Methods and Strategy for Monitoring Race Distribution and Identification of Resistance Genes to Bacterial Leaf Blight (*Xanthomonas campestris* pv. *oryzae*) in Rice

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Abstract

For controlling bacterial leaf blight of rice, caused by Xanthomonas campestris pv. oryzae, the use of resistant cultivars is the most economical and effective method due to the scarcity of effective bactericidal agents and to the need for preserving the environment. Against this background, the resistance genes to this disease so far identified will be reviewed. Under the collaboration between the Tropical Agriculture Research Center, Japan and the International Rice Research Institute, Philippines, the genes identified were rearranged from Xa-1 to Xa-12 based on the numbering system of rice gene symbols and them near-isogenic lines with single resistance genes were developed. By using these near-isogenic lines, the strategy for monitoring the race distribution and the methods of identification of new resistance genes are reviewed.

Discipline: Plan breeding Additional key words: allelism test, differentials, near-isogenic line, plant disease

Introduction

Bacterial leaf blight caused by *Xanthomonas* campestris pv. oryzae is responsible for heavy damage to rice in the rice-growing countries. For controlling the disease, the use of resistant cultivars is the most economical and effective method due to the scarcity of effective bactericidal agents and to the need for preserving the environment.

Since the pathogenic specialization of the causal bacterium of rice bacterial leaf blight was first reported in Japan, a number of reports have been published on the variability of the pathogenicity of the bacterium and of the resistance of rice cultivars.

Since the rice cultivars and bacterial races used as differentials in each country were different, the respective groups of scientists found it difficult to distinguish the resistance gene(s). In order to control the disease, it was deemed important to set up a common base to define the relationship between the virulence of the bacterial races and the resistance of rice cultivars to the races. Recent research on bacterial leaf blight has been carried out mostly in Japan and at IRRI (International Rice Research Institute, Philippines) and in both locations different differential cultivars and bacterial groups were used.

Against this background, the collaborative studies on the resistance to rice bacterial leaf blight between Japan and IRRI were carried out for establishing a common base of research and for controlling the disease.

This paper deals with the results of the collaboration and the strategy for monitoring the race distribution and for the identification of resistance genes using the near-isogenic lines developed under the collaboration.

Resistance genes to bacterial leaf blight of rice

1) Genes identified in various countries

The identification of the resistance genes in each country, except for Xa-kg, was based on analyses using local bacterial isolates. As a result of the genetic studies on the resistance to the disease conducted

Gene identified	Cultivar analyzed	Isolate used	Note	Reference
		Japanese isolates		
X_1	Kogyoku	Giken 44		30)
X2. X3	Shimotsuki	Nara	Complementary gene	30)
		Himeji	for X_1	501
Xa-1	Kogyoku	X-17	Chromosome 11	22)
	Koganemaru		(Nishimura 1961)	
	Pi No. 1		(Adminiara 1901)	
Xa-2	Rantai Emas 2	X-17	Linked with Xa-1	221
	Funda Enhas 2	X-14	(2-16%)	22)
Xa-3	Wase Aikoku 3	Q6808 (1)	Adult resistance	1)
	Java 14	Q7102 (1)	read resistance	•/
	Koentoelan	T7174 (I)		
	Nagomasari	H5809 (11)		
	rugomasari	T7147 (II)		
		Q6809 (111)		
		T7133 (111)		
$Xa-1^{h}$	IR28	T7174 (I)		201
$\Delta u = I$	1R28 1R29	1/1/4 (1)		32)
V t h	IR30	1177701 111		
Xa-kg ^h	IR28	H75304 (V)	Linked with $Xa-I^h$:	32)
	IR29		$(2.0 \pm 0.65\%)$	
V- 11	IR30	TRADIC (D)		2237
Xa-11	IR944-102-2-3-	T7174 (I)		9)
	RP9=3	T7147 (II)		
		T7133 (IIIA)		
		IVA7505 (IV)		
	1	Philippine isolates		
Xa-4	IR20	PXO 25 (1)		21)
	IR22			10.0 M.
	IR1529-680-3			
xa-5	IR1545-339	PXO 25 (1)		21)
	RP291-7	and a second		
Xa-4ª	IR22	PXO 61 (1)		4)
	Sigadis			0.20
	TKM6, etc.			
Xa-4 ^b	Semora Mangga	PXO 61 (1)	Adult resistance	4)
Xa-6	Malagkit	PXO 61 (1)		23)
111111110	Sungsong	2007.000 AL		23)
	Zenith, etc.			
Xa-7	DZ78	PXO 61 (1)	Adult resistance	24)
	DV85		ALCOND. CONTRACT	
	DV86			
xa-8	P1231129	PXO 61 (1)		24)
xa-9	Khao Lay Nhay	PXO 61 (1)	Linked with Xa-6	26)
112.00	Sateng		(5.9%)	20)
Xa-10	Cas209	PXO 61 (1)	Linked with Xa-4	34)
unite suite fille	10.110.000	PXO 86 (2)	(27.6 ± 0.2)	24)
		PXO 79 (3)	Chromosome 5	
		PXO 71 (4)	(Shastry et al. 1960)	
		1/11/11/11/11	DITAMENT CLAIL 1900)	

Table 1. Resistance genes to bacterial leaf blight originally identified in rice^{1,3)}

(Table 1, continued)

Gene identified	Cultivar analyzed	Isolate used	Note	Reference
	S	ri Lankan isolates		
Xa-a,	Wase Aikoku 3	CARI	Multiple genes	31)
Xa-k				
Xa-i	P1209938		Multiple genes	31)
	Zenith			
	RL Gopher			11111
Xa-p	P1209938		Multiple genes	31)
	Zenith			
Xa-b	Bluebonnet/Rexark		Incomplete	31)
	li	ndonesian isolates		
Xa-kg	Kogyoku	Xo-7306	Linked with Xa-1	8)
	Java 14	(V)	(2%)	
	h	ndian isolates		
Xı	BJ1	H14		2)
X		H89		
Xi		H146		
$I-X_1$	IR8	H14, H89, H146	Inhibitor to X_1 , X_2 and X_3	2)
A	Malagkit, Sungsong	X010		5)
B		X032		10740
P_1	Lacrosse/Zenith-Nira			
R	IRR1 69/469			
	IRRI 70/470			
I_p	IR8		Inhibitor to P_1	
		hinese isolates		
Xa-a	1R28			36)
Xa-h		Linked with Xa-a (17%)		35)

mainly in Japan and at IRR1, Xa-1, Xa-2, and Xa-3 were identified using Japanese isolates in Japan^{1,22}, while Xa-kg was identified using an Indonesian isolate in Japan⁸). Furthermore, two alleles of Xa-1 and Xa-kg were recognized using Japanese isolates in Japan and they were designated as $Xa-1^{h}$ and $Xa-kg^{h}$, respectively³²). On the other hand, Xa-4, xa-5, Xa-6, Xa-7, xa-8, xa-9, and Xa-10 were identified using Philippine isolates at IRRI^{4,20,21,23,24,26,34}). $Xa-4^{h}$ was recognized as an allele of $Xa-4^{4,25}$.

Genetic studies on the resistance to the disease have also been conducted in Sri Lanka, India and China using isolates obtained in the respective countries. Xa-a and Xa-k in Wase Aikoku 3, and Xa-p and Xa-i in PI209938 were identified using Sri Lankan isolates³¹⁾. The incompletely dominant gene, Xa-bwas also identified in Bluebonnet/Rexark using Sri Lankan isolates³¹⁾. The three complementary genes, Xa_1 , Xa_2 , and Xa_3 , and the inhibitor of Xa_1 , $I-X_1$, were detected in IR8 using Indian isolates2). The presence of two complementary dominant genes, A and B, in Malagkit Sungsong, one dominant gene, R, in IRRI69/469 and one dominant gene, P1, in Lacrosse/Zenith-Nira, was suggested using two Indian isolates⁵⁾. Furthermore, two dominant genes, Xa-a (different from the Xa-a described earlier) and Xa-h, were identified using Chinese strains^{35,36)}. Genetic studies on the resistance of rice cultivars to the disease have also been carried out in Korea, Bangladesh, and Indonesia. However, the genes have not been designated. The identified resistance genes to bacterial leaf blight are summarized in Table 1.

2) Rearrangement of identified genes

The results of identification of resistance genes to the disease obtained from each country can not be compared because each researcher used isolates collected in the respective countries. However, the genes identified in Japan and at IRRI were compared with each other using Japanese and Philippine isolates during the collaborative studies. As a result, the resistance genes, Xa-1, Xa-2, Xa-3, Xa-4, xa-5, Xa-7, xa-8, Xa-10, and Xa-kg were confirmed to be different from each other^{13,14}). In addition, a new resistance gene to the Japanese isolates, Xa-11 was identified in IR8, the susceptible differential to Philippine isolates^{9,18)}. However, Xa-6, xa-9 and $Xa-4^{b}$ identified at IRRI were allelic to Xa-3 identified in Japan¹⁵⁻¹⁷⁾. Based on these results, gene symbols for the resistance genes to bacterial leaf blight were rearranged following the numbering system of the rice gene symbols indicated in Table 2¹⁰⁾. Therefore, the Xa-kg symbol was rearranged as $Xa-12^{10}$.

The rearrangement of the genes has created problems which should be solved in future. It is generally recognized that Xa-1, Xa-2, and Xa-12 are very closely linked. It is also possible that Xa-1, Xa-2 and Xa-12 are alleles at the same locus. In

Rearranged gene	Dominance	Original designation	Representative cultivar
Xa-1	Dominant	Xa-1	Kogyoku
Xa-1 ^h	Dominant	Xa-1 ^h	IR28, IR29, IR30
Xa-2 Xa-3	Dominant Dominant	Xa-2 Xa-w	Rantai Emas 2, Te-tep Wase Aikoku 3
		Xa-4 ^b	Semora Mangga
		Xa-6	Zenith
		xa-9	Sateng
Xa-4	Dominant	Xa-4	TKM6, IR20, IR22
		$Xa-4^{a}$	and a service of the second constraints
xa-5	Recessive	xa-5	DZI92, IR1545-339
Xa-7	Dominant	Xa-7	DV85
xa-8	Recessive	xa-8	P1231129
Xa-10	Dominant	Xa-10	Cas209
Xa-11	Dominant	Xa-11	RP9-3, IR8
Xa-12	Dominant	Xa-kg	Kogyoku, Java 14
Xa-12h	Dominant	Xa-kgh	IR28, IR29, IR30

Table 2. Rearranged genes for resistance to bacterial leaf blight

Table 3. New genes for resistance to bacterial leaf blight recently identified

Identified gene	Dominance	Original donor	Representative cultivar
xa-13	Recessive		BJ1, Chinsurah Boro II
Xa-14	Dominant		Taichung Native 1
xa-15* Xa-16	Recessive Dominant	Harebare	M41 Te-tep
Xu-17	Dominant		Asominori
Xa-18	Dominant		IR24, Milyang 23, Toyonishik
xa-19	Recessive	IR24	XM5
xa-20	Recessive	IR24	XM6
Xa-21	Dominant	O, longis- taminata	IR-BB 21

* Not approved yet.

R-gene designation	Generation	Line no.	Cross
Xa-1 (Xa-12) ^{a)}			
IR-BB 1	BC ₄ F ₄	IS630	IR24 * 5/Kogyoku
IR-BB 101	BC ₄ F ₄	IS638	Toyonishiki * 5/Kogyoku
1R-BB 201	BC ₄ F ₄	IS634	Milyang 23 * 5/Kogyoku
Xa-2 (Xa-1) ^{a)}			
IR-BB 2	BC ₄ F ₅	B174	IR24 * 5/Te-tep
IR-BB 102	BC ₄ F ₅	B205	Toyonishiki * 5/Te-tep
IR-BB 202	BG ₄ F ₅	B221	Milyang 23 * 5/Te-tep
Xa-3			
IR-BB 3	BC ₄ F ₆	IS 22	IR24 * 5/Chugoku 45
IR-BB 103	BC ₄ F ₆	IS103	Toyonishiki * 5/Chugoku 45
IR-BB 203	BC ₄ F ₆	IS 13	Milyang 23 * 5/Chugoku 45
IR-BB 3J	BC ₄ F ₆	IS 40	IR24 + 5/Java 14
IR-BB 103J	BC ₄ F ₆	IS 27	Toyonishiki * 5/Java 14
IR-BB 203J	BC ₄ F ₆	IS 37	Milyang 23 * 5/Java 14
IR-BB 3Z	BC ₄ F ₆	IS 74	IR24 * 5/Zenith
IR-BB 103Z	BC4F6	IS283	Toyonishiki + 5/Zenith
IR-BB 203Z	BC ₄ F ₆	IS 68	Milyang 23 * 5/Zenith
IR-BB 3S	BC ₄ F ₆	IS 91	IR24 * 5/Sateng
IR-BB 103S	BC4F6	IS 79	Toyonishiki * 5/Sateng
IR-BB 203S	BC ₄ F ₆	IS341	Milyang 23 * 5/Sateng
Xa-4			
IR-BB 4	BC4F6	IS110	1R24 + 5/1R20
IR-BB 104	BC4F6	IS 98	Toyonishiki * 5/1R20
IR-BB 204	BC ₄ F ₆	IS104	Milyang 23 * 5/IR20
xa-5			
1R-BB 5	BC ₄ F ₅	IS133	1R24 + 5/1R1545-339
IR-BB 105	BC_4F_4	IS118	Toyonishiki * 5/FIR1545-339
IR-BB 205	BC ₄ F ₅	IS299	Milyang 23 * 5/IR1545-339
Xa-7			
IR-BB 7	BC ₄ F ₇	IS165	IR24 * 5/DV85
IR-BB 107	BC_4F_4	15499	Toyonishiki * 5/DV85
IR-BB 207	BC_4F_5	IS491	Milyang 23 + 5/DV85
xa-8			
IR-BB 8	BC ₄ F ₅	18513	IR24 * 5/PI231129
IR-BB 108	BC ₄ F ₅	IS831	Toyonishiki + 5/PI231129
IR-BB 208	BC ₄ F ₅	IS818	Milyang 23 + 5/P1231129
Xa-10	and the second sec		ARTMENTATI UNIVERSI - PROPERT
IR-BB 10	BC ₄ F ₆	IS154	IR24 * 5/Cas209
IR-BB 110	BC ₄ F ₅	IS140	Toyonishiki * 5/Cas209
1R-BB 210	BC_4F_6	IS150	Milyang 23 = 5/Cas209
Xa-11			
IR-BB 11	BC_4F_4	IS618	IR24 * 5/IR8
IR-BB 111	BC_4F_4	IS627	Toyonishiki * 5/1R8
IR-BB 211	BC_4F_4	IS624	Milyang 23 + 5/1R8

Table 4. Near-isogenic lines for resistance to bacterial leaf blight of rice developed under TARC-IRRI collaboration¹⁹⁾

a): Not segregated.

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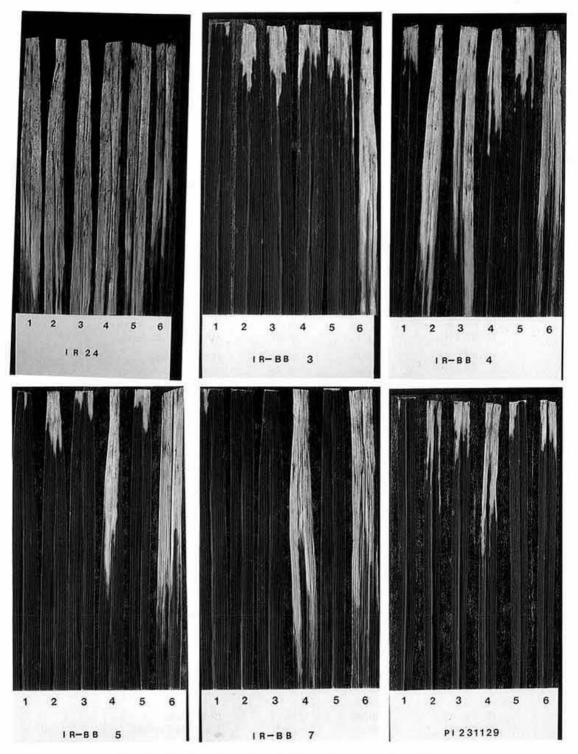
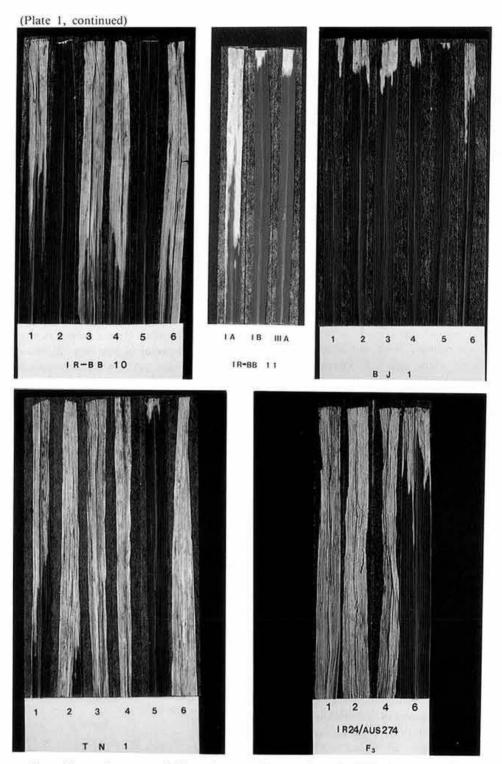


Plate 1. Reaction of near-isogenic lines and representative cultivars to Philippine and Japanese races



Note: The numbers on top indicate the respective races from the Philippines (except for Japanese race IR-BB 11).

IR24/AUS274 F₃ indicates the reaction of the segregant from the cross between IR24 (susceptible) and AUS274 (xa-5, xa-13). The plant carries only the xa-13 gene.

addition, $Xa-1^h$ and $Xa-12^h$ were reported to be allelic genes of Xa-1 and Xa-12. Analysis using IR28, IR29, and IR30 showed that these cultivars harbor Xa-4, which is also effective against the Japanese isolates. Therefore, $Xa-1^h$ and $Xa-12^h$ should be compared with Xa-1 and Xa-12 based on the resistance gene Xa-4 of IR28, IR29, and IR30 to Japanese isolates.

3) Resistance genes recently identified

During the research collaboration between Japan and IRRI, two new genes, xa-13 and Xa-14, were identified using Philippine races^{11,29)}. xa-13 in BJ1, AC19-1-1, AUS274, Chinsurah Boro II, and Kalimakri77-5 is resistant only to race 6 of the Philippines¹¹⁾. Xa-14 in Taichung Native 1 is resistant only to race 5 of the Philippines²⁹⁾. However, it has not been determined whether the two genes are resistant to the Japanese isolates. Although the presence of a recessive gene, xa-15 (a mutant from Harebare), was reported, it has not been confirmed yet because no allelic test with known recessive genes⁶⁾ was conducted.

Xa-16 in Te-tep, and Xa-17 in Asominori were identified using Japanese isolates^{7,12)}, while Xa-18 in Toyonishiki, Milyang 23, and IR24 was identified using a Myanmar isolate³³⁾.

Two recessive genes, xa-19 and xa-20, were induced in IR24 by N-methyl-N-nitroso-urea $(MNU)^{27,28}$. The two genes were resistant to all the Philippine races.

The latest resistance gene identified is Xa-21, which was introduced into IR24 by backcrossing from a wild rice variety, *O. longistaminata*³⁾. The resistance genes to bacterial leaf blight recently identified are summarized in Table 3.

Breeding of near-isogenic lines

Near-isogenic lines with various genes for resistance to major diseases and insects can be useful for identifying races and biotypes of diseases and insects as well as new genes for resistance. Moreover, isogenic lines can serve as donors of resistance in breeding programs and be excellent materials for studying the mechanism of resistance. In the case of rice diseases and insects, no near-isogenic lines can be used as common differentials internationally due to the difficulty in exchanging materials among rice-growing countries.

To establish a common basis of research on resistance to bacterial leaf blight, attempts were made to develop near-isogenic lines with diverse genes for the resistance to the disease under the above collaboration. As a result, the initial set of near-isogenic lines (more advanced generation than BC_4F_4) was ceveloped using IR24, Milyang 23, and Toyonishiki as recurrent parents (Table 4)¹⁹⁾

Strategy for monitoring race distribution and identification of new genes

Proposed international differentials for bacterial leaf blight pathogen.

The near-isogenic lines were developed with IR24 for use as international differentials to the bacterial leaf blight pathogen and as testers to identify new resistance genes to the disease. However, the genes recently identified are not related to these lines because the breeding of near-isogenic lines carrying the new resistance genes is currently underway.

Therefore, it is recommended to use the lines and

Table 5.	Proposed international differentials for monitor-					
	ing the race distribution of the bacterial leaf blight pathogen					

Differentials	Ecotype	Resistance gene
I'roposed internation	al differentials:	
Toyonishiki	Japonica	Xa-18
IR24	Indica	Xa-16
IR-BB 1	Indica	Xa-1, Xa-12
IR-BB 2	Indica	Xa-2
IR-BB 3	Indica	Xa-3
IR-BB 4	Indica	Xa-4
IR-BB 5	Indica	xa-5
IR-BB 7	Indica	Xa-7
IR-BB 8	Indica	xa-8
IR-BB 10	Indica	Xa-10
IR-BB 11	Indica	Xa-11
IR-BB 21 ^{a)}	Indica	Xa-21
BJ1	Indica	xa-5, xa-13
Taichung Native 1	Indica	Xa-14
Asominori	Japonica	Xa-17
Optional differentials	\$:	
M41 ^{b)}	Japonica	(xa-15)
XM5 ^{c)}		xa-19
XM6 ^{c)}		xa-20

a): Newly developed³⁾.

5): Mutant from Harebare.

c): Mutant from IR24.

cultivars shown in Table 5 for monitoring the race distribution of the bacterial leaf blight pathogen.

By using the 18 cultivars listed above, it is likely that most races could be identified and effective resistance genes could be recognized in each country.

2) Methods for identification of a new resistance gene

For the identification of a new resistance gene to bacterial leaf blight, the following steps are recommended:

Step 1: Comparison of reaction pattern; the above 18 differentials should be subjected to inoculation tests together with the resistant cultivar where the resistance gene is expected to be identified. If the reaction of the resistant cultivar is clearly different from that of the differentials and if it is confirmed that the resistant cultivar carries only one resistance gene in **Step 3**, the resistant cultivar can be considered to carry a new resistance gene.

Step 2: Hybridization; it is always necessary to obtain the F₁ hybrids between resistant and susceptible cultivars.

Step 3: Determination of the number of resistance genes; by breeding the F_2 population between susceptible and resistant cultivars, the number of resistance genes in the resistant cultivar should be estimated from the ratio of segregation in the population.

Step 4: Allelic test with dominant genes; when the F_1 hybrids obtained in Step 2 are resistant to the isolates, it is necessary to develop F_2 hybrids between the resistant cultivar and the above differentials which carry dominant genes and show a similar reaction to that of the tested resistant cultivar. If susceptible plants are detected in every F_2 population, the resistant cultivar can be considered to carry a new resistance gene.

Step 5: Allelic test with recessive genes; when the F_1 hybrids obtained in **Step 2** are susceptible, the resistant cultivar should be crossed with differentials, which carry a recessive gene and show a similar reaction to that of the resistant cultivar, to obtain the F_1 hybrids. If every F_1 hybrid is susceptible to the isolates, it is assumed that the resistant cultivar carries new resistance gene.

If there is more than one resistance gene in the tested resistant cultivar in **Step 3**, a similar procedure should be adopted from **Step 1** onward except for Step 3 after obtaining segregants carrying only one resistance gene from the hybridization between susceptible and resistant cultivars.

Resistance reactions of cultivars

There are various kinds of resistance reactions to the bacterial leaf blight pathogen in rice cultivars. Usually, it is recommended to observe rice plants during 2 to 4 weeks after inoculation by applying the clipping method. Suitable concentration of bacteria for inoculation may be 10^8 cells/m/. The resistant plants show a lesion length below about 6 cm at 3 weeks after inoculation. However, the reactions vary depending on the virulence of the inoculum, weather conditions, plant age, etc.

The resistance reactions of cultivars can be classitied into the following categories.

1. Highly resistant; no or minimal lesion development after inoculation (reaction of cultivar with Xa-10 gene to Philippine race 2).

2. Resistant; lesion length below about 6 cm at 3 weeks after inoculation (reaction of cultivar with Xa-4 gene to Philippine race 1).

3. Resistant with lesions showing a brown margin; lesions are less than about 6 cm long at 3 weeks after inoculation and they are characterized by a brown margin or spots around the lesions (reaction of cultivar with Xa-3 gene to Philippine races 1 to 4). 4. Moderately resistant or susceptible, i.e. variable; lesions continue to develop after inoculation, but more slowly than in the case of the susceptible cultivars (reaction of cultivars with Xa-4 and xa-5 genes to Philippine race 4).

 Susceptible; lesions continue to develop after inoculation. These reactions are illustrated in Plate 1.

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