			
V	P_1 Fukei 67 (M, M)	① P-2 b (Inj.)	r m s	76(P_1)		76	(3 : 1) 0.5~0.7
	P_2 Kamenoo (S, S)	② Ken 53-33 (Inj.)	Total	76	22	98	(rr:ss=3:1) 0.5~0.7
			$P_{②}$	(3 : 1) 0.5~0.7			
VI	P_1 Fukei 67 (R, M)	① Ken 54-04 (Spr.)	r m s	75(P_1)		75	(3 : 1) 0.5~0.7
	P_2 Kamenoo (S, S)	② Ken 54-20 (Inj.)	Total	75	22	97	(rr:ss=3:1) 0.5~0.7
			$P_{②}$	(3 : 1) 0.5~0.7			

* : Showing corresponding position of the parents.

** : ① and ② mean the first and second inoculations respectively.

*** : $P_{①}$ and $P_{②}$ mean the P values for the first and second inoculations respectively.

**** : Spr.=Spraying Inj.=Injection

For the second fungus strain, a segregation ratio of 3:1 was obtained. For both the fungus strains, a segregation ratio of the four reactions (rr:rs:sr:ss) agreed with 9:3:3:1 expected when one of two genes controlling resistance to Ina 72 was the same as the gene controlling resistance to Hoku 1.

The same 98 lines were inoculated with two fungus strains, P-2 b and Ken 53-33. The

Table 3. Analyses of F_3 lines of Fukei 67 $\times$ Kamenoo for reaction to the blast fungus strain, Ina 168, using injection method

Expt. no.	Parent	Fungus strain	Number of lines			P value
			r	m	s	
VII	Fukei 67(R)	Ina 168	44	2	46	(15 : 1) 0.3~0.5
VIII	Kamenoo (S)		17		17	
Total			61	2	63	

result (Expt. V) indicated that one and same gene controls resistance to the two fungus strains. A different set consisting of the same 98 lines was inoculated with other two fungus

Table 4. Synthesized results of F_3 analyses of Fukei 67 $\times$ Kamenoo

Fungus strain		Number of lines	P value (12 : 3 : 1)
Ina 72 Ina 168	P-2 b Ken 53-33 Hoku 1 Ken 54-20 Ken 54-04		
r	r	76*	0.8~0.9
r	s	16	
s	s	6	
Total		98*	

* : For Ken 54-04, one line less than the number of lines described.

strains, Ken 54-04 and Ken 54-20, and the result obtained indicated that the same gene controls resistance to both the fungus strains (Expt. VI).

Out of these 98 lines, 63 lines which were not tested in the Expt. III were inoculated with Ina 168 in two separate sets, and a digenic segregation was again obtained (Expts. VII and VIII).

The results of F_3 analyses are partially different from those of F_2 analyses for Ina 168 and Ken 54-04. Impurity of Fukei 67 which was confirmed in tests of plant progenies seems to be responsible for the disagreement for Ina 168; 3:1 ratio in F_2 and 15:1 ratio in F_3 . The disagreement between 15:1 in F_2 and 3:1 ratio in F_3 for Ken 54-04 may be due to a difference of experimental conditions under which plants were grown and inoculated; the susceptible parent Kamenoo showed MS reaction in F_2 test and S reaction in F_3 test, and F_2 or F_3 plants showing the same level of resistance as Kamenoo were classified in "m" group in the F_2 test and in "s" group in the F_3 test. The impurity of Fukei 67 may also be responsible for the disagreement observed between F_2 analyses for Ina 72 (Expts. I-2 and II-1).

Taking all the experimental results on F_3 lines into consideration (Table 4), it is concluded that Fukei 67 carries two genes, one controlling resistance to Ina 72 and Ina 168, and another controlling resistance to all fungus strains used in the present study.

In order to know linkage relationships between two genes in Fukei 67 and the four genes carried in the four tester varieties, Norin 17, Kanto 51, Fujisaka 5 and Pi No. 1,

Table 5. Analyses of F_2 populations of crosses between Fukei 67 and various varieties with known resistance genes

Expt. no.	Population	Fungus strain	Number of plants		P value
			r m s	Total	
K-1	Fukei 67 (R^h)	Ina 72 (Spr.)	34	34	(1 : 0)
	Norin 17 (R)		33	33	
	F_2		265	265	
K-2	Fukei 67 (M)	Ken 54-20 (Inj.)	32	33	(15 : 1) <0.01
	Kanto 51 (M)		32 2	34	
	F_2		338 9 7	354	
K-3	Fukei 67 (R^h)	Hoku 1 (Inj.)	4 29	33	(15 : 1) 0.5~0.7
	Kanto 51 (R^h)		29 1	30	
	F_2		169 69 14	252	
X-1	Fukei 67 (R^h)	Ken 54-20 (Spr.)	34	34	(15 : 1) 0.01~0.2
	Pi No. 1 (R)		32	32	
	F_2		237 5 26	268	
X-2	Fujisaka 5 (R)	Ken 54-20 (Spr.)	5 28	33	(r:m+s=3:1) <0.01 (r+m:s=15:1) <0.01
	Fukei 67 (R^h)		34	34	
	F_2		272 43	272	
X-1	Fujisaka 5 (R)	Ken 54-20 (Spr.)	17	17	(r:m+s=3:1) <0.01 (r+m:s=15:1) <0.3~0.5
	Fukei 67 (R^h)		17	17	
	F_2		89 40 6	135	
X-2	Fujisaka 5 (R)	Ken 54-20 (Spr.)	17	17	(r:m+s=3:1) 0.2~0.3 (r+m:s=15:1) 0.3~0.5
	Fukei 67 (R^h)		17	17	
	F_2		95 30 9	134	
X-3	Fujisaka 5 (R)	Ken 54-20 (Spr.)	17	17	(r:m+s=3:1) 0.01~0.02 (r+m:s=15:1) <0.01
	Fukei 67 (R^h)		17	17	
	F_2		114 21	135	
X-4	Fujisaka 5 (R)	Ken 54-20 (Spr.)	17	17	(r:m+s=3:1) 0.2~0.3 (r+m:s=15:1) 0.05~0.10
	Fukei 67 (R^h)		17	17	
	F_2		95 36 3	134	
X-5	Fujisaka 5 (R)	Ken 54-20 (Spr.)	1 16	17	(r:m+s=3:1) 0.05~0.10 (r+m:s=15:1) 0.3~0.5
	Fukei 67 (R^h)		17	17	
	F_2		92 31 11	134	
X-6	Fujisaka 5 (R)	Ken 54-20 (Spr.)	1 16	17	(r:m+s=3:1) 0.02~0.05 (r+m:s=15:1) <0.01
	Fukei 67 (R^h)		17	17	
	F_2		91 44	135	
X-7	Fujisaka 5 (R)	Ken 54-20 (Spr.)	17	17	(r:m+s=3:1) <0.01 (r+m:s=15:1) <0.01
	Fukei 67 (R^h)		16 1	17	
	F_2		79 56	135	
Total (X-2 ~ X-7)	Fujisaka 5 (R)	Ken 54-20 (Spr.)	7 145	152	(r:m+s=3:1) 0.05~0.10 (r+m:s=15:1) <0.01
	Fukei 67 (R^h)		152 1	153	
	F_2		1185 301 29	1214	

* : An evidence showed that this plant is a susceptible segregant from Fukei 67.

Fukei 67 was crossed with these tester varieties. These tester varieties have been known to carry genes, *Pi-a*, *Pi-k*, *Pi-i* (YAMASAKI and KIYOSAWA, 1966) and *Pi-a* and *Pi-ta* (KIYOSAWA, 1966 d), respectively. F_2 populations of these crosses were inoculated with fungus strains which showed avirulent reac-

tions to both of Fukei 67 and these tester varieties (Table 5).

When F_2 population of Fukei 67 $\times$ Norin 17 was inoculated with Ina 72, susceptible plants were not found. This indicates that one of two genes in Fukei 67 is the gene *Pi-a*. Linkage relationship between another gene in Fukei 67 and the gene *Pi-k* was tested by inoculating individually Ken 54-20 and Hoku 1 to F_2 populations of Fukei 67 $\times$ Kanto 51. Digenic segregation was obtained for Ina 72 but not for Ken 54-20, although in the latter susceptible plants segregated. This indicates that the gene in Fukei 67 is not located at least in the same locus as the gene *Pi-k*.

In order to determine the linkage relationship between the gene in Fukei 67 and the gene *Pi-i*, F_2 populations of hybrid of Fujisaka 5 $\times$ Fukei 67 were used. In a first experiment, two families of F_2 generation were inoculated with Ken 54-20 (Expt. X in Table 5), without an appearance of susceptible plants. Here, a family is an F_2 population originated from an F_1 plant. This is not due to a failure of crossing, because plants showing the Fukei 67-type reaction appeared numerous in F_2 populations. The success of crossing was examined by injecting secondly Hoku 1 which is virulent to the maternal parent, Fujisaka 5, to the same F_2 populations. This test showed that the two populations segregated to 3 resistant: 1 susceptible to the fungus strain, and therefore indicated again the success of crossing because the resistant plants are considered to depend on the resistance gene in Fukei 67.

In a second experiment (Expt. XI. in Table 5) a larger number of F_2 families of the same hybrid were tested. In this experiment, some susceptible plants were found in some families. A pooled segregation ratio, $r:m+s$, in the two experiments agreed with a ratio of 3:1, indicating the success of crossing and that the resistance of Fukei 67 is epistatic to that of Fujisaka 5. Another segregation ratio, $r+m:s$, was not in

agreement with the ratio 15:1, which is expected when two genes in both the parental varieties behave independently of each other. This indicates that the two genes are linked. The crossing-over value very roughly calculated is 30.9%. This value should be re-examined in further experiments, since its reliability is low for the value calculated from materials having in repulsion a pair of dominant genes.

These results indicate that one gene in Fukei 67 is located on a locus different from genes, *Pi-a*, *Pi-k*, *Pi-i* and *Pi-ta*, found previously. This gene is designated *Pi-z*, because this gene is thought to be introduced from the variety Zenith. Accordingly, it is concluded that Fukei 67 carries two genes, *Pi-a* and *Pi-z*.

B) Gene analyses of Zenith. F_2 populations of Zenith $\times$ Shin 2 were inoculated with seven fungus strains (Table 6), and monogenic segregations were obtained for P-2 b, Ken 53-33, Hoku 1, Ken 54-20 and Ken 54-04. This indicates that one dominant gene controls

Table 6. Analyses of F_2 populations of Zenith $\times$ Shin 2 for reactions to seven blast fungus strains using injection method

Fxp. no.	Population	Fungus strain	Number of plants		P value
			r m s	Total	
XII-1	Zenith (M)	P-2 b	17	17	(3 : 1) 0.1~0.2
	Shin 2 (S)		1 14	15	
	F_2		105 6 20	131	
XII-2	Zenith (M)	Ken 53-33	17	17	(3 : 1) 0.5~0.7
	Shin 2 (S)		17	17	
	F_2		102 9 21	132	
XII-3	Zenith (MR)	Ina 72	15	15	(15 : 1) 0.2~0.3
	Shin 2 (S)		17	17	
	F_2		122 5	127	
XII-4	Zenith (M)	Hoku 1	16	16	(3 : 1) 0.5~0.7
	Shin 2 (S)		1 15	16	
	F_2		94 8 26	128	
XII-5	Zenith (M)	Ken 54-20	5	5	(3 : 1) 0.02~0.05
	Shin 2 (S)		9	9	
	F_2		106 1 21	128	
XII-6	Zenith (M)	Ken 54-04	17	17	(3 : 1) 0.3~0.5
	Shin 2 (S)		1 6 10	17	
	F_2		100 11 17	128	
XII-7	Zenith (M)	Ina 168	17	17	(15 : 1) 0.2~0.3
	Shin 2 (S)		15	15	
	F_2		121 1 4	126	

resistance to each of these fungus strains. Digenic segregations were obtained for Ina 72 and Ina 168, indicating participation of two genes for resistance to each of these fungus strains.

It was considered above that one gene in Fukei 67 is originated from Zenith. It was investigated by inoculating F_2 population of Zenith $\times$ Fukei 67 with Hoku 1 (Table 7). No susceptible plants were found, indicating that both of the varieties carry the same gene, *Pi-z*.

Zenith shows the same reactions to each of the seven fungus strains as Fukei 67. Therefore, it was considered that Zenith has the gene *Pi-a* in addition to the gene *Pi-z*. This was examined by inoculating the F_2 population of Zenith $\times$ Norin 17 with Ina 72; the latter having the gene *Pi-a*. Results (Table 8) did not show segregation of susceptible plants and indicated that Zenith carries the gene *Pi-a*.

In order to confirm these results, a mutant (Ina 168- a^+k^+) which was originated from Ina 168 and became virulent to Aichi Asahi and Kanto 51 was inoculated (Table 9). In this test, Zenith, Fukei 67, To-to and Aichi Asahi showed lowered resistance to this mutant, but Fujisaka 5 did not do so. However, these varieties did not show changed resistance to a mutant in which only virulence to Kanto 51 changed. This indicates that Zenith, Fukei 67 and To-to carry the same gene *Pi-a* as Aichi Asahi.

Table 7. Analysis of F_2 population of Zenith $\times$ Fukei 67 for reaction to the blast fungus strain, Hoku 1, using injection method

Expt. no.	Population	Fungus strain	Number of plants		P value
			r m s	Total	
XIII	Zenith (M)	Hoku 1	16	16	(1 : 0)
	Fukei 67 (MR)		17	17	
	F_2		125	125	

Table 8. Analysis of F_2 population of Zenith $\times$ Norin 17 for reaction to the blast fungus strain, Ina 72, using injection method

Expt. no.	Population	Fungus strain	Number of plants		P value
			r m s	Total	
XIV	Zenith (R)	Ina 72	24	24	(1 : 0)
	Norin 17 (R)		32	32	
	F_2		233	233	

Table 9. Reactions of Zenith, Fukei 67 and some other varieties to mutants which originated from Ina 168, using injection method

Variety	Fungus strain	Ina 168	Ina 168- a^+k^+	Ina 168- k^+
		Genotype*		
Zenith	—	<i>Av-a</i>	<i>Av-a</i>	<i>Av-a</i>
		<i>Av-k</i>	<i>Av-k</i>	<i>Av-k</i>
		<i>Av-i</i>	<i>Av-i</i>	<i>Av-i</i>
		<i>Av-ta</i>	<i>Av-ta</i>	<i>Av-ta</i>
Fukei 67	—	R ^h	M	R ^h
To-to	<i>Pi-a, Pi-k</i>	R	M	R
Aichi Asahi	<i>Pi-a</i>	R ^h	S	R
Fujisaka 5	<i>Pi-i</i>	R	S	R
		M	M	M

* : For the host genotype, only resistance alleles were described.

Discussion

Results of the present study indicated that Fukei 67 and Zenith carry two genes, *Pi-a* and *Pi-z*; the latter was found for the first time.

Fukei 67 is a selection obtained from hybridization program that three Japanese varieties were repeatedly crossed with Zenith, as shown in Fig. 1. An intermediate line 54BC-68, in the process of breeding of Fukei 67, shows M reactions to all the fungus strains. This type of reaction is considered to be

Fig. 1. Genealogical relationship of derivatives from Zenith. (According to HIRANO *et al.* (1964), and TORIYAMA (personal communication))

Table 10. Summarized results of the gene analyses of Zenith and Fukei 67

	Fungus strain	P-2 b	Ken 53-33	Ina 72	Hoku 1	Ken 54-20	Ken 54-04	Ina 168
Variety	Genotype*	<i>Av-k</i>	<i>Av-z</i>	<i>Av-a</i>	<i>Av-k</i>	<i>Av-k</i>	<i>Av-k</i>	<i>Av-a</i>
		<i>Av-i</i>		<i>Av-i</i>	<i>Av-ta</i>	<i>Av-i</i>	<i>Av-i</i>	<i>Av-k</i>
		<i>Av-z</i>		<i>Av-ta</i>	<i>Av-z</i>	<i>Av-ta</i>	<i>Av-ta</i>	<i>Av-i</i>
				<i>Av-z</i>		<i>Av-z</i>	<i>Av-z</i>	<i>Av-z</i>
Zenith	<i>Pi-a</i> , <i>Pi-z</i>	▲ M	▲ M	▲ R	▲ M	▲ M	▲ M	▲ R
Fukei 67	<i>Pi-a</i> , <i>Pi-z</i>	▲ M	▲ M	▲ R	▲ M	▲ M	▲ M	▲ R
Shin 2	+	S	S	S	S	S	MS	S
Kamenoo	+	S	S	S	S	S	MS	S
Norin 17	<i>Pi-a</i>			▲ R	S	S	S	▲ R
Kanto 51	<i>Pi-k</i>	S	S	R	S	S	S	R
Fujisaka 5	<i>Pi-i</i>	● M	S	S	R ^h	R ^h	R ^h	R ^h
Pi No.1	<i>Pi-ta</i> , <i>Pi-a</i>	● M	S	● M	S	● M	● M	● M
		S	S	▲ R	□ M	□ M	□ M	▲ R

===== : non-segregation

————— : monogenic segregation

----- : digenic segregation

} when F₂ plants or F₃ lines of the cross between the varieties at both ends of these lines were inoculated with the corresponding fungus strain.

*: Resistance and avirulence alleles were described but the corresponding susceptibility and virulence alleles were not described.

typical reaction of the gene *Pi-z*. The gene *Pi-a* in Fukei 67 may be originated from Sasashigure which is a parent of Fukei 67.

The gene *Pi-z* have been utilized at present in a registered variety, Fukunishiki, which was bred as highly blast-resistant variety in the Tohoku National Agricultural Experiment Station, Japan. (HIRANO *et al.*, 1964).

ATKINS (1965) found one gene symbolized as *Pi₆* in Zenith, which controls resistance to race 6. The resistance gene *Pi₆* is different from *Pi-a* found in the present study, because race 6 shows virulent reaction to Aichi Asahi which include the gene *Pi-a*. The gene *Pi-z* may be the same as the gene *Pi₆*, although further genetic studies are required for such conclusion.

The variety Fukunishiki and 54 BC-68 which is a common intermediate progenitor of Fukei 67 and Fukunishiki are considered to have the identical genotype, *Pi-z*, *Pi-a*⁺, which is different from Zenith and Fukei 67 in relation to the *Pi-a* gene.

A summary of the above mentioned results is given in Table 10, and genotype with regard to pathogenicity of the fungus strains are also shown, which were presumed according to the FLOR's gene-for-gene theory. According to the theory, the fungus strain showing avirulent reaction to the variety having the gene *Pi-z* is presumed to carry the avirulence gene *Av-z*, and the strain showing susceptible reaction to the variety to carry the virulence gene *Av-z*⁺.

Summary

Rice variety, Zenith, and its derivative, Fukei 67, were studied in relation to the inheritance of resistance to the several strains of the blast fungus. The two varieties show the same reactions to each of the several fungus strains. It was found that these reactions were controlled by two genes, *Pi-a* and *Pi-z*, the latter being newly found. The gene *Pi-z* controls semi-resistance to the fungus strains used and is on a locus indepen-

dent of or distant from the genes, *Pi-a*, *Pi-k* and *Pi-ta*. A loose linkage was recognized between *Pi-z* and *Pi-i*. On the base of these results, genotypes of the seven fungus strains used in relation to pathogenicity were presumed. Variety Fukunishiki, derivative from Zenith, was presumed to carry the gene *Pi-z* but not *Pi-a*, based on its reactions to many fungus strains and its parentage for Zenith and Fukei 67.

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水稻 Zenith 型品種のいもち病抵抗性の遺伝

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アメリカの水稻品種 Zenith と、それに日本水稻を繰返し交雑した結果育成された系統ふ系 67 号の遺伝子分析を行なった。両品種とも、菌系 P-2 b, 研 53-33, 稻 72, 北 1, 研 54-20, 研 54-04, 稻 168 に対する中度抵抗性を支配する 1 優性遺伝子と、菌系稻 72 と稻 168 対

する高度抵抗性を支配する 1 優性遺伝子を含む。前者は新しく見いだされた遺伝子で、*Pi-z* と名付けられ、後者は既知の *Pi-a* である。*Pi-z* は *Pi-a*, *Pi-k*, *Pi-ta* とは独立に行動し、*Pi-i* との間に連鎖関係を示す。フクニシキもまた *Pi-z* をもつものと考えられる。