

**SOME EXPERIMENTAL STUDIES ON THE INHERIT-
ANCE OF RESISTANCE AND SUSCEPTIBILITY
TO RICE LEAF BLAST DISEASE,
PIRICULARIA ORYZAE CAV.⁽¹⁾**

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Since questions concerning: 1) the number of physiologic races of blast disease, 2) the genic constitution for hostal plants in relation to those races and 3) the influence of environment to the manifestation of this disease, are not completely understood, they make difficulties for rice breeders whenever and wherever this disease is a menace to that locality. For instance, variety Taichung No. 65, one of the popular commerical varieties on the island of Taiwan was reported as a resistant variety in 1934 by Hashioka (1952). Nevertheless, since 1937 its resistance has gradually lost, and now it becomes susceptible to all physiologic races of the pathogen in this country. Previous studies of the disease infections had been investigated by Ou (1954), Ou and Lin (1958), Hung and Chien (1961) and Kou *et al.* (1963) in this island, and also by Toyoda and Suzuki (1952), Abumiya (1955), Nakanishi and Imamura (1960), Latterell *et al.* (1960) and Atkins (1962) in Japan and U. S. A. In the view of these findings, this paper reports the use of three physiologic races of blast fungus applying on several hybrid families for the purpose of revealing the relationships between the genotypes of the plant and the pathogen used.

Materials and Methods

Eight hybrid populations were made in the summer of 1962. Their parents and inoculums were derived from the differentials and physiologic cultures mentioned in the paper of Kou *et al.* respectively (1963). Those plants for the crosses have been selfed two generations for purification, and those cultures were developed from a single spore isolation for the same purpose. Seedlings of hybrid progenies and their parental lines were grown together in the green-

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house with temperature at 15-25°C for twenty days or until five to six inches tall, and the method of water conidium suspension was applied for the reaction.

In studying the blast infection types, many criteria have been set by various workers. Hashioka (1950) established a scale of five categories designated as A, B, C, D and E from susceptible to resistant. Ono (1953) classified the lesions into: brown, white, acute and chronic types of four classes. Abumiya (1955; 1958) described lesion zones as white (w), purple (p), brown (b), green (g), and yellow (y) regions. Toyoda and Suzuki (1952) classified lesions into five classes according to their size and degree of discoloration. Padmanabhan *et al.* (1953) classified lesions into A, B, C, D and F from resistant to susceptible and added I, II, III to each group for indicating the number of lesions. Atkins (1956) made two scales of six classes: 0, 1, 2, 3, 4, and 5 for greenhouse; 0-1%, 1-5%, 5-10%, 10-50%, 50-80% and complete killing of leaves for field study. Goto *et al.* (1961) classified R, RS, MS and S types of reactions. Latterell *et al.* (1960) used 0, 1, 2, 3, 4 and 5 six grades for grouping lesions. And in this country, Hung and Chien (1961) and Hung *et al.* used I, R, M and S at Taiwan Agricultural Research Institute. Really there are too many systems of criteria in use. However, at Academia Sinica, twelve reaction types of initial, preceding and final stages (Kou, unpublished) were used at the early stage of our work, but those reactions were terminally classified only as R and S to represent resistant and susceptible series respectively. This makes the classification definite and clear cut. Those systems used for grouping reaction types are compared in Table 1 (Chiu *et al.*, 1963).

Results and Discussion

In the experiment, four isolates belonged to three physiologic races were involved in the study. Because of those isolates showing various reactions to different differentials, they were assumed of carrying different genotypes for virulency (Kou *et al.* 1963). And the host plants showing various reactions to the isolated cultures were presumably identified of having different blast-conditioning genes. Those genotypes can be identified by using the isolate cultures against those hybrid populations. In the trials, a tester-variety, Kung-shan-wu-shung-keng (KSWSK) was used as one parent in each of the crosses because of its susceptibility to all of the physiologic races collected in our laboratory. And depending upon its high susceptibility, KSWSK was tentatively assumed to carry recessive genes for the reaction. However, since the trials were carried out, reactions for susceptibility to blast pathogen showed dominance in some of the crosses, so it can be easily seen that susceptibility to the disease may be conditioned by dominant genes in certain cross (Hsieh, 1961; Suzuki, 1963). Furthermore, complementary reactions may also exist.

Table 1. Comparison of the classifying systems of reaction types

Descriptions	Academia Sinica	IARI		Abumiya 1955-58	Atkins 1956	Goto <i>et al.</i> 1960	Hashioka 1950	Latterell 1960	Padmanabhan <i>et al.</i> 1959
		1958-9	1960-2						
No response	Escaped*	I	R	0	0	HR	E	0	0
Small brown lesions, without enlarging tendency, diameter 0.5-1.0 mm	R (1)	R	R	b-g	1	R	D	1	A
Small brown lesions, with necrotic center, surrounded by yellowish ring, enlarging very slowly, 1.0-1.5 mm	R (2)	R	R	y	2	R	C	2	B
Violet or gray lesions with a pale center, surrounded by chlorosis, enlarging fairly slowly	S (3)	M	M	w	3	RS	B	3	C
Spindle shape lesions, with a pale or whitish center surrounded by light chlorosis of greenish tissue, enlarging rapidly	S (4)	S	S	p	4	MS	A	4	D
Expanding lesions of large size usually with water-soaked appearance, brown border and a pale center, enlarging very rapidly	S (4)	S	S	p	5	S	A	5	E

* Escaped = escaped plants; I = immune; HR = highly resistant; R = resistant; RS = resistant-susceptible; MS = moderate susceptible; S = susceptible; b = brown; g = green; y = yellow; w = white; p = purple

Therefore, the tester has shown a perfect susceptible phenotype to all races found; its genotypes for the disease reaction are neither completely dominant nor fully recessive, and the complementary factors are also present.

Of the results given in tables 2 and 3, hybrid generations of F_1 and F_2 are included. Notes of the F_2 reactions were dependent on single plants basis. However, seedlings being heavily inoculated, especially the susceptible plants, could not completely survive. So the F_3 population was not included in the study.

Of the inheritance of the hybrid progenies, crosses 62.106 (against races 3, 5 and x), 62.105 and 62.107 (against race 5 (3e)) gave a simple Mendelian ratio 3:1 with resistance dominant over susceptibility. The result agrees with those of Sasaki (1922), and reveals that the varieties of Taichung No. 179, Taichung No. 178, Chianungyu No. 280 and other have a single gene difference from the other parent of the crosses, governing the blast resistance. On the contrary, a single factor difference also occurred in the dominance of susceptibility. Crosses 62.102, 62.104 and 62.108 (against race 3(9a)) etc. provided with the evidences. In field condition, natural infection of the disease found to be varied continuously from resistant to susceptible by Oka and Lin (1957); biometrical method was applied to a hybrid progenies of Pei-ku (Indica) x Taichung No. 65 (Japonica). By using the method of K. Mather and by estimating the variance of heritable and non-heritable components, they found that one major gene was responsible for the resistance, and the susceptibility seemed to be dominant. Two dominant factors controlling resistance were found in cross 62.101 (against races 3(9a) and x (4a)). It supports Okada and Maedas' (1956) hypothesis that two to three dominant genes are concerned with blast resistance.

Susceptible varieties may also carry complementary genes for resistance. In cross 62.103 (against race x(4a)), a typical 9:7 ratio was segregated from Taichung No. 65 x KSWSK. Other examples as crosses 62.105 and 62.107 (against race 3(9a)) also confirm the results. These phenomena help to explain that the parents of the crosses may carry a pair of complementary genes. And a pair of the complementary gene can not exert their influence unless they are combined with the gene from the other pair. Similar results were reported by Hsieh (1961) under field condition.

Ratio of 3:13 of involving an inhibitor (crosses 62.103 and 62.108 against race 5(3e)) obtained from the crosses of two susceptible parents are also observed. These facts would be considered that the variety Taichung No. 65 (cross 62.103) and Taichung spe. No. 6 (cross 62.108) may have a pair of inhibitors and resistance genes. As soon as the segregation does, a small number of individuals which do not carry the inhibitor reveal resistance. For this point, more efforts should be paid for seeking further evidence to prove this results.

Table 2. Segregation for leaf-blast reactions in the progenies of several crosses at seedling stage to the isolates 9a of race 3 and 3e of race 5.

Parents & crosses	Races and isolates															
	3(9a)							5(3e)								
	Res.		Susc.			ratio	X ²	P	Res.		Susc.			ratio	X ²	P
	1	2	3	4	1				2	3	4					
Taichung spe. No. 6 KWSK (X62.108) F ₁ F ₂	16	12	72	24	1:3	0.125	0.75-0.50	34	20	38	184	3:13	0.115	0.75-0.50		
Taichung No. 65 KWSK (X62.103) F ₁ F ₂	40	10	30	41	27:37	0.037	0.90-0.75	30	18	5	8	3:13	0.059	0.90-0.75		
Taichung No. 154 KWSK (X62.104) F ₁ F ₂	16	8	32	20	1:3	1.753	0.25-0.10	36	4	26	64	27:37	0.234	0.75-0.50		
Taichung No. 178 KWSK (X62.105) F ₁ F ₂	5	72	24	8	9:7	0.347	0.75-0.50	100	36	3	12	3:1	0.029	0.90-0.75		
Taichung No. 179 KWSK (X62.106) F ₁ F ₂	3	40	8	10	3:1	0.000	1.0	3	16	8	14	3:1	2.541	0.25-0.10		
Kwan-fu No. 401 KWSK (X62.101) F ₁ F ₂	62	134	10	2	15:1	0.081	0.90-0.75	76	4	22	58	9:7	1.297	0.75-0.50		
Hsinchu No. 50 KWSK (X62.102) F ₁ F ₂	26	8	41	51	1:3	0.132	0.75-0.50	42	26	3	210	3:13	1.898	0.25-0.10		
Chianungyu No. 280 KWSK (X62.107) F ₁ F ₂	2	32	12	18	9:7	0.309	0.75-0.50	120	3	28	36	3:1	0.103	0.75-0.50		

Table 3. Segregations for leaf-blast reactions in the progenies of several crosses at seedling stage to the isolates 4a and 5a of race x.

Parents & crosses	Races and isolates															
	race x(4a)							race x(5a)								
	Res.		Susc.			ratio	X ²	P	Res.		Susc.			ratio	X ²	P
1	2	3	4	1	2				3	4						
Taichung spe. No. 6 KWSK (X62.108) F ₁ F ₂	*	6	3	25	0	3:1	0.158	0.75-0.50	21	*	4	52	80	1:3	0.150	0.75-0.50
Taichung No. 65 KWSK (X62.103) F ₁ F ₂	43	0	3	21	11	9:7	0.116	0.75-0.50	*				All			
Taichung No. 154 KWSK (X62.104) F ₁ F ₂	83	2	3	19	8	3:1	0.073	0.90-0.75	22	16	3	78	63	1:3	1.357	0.75-0.50
Taichung No. 178 KWSK (X62.105) F ₁ F ₂	56	3	8	12	5	3:1	0.694	0.50-0.25	5	38	11	18	18	3:1	0.149	0.75-0.50
Taichung No. 179 KWSK (X62.106) F ₁ F ₂	83	6	3	19	8	3:1	0.073	0.90-0.75	5	22	12	19	19	3:1	0.126	0.50-0.25
Kwan-fu No. 401 KWSK (X62.101) F ₁ F ₂	86	5	85	7	3	15:1	0.162	0.75-0.50	68	4	26	28	28	3:1	1.000	0.50-0.25
Hsinchu No. 50 KWSK (X62.102) F ₁ F ₂	2	56	6	19	4	3:1	0.192	0.75-0.50	38	1	29	38	38	9:7	0.050	0.90-0.75
Chianungyu No. 280 KWSK (X62.107) F ₁ F ₂	3	74	5	15	6	3:1	0.855	0.50-0.25	5	46	25	12	12	3:1	0.416	0.75-0.50

Ratio of 27:37 occurs in cross 62.103 (against race 3) and cross 62.104 (against race 5); this ratio furnishes the hint that there are three factors being involved in the hybrid families. Nevertheless, in cross 62.103, parent Taichung No. 65 gives a susceptible reaction of type 3; it still has two genes conditioning the reaction. On the other hand parent KSWSK has one gene conditioning the reaction. At the meantime, only the individuals carrying more than two pairs of genes show resistance. Besides, cross 62.104 has the same evidence of three factor; the cross includes one resistant parent and one susceptible. Therefore in the latter case the resistant parent should be assumed of having three resistance genes against race 5 and the other none. This fact can be considered as a cause of making blast inheritance complex.

Genic symbols used for blast-conditioning genotypes had been previously designated as Pi_1 , Pi_2 by Sasaki (1922), Nakatomi (1926) and Ramiah and Ramaswami (1936), and as R_1 , R_2 , R_3 by Okada and Maeda (1956). However, those designations do not seem to be applicable in representing the responses of the complex blast-conditioning genes as found in this study. A new symbolic model is hereby suggested by the author tentatively. Genotypes of the several major varieties used are postulated in table 4.

Of the genic symbols suggested in table 4, the letters "Pi" stand for dominant resistance, whereas "Cpi" is for complementary genes causing of resistance. "Spi" is suggested for susceptibility genes and the "I-pi" for dominant inhibitor. The subscript is for gene identification. For examples, " Pi_3 " means the dominant resistance gene identified by race 3; " Cpi_5 " represents the complementary gene which was found by race 5 and can create complementary resistance with gene " Cpi_5' ". " $I-pi_5$ " means the dominant inhibitor which can

Table 4. Symbols suggested for blast-conditioning genes

Varieties	race and isolates			
	3(9a)	5(3e)	x(4a)	x(5a)
Taichung spe. No. 6	Spi_3	Pi_5 I- pi_5	Pi_x	spi_x
Taichung No. 65	$Pi_{(1-2)'}?$	Pi_5 I- pi_5	Cpi_x	pi_x
Taichung No. 154	spi_3	$Pi_{(1-3)'}?$	Pi_x	spi_x
Taichung No. 178	Cpi_3	Pi_5	Pi_x	Pi_x
Taichung No. 179	Pi_3	Pi_5	Pi_x	Pi_x
Kwan-fu No. 401	Pi_3 Pi_7	Cpi_5	Pi_x Pi_7	Pi_x
Hsinchu No. 50	spi_3	I- pi_5	Pi_x	Cpi_x
Chianungyu No. 280	Cpi_3	Pi_5	Pi_x	Pi_x
KSWSK	Spi_3	i- pi_5 pi_3	pi_x	Spi_x
	$pi_{(1)'}?$	Cpi_5'	cpi_x'	
	Cpi_3' pi_3	$pi_{(1-3)'}?$		

inhibit the effect of resistance gene "Pi₅".

As the facts discussed, some entirely different segregations are found in the study. Generally, resistance appears dominant over susceptibility about one half out of the thirty-two tests (Goto, 1959; 1960); the recessive and other segregations show the other one half. Incidentally, it seems to be obvious that different types of segregations may be possibly obtained from the same cross against different pathogenic cultures as well as from a single culture against different hybrid progenies. In concerning with Goto *et al.*'s (1961) report, they found that variety Asahi was susceptible to many physiologic races in Japan; however, it showed high resistance to some others. This apparent evidence supplies the idea that the blast infection is conditioned by many genetic factors. Takahahi (1963) concluded that five to nine pairs of genes may be involved in conditioning blast phenotypic reactions. These facts found and reviewed suggest that the resistance appears only at the combination of certain host to a specific physiologic race. The interactionship being found lends to the conclusion that a host-parasite interaction similar to those of flax and flax rust (Flor, 1955), sorghum and smut disease (Holton, 1969), apple and apple scab (Weitt *et al.* 1959) or potato and late blight disease (Gallegly and Niederhauser, 1959) may exist in rice plants and blast fungus (Takahahi, 1963). Whether and when the mechanism of the genetic relationship may be worked out, it should depend upon the successful development of artificial sexual or asexual hybridization of the fungus.

Summary

Inheritance of the resistance to rice blast disease in the present study was investigated on lesion basis. Several varieties from the differentials, and four isolates belonged to three physiologic races of blast fungus were used to study the resistance behavior of rice plants. Variety, Kung-shan-wu-shung-keng found susceptible to all of the physiologic races used as one parent of the crosses, for the purpose of identifying numbers of blast-conditioning genes carrying by the varieties. Blast-conditioning genes were found to be differed from one, to three factors. And an inhibitor was also involved in one of the crosses. Those factors investigated may be dominant, recessive or complementary, depending upon the cultures used.

水稻抗稻熱病遺傳習性之研究

吳 旭 初

本試驗研究稻熱病的反應，是根據水稻苗期所發生病斑的形狀作研究的基礎，八種鑒別品種和三種病菌生理小種作為本研究的材料。崑山五香粳種因為受感於所有的生理小種，用做親本和其他品種雜交，測驗不同品種所含的抗病基因數。一般水稻品種具有一到三個抗病基因，此外尚發現一個抑制基因。這些抗病基因，有顯性的，有隱性的，亦有互補的。

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