GENIC ANALYSIS IN RICE

V. Genes for the resistance to leaf and neck blast diseases in rice

SUNG-CHING HSIEH⁽¹⁾
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Knowledge of genetics for resistance to blast disease is important to rice breeders. It has been suggested that the *indica* type is more resistant to the blast disease than the *japonica* type (Hashioka 1950, Takahashi 1951, Hsieh *et al.* 1961), In the past, many genetic experiments on the resistance to blast disease were conducted by using mainly *japonica* varieties (Nakamori 1936, Yamazaki 1959, Uzihara 1960); few workers (Hashioka 1950, Okada and Maeda 1956) compared the inheritance of resistance between the two types.

The method to determine the degree of disease infection was one of unsolved problems in carrying out genetic experiments on blast resistance. As methods used by various workers different, their results can not be easily brought together.

The writer (1961) previously studied the inheritance of blast disease resistance using *indica* and *japonica* varieties by the seedling inoculation method. It was found that at least two genes are concerned for the resistance. In the present experiment, beside the leaf blast, neck blast resistance was also studied with F_2 plants grown under the condition of natural infection. In addition to this, heritability and genetic correlation for both leaf and neck blasts were estimated.

Materials and Method

During the second crop-season of 1958, 16 F_2 crosses and their parents were planted in an experimental field located at Tunshu, Taichung Prefecture, where the blast disease prevails in both the first and second crop-seasons. In the first crop of 1960, six F_2 crosses were planted in Kwanyin, Taoyuan Prefecture. List of the materials used is shown in Table 1.

In order to promote disease epidemic, a highly susceptible variety Wuhsiang-ken, was grown in "spreader-rows" around the plots and inside the

⁽¹⁾ Senior Agronomist of Taiwan Agricultural Research Institute, Taipei, Taiwan

Table 1. Strains used for genetic studies of blast disease resistance

Strain No.	Variety name	Source	Strain No.	Variety name	Source	
P123	Taichung No. 65	Taiwan (Ponlai)	J 303	Aikoku	Japan (<i>japanica</i>)	
P124	Taichung No. 150	Taiwan (Ponlai)	J 309	Chao-ei-tao	Japan (japanica)	
P 130	Taichung No. 171	Taiwan (Ponlai)	J 312	Bansaku	Japan (japanica)	
P137	Kuwan-fu No. 401	Taiwan (Glutinous)	J 311	Hats-nishiki	Japan (japanica)	
P138	Taichung-gl. No. 46	Taiwan (Ponlai)	J 314	Zuiho	Japan (japanica)	
P140	Chianung-yu No. 242	Taiwan (Ponlai)	J 320	Toyokuni No. 1	U.S.A.	
P148	Kauhsiung No. 18	Taiwan (Ponlai)	J 321	Nolin No. 11	Japan (japanica)	
P161	Taitung No. 24	Taiwan (Ponlai)	U401	Century patna 52	U. S. A.	
P163	Nung-yu gl. No. 8	Taiwan (Glutinous)	M503	Siau-nan-sien	China mainland	
P165	Chianunyu No. 478	Taiwan (Ponlai)	M511	Nan-te-how	China mainland	
P167	Pai-kan-tao	Taiwan (Ponlai)	M513	Kinmen-red rice	China mainland	
P168	Tainung No. 38	Taiwan (Ponlai)	M514	Hong-nao	China mainland	
P169	Chia-nung-yu No. 280	Taiwan (Ponlai)	D-155-8	Mutant	Taiwan (Ponlai)	
P170	Taichung No. 177	Taiwan (Ponlai)	C-1	Wu-sian-ken	China mainland	
T201	Pai-mei-fuen	Taiwan (Native)	D-65-1	Mutant	Taiwan (Ponlai)	
T203	I-kun-pao	Taiwan (Native)	La-8-4	Mutant	Taiwan (Ponlai)	
T208	Wu-liap-chin-yu	Taiwan (Native)	7101	Jodon's marker	U. S. A.	
T213	Liu-to-tze	Taiwan (Native)	7111	Jodon's marker	U. S. A.	
T215	Wu-liap	Taiwan (Native)	7114	Jodon's marker	U. S. A.	
T220	Swan-chian	Taiwan (Native)	7163	Jodon's marker	U. S. A.	
T233	Taliap-chin-yu	Taiwan (Native)	7164	Jodon's marker	U. S. A.	
T237	Wou-lan-chu	Taiwan (Native)	7165	Jodon's marker	U.S.A.	
T234	Wu-kao	Taiwan (Native)	7237	Jodon's marker	U.S.A.	
Т248	Taipei-wu-kao	Taiwan (Native)				
J 302	Nakamura	Japan (<i>japonica</i>)				

plots between rows to be tested. The inoculum was furnished from natural deposits of spores from the air. To induce heavy infection, the field was flooded and drained as often as possible. Spray of water was given on the leaves after the evaporation of dew drops on dry days. The field was dressed with 250 kgs of nitrogen per ha.

The leaf infection of adult plants was scored by an index number indicating the percentage of lesion area which is shown in Table 2.

Table 2. Index-numbers showing the percentage of diseased leaf area

<u> Caralina e esperar de la plane de la colo</u>		<u> </u>	120	11 A. A. A.		artini di Ta			industria.		
% of diseased	50 100	Maria Albania						***	256		
	0 0.2	0.5	1	2	5	11	25	55	80	100	120
leaf area											
						1.00			1	F. P. S. S. S. S.	
Index number	0 1	2	3	4	5	6	7	- 8	8.5	8.8	9
	Path A Labada										

Since this classification was too complicated, the writer tried further to group index number into five classes by a statistical method so as to maximize the difference between line means relative to that within lines. However, the result showed that the grouping differed according to the season. Therefore, the resistant and susceptible classes in F_2 had to be determined by comparing with the mode of variation in parental lines.

1. Inheritance of leaf-blast resistance under field condition

Table 3. Variations in leaf-blast resistance of F_2 and parental plants (a) Tunshu Experimental field

Parents and				Dis	ease	ind	ex r	um	ber		**	1	Segr.		
crosses	0	1	2		4			7		0 =	8.8	To	tal	X^2	P
	1				4		- 0		-	8.5	8.8	9	ratio	'	
P169		13	* 3	1] 1	7		
P169×T220	77	26		1	1							10	5 1:0		
T220	67	95	14	13	6							19	5		
T248	34	4										3	8		
T248 × M511	370	90	42	11	2	10	2					52	7 1:0		
M511	142	48	2	1								19	3		
$T220 \times T248$	71	24	10	3		3	2	1				11	4 1:0(?)		
P123						5	3	15	19			4	2		
P123 × D-65-1							3	103	204	58	2	6 37	6 0:1		
D-65-1								6	16	14	2	3	8		
P123 × C-1							1	36	188	67	23 3	2 34	7 0:1		
C-1						19	20	25	30	21	5	12	0		
P123×7164						1		19	37	45	55 9	- 1			
7164									7	19	17	3 4	1 1		
J 321									4	10	17 7) 11	0		
J 321 × P123							6	10	17	52	25	11	0 0:1		
P123×7165	1	13	19	24	17	8	5	7	1	V.		9	5		
		5	7		-		38	3	•				9:7	0.542	0.3-
7165					15	22	14	22	25	3		10	1		0.5
P123×T248	. 7	25	12	12	4	9	9	4	2	1		7	8		1.50
A CONTRACTOR			53					25				4 4	3:1	1.610	0.2-
T248	116	67	20	3								20	6		0.3
P123×7237	6	50	24	23	16	19	9	4	6	,		15			
			119				3	8	ı				3:1	0.049	0.8-
7237	21	54	5	3	1							8	4		0.9
J 321									4	10	17 7) 11	0		
J 321 × U401		57	42	67	43	35	34	24	15	6	4	3 33	i .		
in the second se				244						86		-	3:1	0.198	
U401	1	89	32	18	9	2						15	1		0.7

		T7 .		
1	(b)	Kwanvin	experimental	held
١	. ~ /	12 11 (411) 411	CAPCILITICAL	IICIG

Parents and			I	Disea	ise i	inde	x nt	ımbe	r			m . 1	Segr.	779	
crosses	0	1	2	3	4	5	6	7	8	8.8	9	Total	ratio	X ²	P
P123						1.	12	25	20	2		60			
$P123\times M514$			6	13	11	8	6					44			100
Section 1				30		. 1	4						3:1	1.091	0.2-0.3
M514	8	8	15	5	1							37			
P167		2	35	18	4	•						59	-		
$P167 \times D-155-8$		2	10	77	88	71	23	13	4			288			
				177			11	1					9:7	3.175	0.05-0.1
D-155-8						20	19	14	3			56			1 1
J 314			*			. 5	12	17	22	4		60			
$J314\times T203$		64	27	3 1		2	13	7	_1			114			
and a contract of		9	1				. 2	3			*		3:1	1.415	0.2-0.3
T203	29	11										40			
T201	. 18	2										20			
$T201 \times J302$		27	13	9		46	71	62	21	8	9	266		·	
			49			-		21	7				3:13	0.019	0.8-0.9
J 302						4	24	5	6	1		40			
M513	19	1										20	-		
M513× J 312	8	5	3	1		18	31	18	2			86			
		17					69)-					3:13	0.062	0.7-0.8
J 312							1	12	13			26			
M153	19	1			. : "		۷.					20			100
M513× J 309	119	13	21	-5		8	50	. 9				245			
		178					67						3:1	0.733	0.3-0.5
J 309							7		14	2	1	57			

According to the above mentioned criterion, segregation of leaf-blast resistance was observed. The frequency distributions as shown by the index numbers in Table 2 are given in Table 3.

As Table 3 (a) shows, the F_2 plants of most crosses between resistant strains, were all resistant but in crosses $T248 \times M511$ and $T220 \times T248$, a few were moderately resistant.

As shown in the same table, crosses between susceptible strains, P123×D-65-1, P123×C-1, P123×7164 and J321×P123, the F_1 s were susceptible and all F_2 plants were also susceptible. In the F_2 of P123 and 7165, both parents being susceptible, 57 highly resistant and 38 susceptible plants were found. They fitted quite well to a 9:7 ratio. In crosses between susceptible and resistant strains, P123×T248, P123×7237 and P123×U401, the F_1 s were resistant, and the F_2 showed a 3 resistant to 1 susceptible ratio. These differences in

segregation ratio indicated that different genes are responsible for the resistance of parental strains. We may assume that a resistant gene Pi_1 gives stronger resistance than Pi_2 and the presence of both brings about a high resistance to leaf blast disease.

Table 3 (b) shows the data obtained at Kwanyin experimental field in Taoyuan Prefecture in the first crop of 1960. As shown in Table 3 (b), crosses between resistant and susceptible strains, i. e., P123×M514, J314×T203 and M513×J309 showed a 3 resistant and 1 susceptible segregation ratio, indicating that the resistance is controlled by a dominant gene. However, in the cross P167×D-155-8, 9 resistant and 7 recessive plants were segregated showing that at least two genes are concerned for resistance to leaf blast.

In crosses T201 (resistant) \times J302 (susceptible) and M513 (resistant) \times J312 (susceptible), the F₂ ratio seemed to be somewhat different from that obtained previously, fitting a 3:13 ratio. If the 3:13 ratio is true, there should be an inhibitor for the resistance to leaf-blast. Since the expression of blast resistance is largely affected by environmental conditions, further studies of these crosses using different methods are needed to confirm this assumption.

2. Comparison between the percentage of diseased leaf area and the lesion types.

The writer (1961) formerly determined the degree of blast infection by the lesion type. The lesions on the leaves were classified into six types, O, A, B, C, D, and E. Among them, types O, A and B were considered as resistant, while types C, D and E to be susceptible. In order to test whether this classification fitted to the percentage of infected leaf area, the number of resistant and susceptible F_2 plants obtained by the two methods were compared. The results are given in Table 4.

Table 4 Comparison between the percentage of diseased leaf area and lesion types in F₂

Localties	Crosses	Res	istant	Susceptible	Total	Segr. ratio	X^2	P
	(a	30	14	44	3:1	1.091	0.2-0.3
	P123×M514 {	ъ	29	15	44	3:1	1.939	0.1-0.2
		a	177	111	288	9:7	3.175	0.05-0.1
	P167 × D-155-8	b	107	83	190	9:7	0.001	0.95-0.98
Kwanyin	(a	408	128	536	3:1	0.358	0.5-0.7
	M503 × J 301 {	ь	433	100	533	3:1	11.032	0.01 <p< td=""></p<>
		a	178	67	245	3:1	0.075	0.3-0.5
	M513×J309 {	b	188	31	219	3:1	13.687	0.01 < P

	P123×M503	ſ	a	61	14	75	3:1	1.604	0.2-0.3
	1 123 × 141,003	1	b	67	14	- 81	3:1	2.577	0.1-0.2
	T201 × J 302	5	a	69	220	289	1:3	0.105	0.1-0.2
Tunshu	1 201 × 3 302]	b	34	143	177	1:3	3.166	0.05-0.1
	T237× J 310	-	a	110	25	135	3:1	3.025	0.05-0.1
	2201 × 3 010	1	b	104	27	131	3:1	1.346	0.2-0.3
	7101 × J 312	[a	92	42	134	3:1	2.876	0.05-0.1
	, 101 1 3 3 3 1	ι	b	104	29	133	3:1	0.724	0.3-0.5

Note: a: Classification by the percentage of diseased area

b: Classification by disease lesion types

As shown in Table 4, the segregation ratios obtained by the two methods fitted very well to the expected ratios in the majority of crosses at both places but in two crosses they were not consistant however. It is then considered that the two methods can be simulteneously used.

3. Inheritance of the resistance to neck blast.

During the first crop season of 1959, 13 F_2 populations were planted at Tunshu experimental field together with their parental lines, in order to get more data on the inheritance of leaf-blast resistance. However, the prevalence of leaf blast was not serious enough in that year. The neck blast was quite serious at maturity, so that the inheritance of neck blast resistance was observed.

The degree of neck resistance was expressed by the percentage of infected panicles. The range of variation in the parental lines was compared with that in F_2 s to estimate the number of resistant and susceptible F_2 plants. The data thus obtained are given in Table 5. As the table shows, 3:1, 9:7 and 27:37 ratios were assumed. There might be at least three genes controlling the resistance to neck-blast disease.

As it will be shown later, the resistance to neck blast is in some crosses, correlated with the resistance to leaf blast, but not in other crosses. This suggests that the genes for leaf blast resistance simultaneously control neck-blast resistance, but there are additional modifiers for the latter. The writer has already assumed two pairs of genes Pi_1 and Pi_2 for leaf blast resistance. They may be operative also for neck blast resistance. Assuming that there are three genes for the neck blast resistance, and the third gene Pi_3 is responsible only for neck blast resistance, the mode of segregation for neck blast may be explained well with a few exceptions.

Strain P123 is susceptible to leaf blast, it may have susceptible genes pi_1 pi_2 . It also showed a serious infection of neck blast; this strain may then be assumed to have susceptible gene pi_3 for neck blast. Strains P124, P138, which showed the same reactions regarding the leaf and neck resistance, may also be of the genotype pi_1 pi_2 pi_3 .

Table 5. F₂ Segregations for neck-blast resistance

	***		%	of d	isea	sed	pani	cle				Segr.		
Crosses											Total		X^2	\mathbf{P}_{i}
	10	20	30	40	50	60	70	80	90	100		ratio		
P123 P123× J 303	10	11	21	14	9	9	4 13	3 3	3 2	3 3	13 95			
	** '	5	6					39	• • •			9:7	0.289	0.5-0.7
J 303 P 123 × P 167	10	11	10	10	2 8	7	2 16	$\frac{2}{12}$	$\frac{2}{10}$	- 3 5	13 99			
			49					50		· ,		9:7	1.561	0.2-0.3
P167 P124 P124 × P140	21	11	8	6	7 22	8 2 6	18 9 6	15 7 5	21 7 3	18 8 1	80 40 89			
	,		6					43				9:7	0.768	0.3-0.5
P140 T124×T208	5 62	4 27	7 18	3 18	21	7	7	10	5	4	19 179			
	89		3	6		35			19			9:3:3:1	7.067	0.05-0.1
T 208 T 124 × T 215	36 12	$\frac{2}{2}$	2	4	7	. 1	11	7	8	15	38 69			
		,	27					42				27:37	0.287	0.05-0.1
T215 P138	7	6		4			1		5	24	30 30			
P138×T215	18	2	4	3 42	7	8	4_	6	0	38	92	27:37	0.456	0.02-0.05
T215	7	6	7	44	6						30	21.01	0.430	0.02 0.00
P140 P140× T233	6 35	3 12	3 10	7	4 8	4	4	4	2	6	23 94			
			74		-	٠		20			5.5	3:1	0.694	0.3-0.5
T233 P140×T215	5 22	4 8		6 12	3 9	8	5	8	4	7	26 95			
	5	, .	63					32				3:1	3.820	0.05-0.10
P167 P167×La-8-4	14	11	14	15	9	8	18 5	15 7	21 8	18 9	80 96			
			63					33				3:1	4.500	0.02-0.05
L-8-4 P167× P168	12 35	7 10	2 4	3 7	- 3 2	2	2	5		8	27 75			
			58			-		17				3:1	0.206	0.5-0.7
P 167 × D -155-8	21	12	11	19	6	2	12	7	6	20	116			
7 POO			69			•	2	47		16	22	9:7	0.478	0.3-0.5
J 302 J 302 × T 234	18	4	10	13	_20	1 4	3 9	7	3 2	15 3	90			
	·		65			•		25			00	3:1	0.370	0.5-0.7
T201 T201 × J 302	7 16	8 3	5 4	5 17	5 13	4	5	5	8		30 95			
udani. Medigijana sum			53			-	, 3	42	3	15	22	9:7	0.007	0.9-0.95
J 302						1			3	10	1 22	1	<u> </u>	<u> </u>

Strain P140 showed a moderate resistance to both leaf and neck blasts. In its cross with P124 $(pi_1 \ pi_2 \ pi_3)$, a 9:7 ratio was found. Its genotype may then be assumed to be $pi_1 \ Pi_2 \ Pi_3$. Strain P167 is resistant to leaf blast and moderately resistant to neck blast; its crosses with P123 $(pi_1 \ pi_2 \ pi_3)$ and P124 $(pi_1 \ pi_2 \ pi_3)$ all showed a 9:7 ratio. Therefore, the genotype of P167 should be $Pi_1 \ pi_2 \ Pi_3$. Next, In the F₂s of crosses of J303×P123 $(pi_1 \ pi_2 \ pi_3)$ a 9:7 ratio was obtained regarding neck blast. In the cross between P124 $(pi_1 \ pi_2 \ pi_3)$ and T208, a 9:3:3:1 ratio was found. Therefore, the genotype of strain T208 should be $Pi_1 \ pi_2 \ Pi_3$.

Strain T215 is highly resistant to both leaf-and neck-blast diseases. When it was crossed with P138 $(pi_1 \ pi_2 \ pi_3)$ which is very susceptible, a 27 resistant to 37 susceptible ratio was found regarding neck blast. Therefore, the genotype of T215 would be $Pi_1 \ Pi_2 \ Pi_3$. The cross T233 (highly resistant to both leaf and neck blasts)×P140 $(pi_1 \ Pi_2 \ Pi_3)$ showed a 3 resistant and 1 susceptible ratio. Then, strain T233 may also have $Pi_1 \ Pi_2 \ Pi_3$.

Thus it was assumed that the resistance to neck blast is due to three dominant genes.

The above-mentioned assumption of genotypes for parental strains, and the F_2 ratios to be expected from the genotypes are listed in Table 6. It is found from the table that the observed ratios fit well to the expected ones.

C		P123	P124	P138	P140	
	rosses	$pi_1 pi_2 pi_3$	pi ₁ pi ₂ pi ₃	pi_1 pi_2 pi_3	pi ₁ Pi ₂ Pi ₃	
P124	pi_1 pi_2 pi_3	(0:1)	(0:1)	(0:1)	9:7	
P167	$Pi_1 pi_2 Pi_3$	9:7	9:7	(9:7)	(9:7)	
J 303	$Pi_1 pi_2 Pi_3$	9:7	(9:7)	(9:7)	(9:7)	
T201	$Pi_1 pi_2 Pi_3$	(9:7)	(9:7)	(9:7)	(9:7)	
T208	$Pi_1 pi_2 Pi_3$	(9:7)	9:3:3:1	(9:7)	9:7	
T215	$Pi_1 Pi_2 Pi_3$	(27:37)	(27:37)	27:37	3:1	
T233	$Pi_1 Pi_2 Pi_3$	(27:37)	(27:37)	(27:37)	3:1	

Table 6. Genotypes assumed for parental strains and F_2 segregation ratios to be expected for neck-blast resistance.

4. Phenotypic and genetic correlations between leaf-and neck-blast resistances and heritability values.

It is usually experienced by rice breeders that the resistance to leaf blast is not always intimately associated with that to neck blast. A question may then arise as to whether the leaf and neck blasts resistances are controlled by

the same genes or not. Hashioka (1950) is of the opinion that resistances in different organs may be independent of one another.

In order to make this point clear, phenotypic and genetic correlation coefficients between leaf-and neck-blast resistances were compared. The formula employed by the writer for computing genetic correlation is

$$rg = \frac{\text{Cov. ab } F_2 - \frac{1}{2} (\text{Cov. ab } P_1 + \text{Cov. ab } P_2)}{\sqrt{\{\text{Va } F_2 - \frac{1}{2} (\text{Va } P_1 + \text{Va } P_2)\}\{\text{Vb } F_2 - \frac{1}{2} (\text{Vb' } P_1 + \text{Vb } P_2)\}}}$$

Table 7. Correlation between leaf-and neck-blast resistances

	Correlation	ı coeficient
Parent and crosses	Phenotypic correlation (r)	Genetic correlation (rg)
P123	0.353**	
P163	0.306*	
P167	0.028	
T234	0.235	
J 311	0.457**	
7101	0.746**	
7111	0.073	
P123×7114	0.497**	0.094
P123×7165	0.354**	0.957**
P123×7101	0.228	0.607**
P123×P130		0.7 55**
° P123×P148		0.910**
P123×P161		0.354*
P123×7237	0.120	
P123×P167	0.013	
P124×T213	0.435**	
P138×T234	0.475**	
P167×D-155-8	0.248	
J 313× T208	0.853**	
M506×T213	0.103	

Where the suffices a and b show leaf and neck resistances respectively. The phenotypic and genetic correlation coefficients thus calculated are shown in Table 7. As the table shows, the phenotypic correlations between leaf and neck resistances were significant in five cross-combinations, and not significant in the other five. The parental strains also showed the same tendency. Therefore, it may be said that whether the leaf-blast resistance is correlated with the neck blast resistance depends on strains. As also shown in table 7, however, genetic correlations were significant in the majority of crosses tested.

This suggests the genes controlling leaf blast resistance exert influence on the neck blast resistance, but there are other modifing genes for the latter. Thus, the writer has assumed as mentioned in the previous paragraph, that two genes Pi_1 and Pi_2 are responsible for both leaf and neck resistances, while the third gene Pi_3 is only for neck blast resistance.

In order to evaluate the efficiency of selection for resistance, heritability values were calculated from the F_2 data by the formula given below.

$$h^2 = \frac{VF_2 - \frac{1}{2}(VP_1 + VP_2)}{VP_2}$$

Table 8. Heritability values for leaf-and neck-blast resistances

Crosses		Heritability values (h²)									
 Crosses		Leaf blast		Neck blast							
P123× P148		0.703		0.852							
P123× P161				0.456							
P123× P165		0.724		0.757							
P123×T248		0.832		0.820							
P123×7101		0.500		0.360							
P123×7114		0.952									

The results are shown in Table 8. As the table shows, heritability values for both leaf and neck resistances were quite high, indicating that selection can be effective under the conditions of this experiment.

Discussion

Sasaki (1922) first reported the inheritance of blast disease resistance. He concluded that the resistance behaves as a simple factor dominant over the susceptibility. Later, Nakatomi (1926) showed that resistance is controlled by two pairs of genes, Nakamori (1936) also made genecological analysis of the resistance of rice varieties to blast disease and noticed a marked difference in susceptibility, that was demonstrated when the same variety was grown at two different places. Hashioka (1950) studied leaf, neck as well as node blast diseases in the cross between distantly related rice varieties, showing that at least two genes would be responsible for the resistance to leaf-and neck-blast diseases. He also assumed that genes controlling leaf-blast resistance are independent of those for neck-and node blast resistance.

In the present study, it was assumed that two dominant genes were responsible for leaf-blast resistance. The monohybrid and dihybrid modes of segregation found by previous workers and also by the present author might be explained to be due to differences in the genotypes of parental lines. It

was assumed further that the neck-blast resistance was controlled by the third gene which would work in cooperation with the two genes for leaf-blast resistance. This assumption is different from that of Hashioka (1950) who assumed that the resistant genes for leaf blast differ from those for neck as well as node resistance. Hashioka's view does not seem, however, to account for the generally recognized tendency for leaf and neck resistances to be correlated (Abumiya 1959).

Abumiya (1959) assumed three genes R_1 R_2 and S for blast resistance. R_1 contributes the strongest resistance, R_2 is thought to have many polymeric alleles which account for varietal differences. S brings about susceptibility, and its effect is active in the spring supressing the action of R_1 and R_2 then the genotype R_1 R_2 S becomes susceptible. But S is inactive in summer, letting R_1 R_2 S to be resistant.

Okada *et al.* (1956) assumed from statistical studies on the inheritance of blast disease that at least three dominant genes are concerned with blast resistance. The three genes for neck blast resistance assumed by the present author may be comparable with Okada's three genes. In addition to these, the resistance may increase due to the presence of various dominant genes, as assumed by Okada *et al.* (1956).

The next problem to be discussed would be physiological races with differencial reactions to varieties. In the Taiwan Agricultural Research Institute, this problem has been studied for years and 19 races have been identified. If in the writer's natural infection experiments, different races were found to be involved, they would work as a disturbing factor for segregation patterns. Therefore, in the future, segregation mode of blast disease resistance should be studied using different races already identified.

Further, "disease-escaping" is an important factor in observing the inheritance of neck-blast resistance. As was pointed out by Hashioka (1950) and others, it results from differences in weather conditions at the heading time. Therefore strictly speaking, it may be difficult to determine the mode of inheritance of neck-blast resistance, Hashioka (1950) assumed however, that disease-escaping due to different heading dates is relatively not important, because the correlation between heading date and neck blast infection was not significant. We may assume that the segregation patterns observed in the fields are as a whole reliable.

Summary

Genetic experiments for leaf- as well as neck-blast resistances were made with 48 varieties from various countries. The inheritance of resistance in adult plants was conducted in the field which was infected by natural infection of

blast disease. The F_2 s of crosses between resistant and susceptible strains generally showed a 3 resistant and 1 susceptible ratio, but some of those between two susceptible strains showed a 9:7 ratio. This suggested that two genes were concerned; two genes Pi_1 and Pi_2 were assumed,

As for neck-blast resistance, 3:1, 9:7 and 27:37 ratios were found from the F_2 data. It seemed that there might be at least three genes. The resistance to neck blast was in some crosses correlated with the resistance to leaf blast but not in others. This suggested that the genes for leaf blast resistance might control neck-blast resistance as well, and the third gene Pi_3 might work as a modifier. Based on this assumption, the genotypes of the strains used in various crosses were assumed.

Heritability value for both leaf-and neck-blast resistances ranged from 0.360 to 0.952, indicating that selection could be effective in the conditions of this experiment.

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稻之遺傳因子分析第五報 葉及穗頭稻熱病抵抗性之遺傳因子

謝順景

本試驗以日本、美國及臺灣各地之 48 種稻品種 爲供 試材料,配合 各種 可能的 組合 (Combination) 互相雜交,其後代分別種植於臺中縣東勢及桃園縣的觀音鄉,任其自然發病,併調查各系統間發病程度及分離情形。葉稻熱病發病之輕重以病斑面積率表示之,穗頸稻熱病則以罹病百分率表示之。

抗稻熱病之分離情形大致與第二報在玻璃室內試驗之結果相同。即抗病×抗病之後代大部分為抗病性,感病×感病之後代大部分為感病,抗病×感病 F_1 為抗病, F_2 大部分為 3:1 之分離比,但亦有 9 抗病: 7 感病之分離比,表示抗病因子有 Pi_1 及 Pi_2 之兩對。 穗 頸熱病有 3:1,9:7 及 27:37 之分離比,如是可能受三對遺傳因子之支配。葉稻熱病與穗 頸稻熱病之表現型相關(Phenotypic correlation)因雜交組合之不同,而有顯著性與不顯著性,因此支配穗頸稻熱病之部分因子,可能與葉稻熱病者相同。除支配葉稻熱病之 Pi_1 , Pi_2 以外,倘有 Pi_3 支配穗頸稻熱病,葉稻熱病與穗頸稻熱病抵抗性之遺傳力(Heritability)介於 0.360 與 0.952 之間,顯示選拔(Selection)之效果大。

Literature Cited

- ABUMIYA, H. Phytopathological studies on the breeding of rice varieties resistant to blast disease. Tohoku Agr. Exp. Sta. Report. No. 17. 1959.
- CHANG, T. T. Techniques in determining varietal reactions to blast pathogen. Plant Industry Division, JCRR Taiwan. Report of Far-east Seed Improvement Conference. Manila 1961.
- HASHIOKA, Y. Inheritance and breeding for blast resistance in rice. Research on Breeding Series 4, 1949.
- HASHIOKA, Y. Studies on the mechanism of prevalence of the rice plant disease in the tropics. Technical Bulletin No. 8. Taiwan Agricultural Research Institute 1950.
- HSIEH, S. C., C. C. CHIEN and S. C. HUANG. Genic analysis in rice II. Inheritance of rice seedlings to blast disease, *Piricularia Qryzae* Taiwan Jour. Agr. Res. **10**: (2) 1-6. 1961.
- NAKATOMI, S. On the variability and inheritance of the resistance of rice plants against the rice blast disease Jap. Jour. Gent. 4(1): 31-38. 1926.
- NAKAMORI, E. Local variability of resistance to blast disease in rice varieties. Agr. and Hort. 11(3): 823-834. 1936.
- NAGAI, I. Japonica rice, Yokendo Ltd, Tokyo pp. 365-370.
- Ou, S. H., and K. M. LIN. Preliminary report on rice breeding for blast disease resistance in Taiwan. Jour. Asso. China. New Series 21:50-58.
- MATHER, K. Biometrical genetics 1949
- OKADA. M., and H. MAEDA. Inheritance of resistance to the leaf blast in crosses, between foreign and Japanese varieties of rice. Tohoku National Agr. Exp. Station Report No. 10: 59-68. 1956.
- OKA, H. I., and K. M. LIN. Genic analysis of resistance to blast disease in rice (by biometrical genetic method). Jap. Jour. Genet, 31(1): 20-27. 1957.
- SASAKI, R. On the inheritance of tolerance to blast disease in rice Jap. Jour. Genet. 1(2): 81-85. 1915.
- TAKAHASHI, Y. Phytopathological and breeding studies on test of resistance to blast disease in rice. Report of Hokaido Agr. Exp. Station 3: 1-59. 1951.
- UZIHARA, K. Breeding on blast disease resistant varieties of rice Jap. Jour. plant Breed. 10: 113-114. 1960.
- YAMAZAKI, G., and N. MURATE. Studies on genetics of blast disease pathogen. Jap. Jour. Genet. 49: 316 1959.
- Proceedings syposium of studies on the cause of low yield of rice in tropical and subtropical regions. Taiwan Agr. Res. Inst. 1961.