

## REVIEW

# Introduction of *Piz-t* and *Pib* Genes for Blast Disease Resistance from Indica Varieties and their Utilization for Genetic Researches in Rice

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### Abstract

Development of varieties with high resistance to blast disease had been an urgent need for rice production in the 1960s and 1970s, since blast epidemics prevailed on excellent varieties with resistance derived from some Chinese, U.S.A. and Philippine varieties. Our breeding project introduced high resistance from typical Indica varieties into the genetic backgrounds of Japanese varieties by backcross breeding, and developed Toride 1, Toride 2 and BL1 to BL7. Toride 1 and Toride 2 inherited *Piz-t* gene for resistance from Indian varieties, and BL1 to BL 7 inherited *Pib* gene from Indonesian and Malaysian varieties. Although *Piz-t* and *Pib* distributed widely among Indica varieties of South Asian countries showed resistance to a number of blast races in Japan, they were vulnerable to naturally-occurring virulent mutants. This paper reviews how *Piz-t* and *Pib* were introduced, identified, and utilized in the breeding and genetic researches conducted by the author and co-workers since 1960.

**Discipline:** Plant breeding

**Additional key words:** epidemic, genetic resource, heading time, linkage, QTL

## Introduction

Utilization of genetic resources in plant breeding is a time-consuming and labor-costing work to find favorable characters and genes in resource plants and to introduce them into active varieties. This paper reviewed the introduction of genes for blast resistance from Indica varieties into Japanese varieties of rice, based on researches conducted by the author and co-workers during the period between 1960 and 2004 in four institutes; National Institute of Agricultural Sciences in Hiratsuka, Tohoku National Agricultural Experiment Station in Omagari, National Agricultural Research Center in Konosu, and University of Tsukuba in Tsukuba.

## Incidence of blast disease on resistant rice varieties

Blast disease caused by *Pyricularia grisea* (*oryzae*) has been a threat to rice production for a long time in

Japan. In the 1940s, Central Agricultural Experiment Station tested resistance of rice collections in blast nurseries to find some resistant Chinese varieties. Rice breeders made the effort to introduce the resistance into Japanese varieties. The first promising variety Kusabue was released for rice production in 1960. Rice farmers and scientists were convinced that Kusabue's plants were completely protected from blast incidence by the resistance. Contrary to their expectation, an outbreak of blast disease happened on Kusabue's plants in 1963, and caused severe loss of rice production from the variety. The blast epidemic continued on the variety for several years until it was withdrawn from farmers' fields.

Rice farmers and scientists had similar experiences that within several years after some excellent varieties were widely grown, having resistance introduced from other Chinese, U.S.A. and Philippine varieties, they also suffered severe incidence of blast disease. Causes of the blast epidemics were later studied intensively and extensively in cooperative research by breeders, geneticists,

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pathologists and statisticians from Japan, U.S.A. and IRRI (International Rice Research Institute) in the late 1960s and 1970s. The above-mentioned varieties were resistant to only some of the major races of blast fungus. Under these circumstances, the Division of Genetics, National Institute of Agricultural Sciences, had conducted the special breeding project of introducing high resistance to most prevalent races from Indica varieties of India, Indonesia, Malaysia, and Thailand since 1960.

**Introduction and utilization of *Piz-t* gene for blast resistance**

Indian varieties TKM1 and CO25 were highly resistant to the standard 7 strains of major blast fungus races (Table 1). In 1964, the author and co-workers in the Division of Genetics obtained some selected lines from crosses of TKM1 and CO25 with a Japanese variety Norin 8 backcrossed as the recurrent parent, from Chugoku National Agricultural Experiment Station, where the selection for resistance was done in blast nurseries under natural conditions.

Homogeneously resistant lines were newly selected based on the result by inoculation tests with the 7 strains in seedling stage and evaluation for agronomic characters in the field. Two resistant lines with agronomic charac-

teristics similar to Norin 8 were named Toride 1 from the cross Norin 8 / TKM1 //4\* Norin 8, and Toride 2 from the cross Norin 8 / CO25 //4\* Norin 8 (Table 1)<sup>7,8</sup>. Toride 1 showed high resistance to a number of isolates of blast fungus collected in Japan<sup>7</sup>. The resistance of Toride 1 was controlled by a new single dominant gene *Piz-t*, different from the known genes such as *Pia*, *Pii*, *Pik*, *Pita*, *Pita-2*, and *Piz*, but allelic to *Piz*<sup>10</sup>. Toride 2 had also *Piz-t* gene<sup>5</sup>.

Spotted lesions were sporadically seen on leaves of Toride 1 when inoculated with dense spores of avirulent strains during the genetic analysis of resistance. Single-spore isolates from these lesions showed strong virulence to Toride 1. Differential reactions of lines or varieties to a virulent mutant isolate and its original strain formed a *Piz-t* group, to which ADT10 and CO4 from India, Kontor and Morak Sepilai from Malaysia, and Chao Leuang and Leuang Tawng from Thailand belonged (Table 2)<sup>2,11,17</sup>. Lines, which have been developed from crosses of these Indica varieties with Japanese varieties since 1960, were discarded from our breeding project due to their uselessness as resistance source of *Piz-t* gene. The breeding needed more than ten years for three- to four-time backcrosses and progeny selection to decrease hybrid sterility and decrease the wide variation of agronomic characters in these remote crosses for intro-

**Table 1. Resistance reactions of developed lines to the 7 strains of blast fungus**<sup>7,8,15</sup>

Line	Donor variety for resistance	Backcrossed parent	No. of backcrosses	Reactions to blast fungus strain						
				P-2b	Ken 53-33	Ina 72	Hoku 1	Ken 54-20	Ken 54-04	Ina 168
Toride 1	TKM1	Norin 8	4	HR	HR	HR	HR	HR	HR	HR
Toride 2	CO25	Norin 8	4	R	R	R	HR	MR	R	R
	TKM1			HR	HR	HR	HR	HR	HR	HR
	CO25			HR	R	R	HR	MR	MR	HR
		Norin 8		S	S	S	S	S	S	S
BL1	Tjina	Norin 25	4	R	MR	MR	MR	MR	R	MR
BL2	Tjina	Norin 25	4	HR	HR	R	MR	MR	MR	MR
BL3	Milek Kuning	Norin 25	4	MR	M	M	MR	M	MR	MR
BL4	Milek Kuning	Norin 25	4	MR	M	M	MR	M	M	MR
BL5	Tjahaja	Norin 25	4	MR	MR	MR	MR	M	MR	MR
BL6	Tjahaja	Norin 25	4	MR	M	M	MR	M	MR	MR
BL7	Milek Kuning	Fujisaka 5	4	MR	M	M	MR	M	MR	MR
	Tjina			HR	MR	HR	MR	MR	MR	HR
	Tjahaja			HR	M	R	R	MR	MR	R
	Milek Kuning			HR	MR	HR	HR	HR	HR	HR
		Norin 25		S	S	S	S	S	M	S
		Fujisaka 5		M	S	M	S	M	M	MR

Resistance reactions: HR(resistant), R, MR, M, MS, S(susceptible).  
TKM1, CO25: India. Tjina, Tjahaja: Indonesia. Milek Kuning: Malaysia.

**Table 2. Indica rice varieties having *Piz-t* and *Pib* genes for resistance**<sup>2,11,17</sup>

Gene	India	Indonesia	Malaysia	Thailand
<i>Piz-t</i>	ADT10		Kontor	Chao Leuang
	Badshabhog		Morak Sepilai	Leuang Tawng
	CO4		Radin Kling	
	CO25			
	TKM1			
<i>Pib</i>	S1092	Bengawan	Engkatek	
	SM6	Peta	Milek Kuning	
		Remadja	Radin China 4	
		Sigadis	Serendah Kuning	
		Tjahaja		
		Tjina		

ducing the resistance of Indica varieties into the genetic backgrounds of Japanese varieties. The results showed a wide distribution of *Piz-t* in Indica varieties of South Asian countries, and this fact made the breeding work wasteful of time and labor, but left several new findings to breeding for blast resistance.

Mutants virulent to *Piz-t* appeared also in blast nurseries where Toride 1 was grown for several years, and *Piz-t* was also vulnerable to blast disease like other genes such as *Pik*, *Pita* and *Piz* under natural conditions. However, Toride 1 was used as a cross parent by the Japan and China joint breeding project to develop three excellent varieties for Yunnan, China, in the 1990s. Recent studies identified *Piz-t* in some of the IRRI-bred rice varieties, inherited from an Indian variety TKM6<sup>1</sup>. Toride 1 is indispensable as a differential variety for identifying and classifying blast isolates with virulence or avirulence to *Piz-t* in breeding and pathological researches on blast resistance<sup>3,22</sup>.

### Introduction and utilization of *Pib* gene for blast resistance

There was another flow of breeding for blast resistance introduced from Indica varieties beside *Piz-t* gene. Backcrossed hybrid progenies of Indonesian varieties Tjina and Tjahaja, and a Malaysian variety Milek Kuning with Japanese varieties were identified to have a new resistance gene from the results of genetic analysis. Seven lines were named BL1 to BL7; BL1 and BL2 inherited *Pib* gene from Tjina; BL3, BL4 and BL7 inherited *Pib* from Milek Kuning; and BL5 and BL6 inherited *Pib* from Tjahaja (Table 1)<sup>15</sup>. These Indica varieties formed a *Pib* group in differential resistance reactions to a mutant virulent to *Piz-t* and its original strain<sup>17</sup>. This

fact urged our breeding project to discard hybrid progenies of other *Pib*-group varieties such as Bengawan, Remadja and Sigadis from Indonesia, Engkatek, Radin China 4, Radin Kuning and Serendah Kuning from Malaysia, and S1092 and SM6 from India (Table 2), because of duplicated introduction of *Pib* gene. *Pit*, a new gene for moderate resistance, was included in BL5, derived from Tjahaja<sup>15</sup>.

Since any mutant isolates with virulence to *Pib* were not obtained in greenhouse tests unlike *Piz-t*, *Pib* was used in active breeding and Hama-asahi variety was developed with *Pib* gene given from BL7 in the Fujisaka Branch, Aomori Agricultural Experiment Station, in 1979. However, Hama-asahi suffered the severe incidence of blast disease in every farmer's field soon. The variety could not tolerate the prevalence of naturally-occurring strains virulent to *Pib* because of its low field resistance. Fukuhibiki variety was developed in Tohoku National Agricultural Experiment Station in 1993 to combine *Pib* originated from a Malaysian variety Engkatek with high field resistance<sup>4</sup>.

Korean rice breeders informed the author that BL1 was resistant to stripe virus disease transmitted by small brown planthoppers. Resistance gene(s) derived from Tjina seemed to be different from already-known genes<sup>15</sup>. Resistance to blast and stripe virus diseases of BL1 and BL7 yielded nine excellent varieties grown widely in Korea through the 1970s and 1980s. BL1 and BL6 were also used as cross parents by the Japan and China joint breeding project to develop four new varieties for Yunnan, China, in the 1990s. The potential or combining ability of BL lines as breeding materials was found out in Korea and China rather than in Japan.

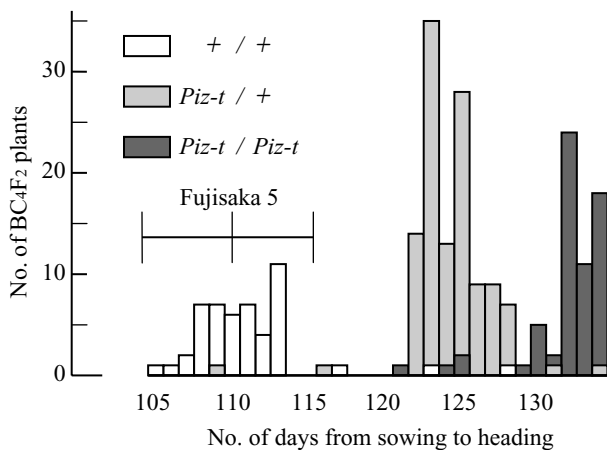
BL1 carrying only *Pib* for resistance became a member of differential varieties for identifying races of

blast fungus, together with Toride 1. Most of the IRRI-bred rice varieties inherited *Pib* from Tjina through an Indonesian variety Peta<sup>1</sup>.

Female sterility governed by two complementary recessive genes was isolated from the cross Fujisaka 5 / Tjina //4\* Fujisaka 5 in the breeding process of BL lines, having abnormal embryos but normal pollen grains<sup>23</sup>. A female sterile line FS1 bore several fertile grains on a panicle, with which the sterility was transmitted to the following generations, and FS1 was used in physiological studies on photosynthate distribution and dry matter accumulation in rice plants<sup>6</sup>.

**Analysis of close linkage between *Piz-t* and *Se1***

The F<sub>2</sub> population of all the backcrosses containing *Piz-t* gene was segregated into a ratio of 1 early : 2 medium : 1 late plants for heading time under natural



**Fig. 1. Frequency distribution for heading time and blast resistance in the BC<sub>4</sub>F<sub>2</sub> population of the cross Morak Sepilai /5\*Fujisaka 5<sup>11</sup>**

conditions, of which their F<sub>3</sub> progenies were mostly homozygous susceptible, segregating for *Piz-t*, and homozygous resistant (*Piz-t/Piz-t*), respectively, having a few recombinants for these two characters (Fig. 1, Table 3)<sup>11</sup>. Thus, the close linkage between *Piz-t* for blast resistance and *Lm* for heading time was found for the first time in rice, and was located on chromosome 6 with other genes *C* for apiculus color and *alk* for alkali reaction of grains (Fig. 2)<sup>11</sup>. The locus *Lm* was later replaced with *Se1*.

The close linkage made the genetic analysis possible, when the quantitative variation for heading time in a hybrid population was partitioned into three *Se1* genotypes by three *Piz-t* genotypes<sup>16</sup>. A pair of two tester lines, ER with an early allele *Se1-e* and *Piz-t*, and LR with a late allele *Se1-u* and *Piz-t*, were selected from Morak Sepilai /5\* Fujisaka 5 and used in crosses with tested varieties. The analyses revealed that *Se1* was a principal locus controlling the earliness and lateness in native and improved, lowland and upland Japanese varieties, and Indica varieties also<sup>14,18,24-26</sup>. The QTL (quantitative trait locus) analysis using Toride 1 as a tester for *Piz-t* and *Se1-n* showed that the earliness in two of the randomly selected 8 artificially-induced early mutants was governed by an early allele of *Se1*<sup>27</sup>. Multiple alleles existed in this locus; an early *Se1-e*, a late *Se1-u* or *Se1-n*, and a very late *Se1-t*<sup>13</sup>.

*Se1* controlled primarily the photoperiod sensitivity of rice plant, and *Se1-e* and *Se1-u* alleles were insensitive and sensitive to short daylength, respectively<sup>20,21,28</sup>. *Se1-e* worked simultaneously for longer basic-vegetative-phase (BVP) and shorter photoperiod-sensitive-phase (PSP), while *Se1-u* for shorter BVP and longer PSP. This caused two turning points in a year to reverse the earliness and lateness between the two genotypes<sup>20,21,28</sup>. *Se1* pleiotropically affected internode elongation and culm length through the time of panicle differentiation and heading<sup>19</sup>.

**Table 3. Segregation for heading time and blast resistance in Indica / Japonica crosses<sup>11</sup>**

Cross combination	Generation	No. of F <sub>2</sub> plants				Recombination value (%)
		Susceptible		Resistant		
		Early	Late	Early	Late	
Fujisaka 5 / Kontor //4* Fujisaka 5	BC <sub>4</sub> F <sub>2</sub>	70	5	7	225	3.9
Morak Sepilai /5* Fujisaka 5	BC <sub>4</sub> F <sub>2</sub>	48	2	2	184	1.7
Ohtori / ADT10 //4* Ohtori	BC <sub>4</sub> F <sub>2</sub>	53	5	3	146	3.6
Norin 8 / TKM1 //4* Norin 8 //Fujisaka 5	F <sub>2</sub>	65	5	11	251	4.8
Chao Leuang /5* Fujisaka 5	BC <sub>4</sub> F <sub>2</sub>	48	4	4	138	4.1
Fujisaka 5 / Leuang Tawng //3* Fujisaka 5	BC <sub>3</sub> F <sub>2</sub>	51	10	8	155	8.1

Kontor, Morak Sepilai: Malaysia. ADT10, TKM1: India. Chao Leuang, Leuang Tawng: Thailand.

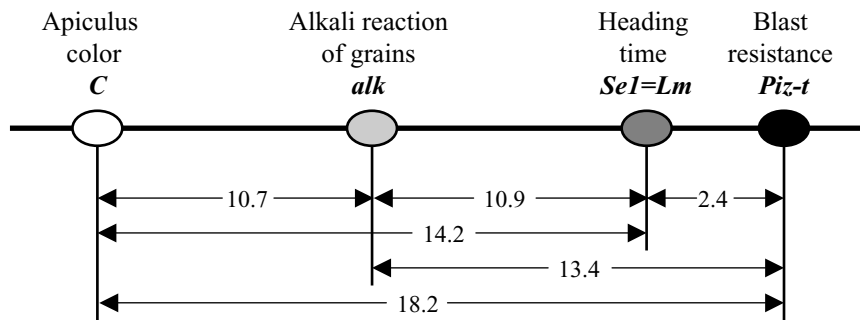
Four isogenic lines with or without *Piz-t* and with *SeI-e* or *SeI-u* were selected from the later generations of Morak Sepilai /5\* Fujisaka 5, and used for genetic and physiological studies on the linkage and the gene expression of *SeI*<sup>9,29</sup>.

**Utilization of *Piz-t* and *Pib* in multiline varieties and with DNA markers**

In the 1960s and 1970s, within a few years after new excellent rice varieties with such a single resistance gene as *Pik*, *Pita* and *Piz*, new virulent races of blast fungus became selectively more prevalent, and the effectiveness of the newly developed commercial resistance was quickly lost; *Piz-t* and *Pib* were no exceptions. To break this resistance-virulence relationship, breeders designed rice varieties protected by field resistance with or without major genes for resistance<sup>4</sup>, and more recently multiline varieties, mechanical mixtures of isogenic lines<sup>12</sup>. *Piz-t*

and *Pib* have been incorporated into component isogenic lines for several multiline varieties.

Our breeding project took almost 20 years since the first hybridization in 1960 to introduce high resistance from Indica varieties into the genetic backgrounds of Japanese varieties by backcrossing, to identify *Piz-t* and *Pib* genes in developed lines, and to locate *Piz-t* on chromosome 6, while *Pib* could not be located on any chromosome yet. However, studies using DNA markers since the 1990s enabled scientists to analyze many blast resistance genes to find the definite position of *Pib* on chromosome 2. The author analyzed only the relationship between *SeI* and other loci for quantitatively-inherited heading time with the help of close linkage with *Piz-t* as a qualitatively-inherited marker. Recent QTL analyses for heading time with DNA markers supported the role of *SeI* on chromosome 6 as a principal locus controlling photoperiod sensitivity of cultivated varieties among many heading time genes.



**Fig. 2. Linkage relationships among four genes on chromosome 6<sup>11</sup>**  
Numbers show recombination values (%).

**Table 4. List of developed lines available from the Gene Bank, Ministry of Agriculture, Forestry and Fisheries**

Accession no.	Line	Cross combination	Genes involved
00008101	TORIDE 1	Norin 8 / TKM1 //4* Norin 8	<i>Piz-t</i>
00008102	TORIDE 2	Norin 8 / CO25 //4* Norin 8	<i>Piz-t</i>
00051073	BL1	Norin 25 / Tjina //4* Norin 25	<i>Pib</i>
00051074	BL2	Norin 25 / Tjina //4* Norin 25	<i>Pib</i>
00051075	BL3	Norin 25 / Milek Kuning //4* Norin 25	<i>Pib</i>
00051076	BL4	Norin 25 / Milek Kuning //4* Norin 25	<i>Pib</i>
00051077	BL5	Norin 25 / Tjahaja //4* Norin 25	<i>Pib</i> , <i>Pit</i>
00051078	BL6	Norin 25 / Tjahaja //4* Norin 25	<i>Pib</i>
00051079	BL7	Milek Kuning /5* Fujisaka 5	<i>Pib</i> , <i>Pii</i>
00038029	FUJISAKA 5 (FEMALE STERILITY)	Fujisaka 5 / Tjina //4* Fujisaka 5	(FS1)
00038030	FUJISAKA 5 (PIZT R LME)	Morak Sepilai /5* Fujisaka 5	<i>Piz-t</i> , <i>SeI-e</i> (ER)
00038031	FUJISAKA 5 (PIZT S LME)	Morak Sepilai /5* Fujisaka 5	+ , <i>SeI-e</i> (ES)
00038032	FUJISAKA 5 (PIZT R LMU)	Morak Sepilai /5* Fujisaka 5	<i>Piz-t</i> , <i>SeI-u</i> (LR)
00038033	FUJISAKA 5 (PIZT S LMU)	Morak Sepilai /5* Fujisaka 5	+ , <i>SeI-u</i> (LS)

DNA marker-assisted genetic researches on blast resistance and heading time in rice were pioneered in the 1960s through 1980s by our project involving the author. Our time-consuming and labor-costing project of introduction and identification of *Piz-t* and *Pib* from remote Indica varieties and their related findings provided a base for new DNA marker-assisted selection techniques to shorten the breeding period for finding useful genes in genetic resources and combining them into active varieties efficiently.

Seeds of the resistant lines and testers developed through our project are stocked in and available from the Genebank, Ministry of Agriculture, Forestry and Fisheries (Table 4).

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