



~~GENETIC~~ STRUCTURE AND VIRULENCE DIVERSITY OF *Pyricularia grisea*

FOR BREEDING FOR RICE BLAST RESISTANCE

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ABSTRACT

Rice blast caused by *Pyricularia grisea* Sacc. is the main production constraint in rice worldwide. Development of resistant cultivars has been the preferred mean to control this disease; however, resistance is defeated by the pathogen shortly after cultivar release.

The blast pathogen population in Colombia's rice growing areas has been grouped into six families genetically different named SRL-1 to SRL-6 by the use of DNA-fingerprinting. The spectrum of virulence of isolates within each family is highly similar differing mainly by single virulences. Although the six genetic families of the fungus share a high number of virulence factors, a high specific interaction between some avirulence/virulence factors in the pathogen and resistance genes in the host is observed. This specific interaction is the base for the selection of progenitors to be included in a breeding program aimed at obtaining more durable blast resistance. Combinations of genes showing complementary resistance to different genetic families of the fungus should exclude any compatible interaction with a blast isolate. The identification of complementary resistance genes is based on the detection of those virulence factors whose combinations in individual isolates within the pathogen

population have a frequency near zero. It is assumed that certain virulence combinations in the blast pathogen may confer a low fitness or deleterious effect on the fungus reducing its frequency in nature.

Frequency of virulence factors to the resistance genes Pi-1 and Pi-2 present independently in two different near isogenic lines is high in the blast fungus population of Colombian genetic families SRL-5 and SRL-1, respectively. The two genes show complementary resistance that exclude all the genetic families of the fungus in Colombia and no isolate with the combination of the two virulence genes infecting both isogenic lines has been detected.

Induced mutations can be a useful technique to produce rice lines with specific resistance genes to different genetic lineages. These lines can be incorporated within breeding programs to combine such genes for the development of durable resistance to blast.

1. Introduction

The rice blast disease caused by *Pyricularia grisea* Sacc., the anamorph of *Magnaporthe grisea* (Hebert) Barr, is a major factor limiting yields of rice (*Oryza sativa* L.) worldwide, particularly under the rainfed and upland conditions prevalent in Latin America. The pathogen produces necrotic lesions on leaves of seedlings, and on leaves, nodes, necks, and panicles of mature plants, with the latter causing the most severe yield losses. Development of resistant cultivars to the pathogen has been the preferred means of controlling the disease, as fungicide applications are expensive and not-environmentally friendly. However, breakdown of this resistance is common in many rice growing areas, often shortly after cultivar release. Developing durably resistant cultivars is thus a high priority for the Rice Program at the International Center for Tropical Agriculture (CIAT) and most rice breeding programs where rice blast occur.

The rice blast pathogen reproduces asexually and is noted for expressing a large number of pathogenic races, being this variability cited as the main cause of resistance breakdown. Nevertheless, it has been proposed that continuous challenge of resistant breeding rice lines with a diverse pathogen population and a detailed genetic information on population structure for understanding the virulence dynamics of the blast pathogen would reduce the risk of resistance breakdown and allow the identification of a more stable blast resistance.

This paper summarizes data on the characterization of the virulence diversity and the genetic structure of a blast pathogen population in Colombia for developing more effective breeding strategies for the production of durable blast resistance.

2. Resistance Breakdown of Colombian Commercial Rice Cultivars

A large breeding effort aimed at combining high yield, good grain quality, earliness, resistance to several insect and diseases including stable blast resistance has been done at CIAT during the last 25 years. Different approaches were taken to develop cultivars resistant to blast including evaluation and selection of lines introduced from the International Rice Research Institute (IRRI), incorporation of several blast resistance sources such as Tادukan, Colombia 1, Tetep, Dissi Hatif, Mamoriaka, and C 46-15, and development of multilines (Rosero, 1979). Later on, breeding for resistance aimed at combining or pyramiding multiple sources of resistance into new cultivars including, besides the above mentioned lines, the resistance source Carreon. The success of this approach was limited by the absence of information on the genetics of resistance in the donors lines and ineffective screening techniques for selection of lines with combinations of appropriate resistance genes (Weeraratne et al, 1981). Mutation breeding, cultivar mixtures and combination of major and minor genes were also used.

Several high yielding-blast resistant lines were selected and released as commercial cultivars as result of these breeding approaches including CICA 4, CICA 6, CICA 7, CICA 8, CICA 9, Metica 1, Oryzica 1, Oryzica 2, and Oryzica 3. However, these strategies were only partially successful as all these cultivars became susceptible to blast within one or three years of commercial planting (Table I).

The CIAT Rice Program changed its strategy in 1985 and moved its breeding work for blast resistance to a site with a high pathogen diversity and a reliable disease pressure ("hot spot"). This site is located in an important rice-growing area where rice blast is a major constraint. Uniform and high blast incidence is maintained in breeding plots (F2-F6) during the entire season using spreader rows composed of a mixture of commercial cultivars and resistance sources with complementary susceptibility to different phenotypes of the blast fungus. Escape to the pathogen is avoided by continuous exposure to the pathogen during the season, at all growth stages, and in several generations (Correa and Zeigler, 1993a, 1993b).

Preliminary data indicated that resistance in some lines selected at this site is stable over time and space (Correa and Zeigler, 1993a; Cuevas y Gaona, 1988). A commercial rice cultivar, Oryzica Llanos 5, exhibiting complete resistance to blast, was developed at this hot spot site and has been grown on more than 300000 ha for more than six years in this blast-prone ecosystem. It has remained resistant since its release (Table I). Studies on the stability of the blast resistance in rice lines selected at this

breeding site indicate that lines exhibiting high levels of resistance since early generations, like the cultivar Oryzica Llanos 5, tended to be more stable than those lines with moderate levels (Correa and Zeigler, 1993a, 1995). The high and relatively durable level of blast resistance in these cultivars is apparently the result of combining different and complementary resistance genes (Correa and Zeigler, 1995).

3. Virulence Diversity of the Rice Blast Pathogen in Colombia

A continuous characterization of the blast pathogen in terms of race composition, compatibility with known resistance genes, and frequency of virulent phenotypes was established as a routine work in the CIAT Rice Program, to evaluate the effectiveness of this hot spot (Santa Rosa, Villavicencio) for the development of blast resistant rice lines. Controlled inoculations of blast isolates collected from different sources in Santa Rosa yielded more than 45 international races. However, this system did not fully describe the virulence spectrum of the isolates as one race could be differentiated in different races when more cultivars were added to the differential set (Correa and Zeigler, 1993b).

Virulence factors compatible with at least 13 known resistance genes were detected in this blast population with no cultivar susceptible to all isolates, a range of virulence frequencies on 42 rice cultivars between 0.0 and 0.86, and no isolate compatible with the cultivar Oryzica Llanos 5 (Table II). Compatibility of blast isolates

recovered from commercial rice cultivars revealed some specialization where some isolates reinfected only the cultivar of origin. The most extreme case was observed in the cultivar Cica 9 where most isolates that reinfected the cultivar originated from the same cultivar. Accumulation of virulence factors to most resistance genes or to the colombian commercial rice cultivars was observed in isolates of the blast pathogen, but none was virulent to all of them. Compatibility with the commercial cultivar Cica 9 was detected in the pathogen population, yet, it was not present in the isolates that exhibited accumulation of a large number of virulence factors (Table III).

The virulence diversity studies on the blast pathogen population collected in Colombia clearly suggest that new resistance genes or combinations of resistance genes that were defeated only by part of this population are needed to control rice blast. Even cultivars that are considered universally susceptible such as Fanny carry resistance genes (Table II).

The high specific compatible interaction observed between some of the commercial cultivars released in Colombia and blast isolates recovered from the same cultivars suggest that useful combinations of resistance genes could be generated from crosses between complementary groups for which the pathogen does not show accumulation of the corresponding virulence genes. This is most clear with cultivar Cica 9 that shows complementary resistance with most of the other rice cultivars (Table III).

Long-term observation of virulence/avirulence frequencies and accumulation of virulence factors would be needed to monitor this strategy. Correa and Zeigler (1993b) suggested that the accumulation of virulence factors observed in blast isolates recovered from recently developed cultivars could be a result of mutation or that some mechanism may exist for recombination, and that the absence of certain virulence combinations could be due to a deleterious effect of such combinations on the pathogen. No evidence for sexual reproduction in the field has been observed despite the fact that it has been developed in laboratory conditions.

4. Genetic Structure of the Rice Blast Pathogen in Colombia

Critical and continuous evaluation of the blast pathogen population at the Santa Rosa screening and selection site for blast resistance indicates that this site exhibits a great pathogen diversity. Selection of virulent phenotypes representing all the diversity of the blast pathogen would be very important to identify under controlled inoculations, diverse germplasm with complementary resistance. This germplasm can then be incorporated in breeding program for rice blast resistance.

A repeated DNA probe (MGR 586) obtained from a rice blast fungus genome (Hamer et al, 1989) was found useful for grouping blast populations in genetic lineages, each with a particular spectrum of virulence characteristics (Levy et al, 1991). The complexity of the virulence structure in the blast fungus found at the CIAT's screening

site prompted the attempt to describe the population in terms of its lineage structure and determine if there was a correspondance between lineage and virulence patterns. This virulence complexitiy was organized into six distinct genetic lineages using the DNA-MGR 586 probe (Levy et al, 1993). The average similarity among all lineages was 49% while isolates within each lineage expressed very similar fingerprints with similarities ranging from 92% to 98% (Levy et al, 1993). In general, each genetic lineage was composed of several pathogenic races, one race could be present in different genetic lineages, and one lineage could be recovered from different cultivars. However, if *P. grisea* populations are generally composed of limited number of lineages and if there is a close relationship between lineage and virulence characteristics of the constituent individuals, population analysis at the lineage level could aid in directing resistance breeding projects that target the pathogen population in question.

5. Virulence Spectrum of Genetic Lineages of the Blast Pathogen In Colombia: Implications for Breeding for Blast Resistance

Characterization of the genetic lineage structure together with the virulence spectrum and virulence frequencies within the whole blast pathogen population should provide a more reliable estimate of the durability of cultivar resistance than only the consideration of virulences or lineages alone.

Analysis of the combination of virulence assays and genetic lineages in the blast

pathogen population studied is shown in Tables IV and V. This analysis was conducted to identify individual isolates within lineages that can be used as representatives of the lineage virulence diversity for use in screening for blast resistance (Correa-Victoria et al, 1994).

Compatibility for all resistance genes studied is present in the blast pathogen population at this screening site. One resistance gene may be defeated by isolates from different genetic lineages, suggesting that a common virulence factor can be shared between genetic lineages. This is the case of resistance gene Pi-a, defeated by five out of six lineages (Table IV). On the other hand, several virulence factors are shared among isolates within the same genetic lineage and may be accumulated in a single blast isolate, or present in individual pathotypes that are a subset of virulence corresponding to the full virulence spectrum of that lineage (Correa-Victoria et al, 1994). Genetic lineages SRL-4, SRL-5, and SRL-6 had wide spectrum of virulences. However, certain specific virulence-lineage-resistance gene interactions were observed, where a resistance gene seems to be effective against all individuals of entire lineages yet susceptible to most individuals of other lineages. This is the case of cultivars Fukunishiki and Tetep with resistance genes Pi-z and Pi-k^h, respectively (Table IV). These two cultivars seem to have complementary resistance which in combination could confer resistance to all the blast pathogen population described.

Virulence changes in the blast pathogen population in Colombia seems to have

been driven by changes in the cultivated commercial rice cultivars in the past. Although genetic lineage SRL-6 exhibits a wide spectrum and accumulation of virulence genes to most of the commercial cultivars released in the past, a high specific interaction between certain rice cultivars and genetic lineages is observed (Table V). As shown in Table IV, some commercial cultivars are incompatible with all isolates tested from some lineages. No lineage is compatible with cultivar Oryzica Llanos 5 explaining the stable resistance exhibited by this cultivar in farmer's fields (Table V).

Several specific single or multiple crosses to combine resistance to all genetic lineages of the blast pathogen can be deduced from Table V. Logical sources of resistance for such crosses would be those showing complementarity for blast resistance to different genetic lineages of the pathogen, as that exhibited by the cultivars Linea 2 or Cica 9, Cica 8, and Oryzica 2. A single or triple cross between these three groups of rice cultivars should theoretically confer resistance to the blast pathogen population present in Colombia. Considering the genetic resistance of a cultivar to completely exclude all the virulence in a lineage of the blast pathogen, suggests that the most important feature of lineage virulence spectrum is its limits, rather than the variation within. The effective exploitation of virulence spectrum of lineages for breeding purposes then would be to combine those resistance genes in combinations which are effective against all lineages within a target population (Correa-Victoria et al, 1994; Zeigler et al, 1994).

6. Stable Resistance to Rice Blast in Commercially Grown Cultivars

As a result of the screening and selection for blast resistance under high pathogen diversity and reliable disease pressure, the CIAT Rice Program identified a rice line released as the cultivar Oryzica Llanos 5. This cultivar was released in 1989 for an environment where the most durable cultivar previously retained resistance for only 3 seasons; nevertheless, Oryzica Llanos 5 has been grown on more than 300000 ha remaining blast resistant for 10 consecutive seasons. Three other sister lines of Oryzica Llanos 5 (namely, FONAIAP 2, MANA 3, and PORVENIR 95-INIA) have been released for commercial production in countries like Venezuela, Guyana, and Peru (Selva), respectively, where rice blast is known to be a serious production constraint.

Selecting high levels of blast resistance from populations with diverse combinations of resistance genes in the presence of a diverse and abundant pathogen population has been a key for the CIAT Rice Program to develop stable blast resistance as in Oryzica Llanos 5 (Correa-Victoria and Zeigler, 1994; Correa-Victoria and Zeigler, 1995). The resistance of Oryzica Llanos 5 did not come from only one of its ancestors, since all were susceptible to at least some isolates to which the cultivar is resistant, and since the parental lines also show susceptible reaction in the CIAT breeding fields where Oryzica Llanos 5 remains resistant (Correa-Victoria and Zeigler, 1995). None of the genetic lineages of the blast pathogen in Colombia exhibit compatibility with all of the parental lines. Instead, complementary resistance to all the

lineages is observed among the different parents (Table VI). It is unlikely that monogenic, vertical resistance could have remained undefeated for very long under this blast-prone environment.

Development of stable blast resistance is then possible through the combination of different sources which exhibit susceptibility to some segment of a blast population. Useful resistance genes would be those for which combinations of the matching virulence factors are absent in the pathogen population. Therefore, identification of these potentially useful gene combinations requires a continuous characterization of the genetic structure (lineages) and monitoring of the virulence frequencies of the blast pathogen.

Using several donors of blast resistance, several near-isogenic lines (NILs) were developed at the International Rice Research Institute (IRRI) for extracting single resistance genes from the donors (Mackill and Bonman, 1992). Inoculations of this group of NILs with blast isolates from different genetic lineages found in Colombia support the results observed in the inoculation of Colombian commercial rice cultivars with the same pathogen population. The single genes Pi-1 and Pi-2 were defeated by isolates of different genetic lineages of the pathogen. These two genes exhibit complementary resistance to all the virulence diversity reported here. There was no single isolate in any lineage compatible with both resistance genes (Table VII). The high virulence frequencies for each individual resistance gene present in the NILs would

suggest that under the circumstances of the existence of any mechanism of reproduction in the pathogen favoring sexual or parasexual recombination, combinations of compatible virulence genes to Pi-1 and Pi-2 should have been detected already. It is possible that the combination of these two virulence genes may confer a deleterious effect on the pathogen affecting the survival of this type of recombinants or simply confer a genetic barrier that avoids the same recombination. In fact, these mechanisms could explain the combination of virulence factors observed for other resistance genes in the NILs or the presence of the same virulence factor in different genetic lineages.

Similar results with these NILs were reported in inoculations with a different blast pathogen population (Zeigler et al, 1994; Zeigler et al, 1995). Combination of resistance genes to exclude all genetic lineages of target pathogen populations as a method to develop durable blast resistance has already been described as the "lineage exclusion hypothesis" (Zeigler et al, 1994).

7. Potential Applications of Induced Mutations for the Development of Durable Blast Resistance

The use of induced mutations is very well known in the development of resistance to pathogens in several crops. Rutger (1991) has described many useful applications of induced mutations in rice; these mutants were classed as "breeding tool" mutants. Although this technique has been successful in many cases, quick

breakdown of mutation induced resistance is also reported very often. One of the reasons for the failure of resistance obtained through mutation is that in most cases single gene changes are responsible for the induced resistance against all the pathogen population . A different alternative that we propose consist in the development of mutants, each with a gene resistant to just one or few genetic lineages of the pathogen. The idea is to identify as many mutants as needed such that combination of these mutants by targeted crosses can combine the different resistance genes to exclude all the genetic lineages of the blast pathogen. The possibility that induced mutation offers for the generation of resistance sources to the different genetic lineages of the blast pathogen is a worthy alternative to pursue for the development of a more stable blast resistance in rice.

8. Conclusions

8.1. Development of rice cultivars with durable blast resistance has been a very difficult task, specially for areas where rice is grown continuously and where climatic conditions are conducive to blast.

8.2. The international set of rice blast differentials can not be used effectively to characterize the high variability found in the blast pathogen population present in Santa Rosa, Villavicencio, Colombia, used as the breeding site for the CIAT Rice Program.

8.3. The MGR-586 probe was very useful for grouping the blast pathogen population in Santa Rosa into six distinct genetic lineages, each with a particular spectrum of virulence.

8.4. The spectrum of virulence for each genetic lineage has been studied and specific virulence-lineage-resistance gene interactions have been found.

8.5. Accumulation of complementary resistance genes in combinations which are effective against all lineages within the target blast population can lead to the development of more durable blast resistance.

8.6. Useful resistance genes would be those for which combinations of the matching virulence factors are absent in the pathogen population. Therefore, a continuous monitoring of the virulence frequencies of the blast pathogen is needed.

8.7. Evaluation and selection for blast resistance under high pathogen diversity, reliable disease pressure and rainfed-upland conditions led to the development and release of Oryzica Llanos 5 in 1989. This cultivar has remained resistant to blast since then; it is resistant to all genetic lineages of rice blast found in Santa Rosa, even though each of its parental lines is susceptible to a given lineage of the pathogen.

8.8. The key elements for the development of stable blast resistance through the

combination of different sources exhibiting susceptibility to some segment(s) of the blast population are:

- a. Characterization of the blast pathogen into distinct lineages.
- b. Characterization of the virulence spectrum of each genetic lineage, specially its limits.
- c. Characterization of each potential parent in terms of its resistance/susceptibility to each genetic lineage.
- d. Make specific crosses aimed at accumulating complementary resistance genes in combinations which are effective against all lineages within the target blast population.
- e. Continuous monitoring of virulence frequencies in the pathogen to confirm absence of targeted virulence gene combinations.
- f. Make use of appropriate field techniques to ensure a high, uniform and constant blast pressure under upland field conditions, repeating this process in each segregating generation.
- g. Multilocation testing of advanced lines.

8.9. Induced mutation offers possibilities for the generation of resistance sources to different genetic lineages of the blast pathogen, which can be combined through targeted crosses for the development of more stable blast resistance in rice.

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TABLE I. Rice cultivars released in Colombia with blast resistance.

Cultivar	Source of resistance	Year of release	Breakdown of blast resistance	Resistance years
CICA 4	Peta	1971	1972	1
CICA 6	IR 822-432	1974	1975	1
CICA 7	Colombia 1	1976	1978	2
CICA 9	C 46-15	1976	1977	1
CICA 8	Tetep	1978	1980	2
METICA 1	Colombia 1	1981	1982	1
ORYZICA 1	C 46-15, Colombia 1, Tetep	1982	1985	3
ORYZICA 3	Colombia 1, Tetep	1984	1985	1
LINEA 2	Oryzica 1	1988	1989	1
Oryzica Llanos 5	IR 36, 5685, Colombia 1, CICA 9	1989	NO	> 5

TABLE II. Virulence frequencies in a rice blast pathogen population in Colombia¹.

Cultivar	Resistance gene	Virulence frequency	Isolates tested (No.)
Oryzica Llanos 5	-	0.00	250
Fujisaka 5	Pi-i, Pi-k ^s	0.14	152
Fukunishiki	Pi-z	0.22	135
Tsuyuake	Pi-k ^m , Pi-m	0.25	118
Tetep	Pi-k ^h	0.26	149
BL-1	Pi-b	0.43	155
K-1	Pi-ta	0.47	138
Shin 2	Pi-k ^s	0.54	136
Pi - No.4	Pi-ta ²	0.64	159
Dular	Pi-k ^a	0.64	154
Kusabue	Pi-k	0.67	141
Aichi Asahi	Pi-a	0.75	145
K 59	Pi-t	0.78	111
Fanny	-	0.86	167

¹ Correa and Zeigler, 1993. Plant Disease 77:1029-1035.

TABLE III. Accumulation of virulence in *Pyricularia grisea* isolates collected in a blast screening site in Colombia.

Cultivar	Resistance gene	Isolates					
		1	2	3	4	5	6
Aichi Asahi	Pi-a	+	+	+	+	+	+
BI-1	Pi-b	+	+	+	-	+	-
Shin 2	Pi-k'	+	+	+	+	-	-
Dular	Pi-k ^a	+	+	+	+	-	-
Fukunishiki	Pi-z	+	-	+	-	-	-
Kanto 51	Pi-k	+	+	-	+	-	+
K-1	Pi-ta	+	+	+	+	-	-
K-59	Pi-t	+	+	+	+	-	-
CICA 9	-	-	-	-	-	+	+

+ = Compatible reaction.

TABLE IV. Virulence spectrum of six Colombian *Pyricularia grisea* lineages on rice cultivars with known resistance genes.

Cultivar	Resistance gene	Pathogen lineage					
		SRL-1	SRL-2	SRL-3	SRL-4	SRL-5	SRL-6
Aichi Asahi	Pi-a	+	+		+	+	+
BL-1	Pi-b		+		+		+
Caloro	Pi-k ^s				+	+	+
Fukunishiki	Pi-z				+		+
Fujisaka 5	Pi-i, Pi-k ^s				+	+	
K 1	Pi-ta			+	+	+	
K 59	Pi-t	+			+	+	+
Tetep	Pi-k ^h					+	

+ = Compatible reaction.

TABLE V. Virulence spectrum of six Colombian *Pyricularia grisea* lineages on colombian commercial rice cultivars.

Cultivar	Pathogen lineage					
	SRL-1	SRL-2	SRL-3	SRL-4	SRL-5	SRL-6
O.Llanos 5						
Linea 2		+				
Oryzica 2						+
Oryzica 1		+				+
Metica 1			+	+		+
CICA 8					+	
CICA 9	+	+				
CICA 6					+	+
CICA 4	+	+			+	+
IR 8	+	+		+	+	+

+ = Compatible reaction.

TABLA VI. Complementary resistance to *Pyricularia grisea* in parental lines of the commercial rice cultivar Oryzica Llanos 5 in Colombia.

Parent	Pathogen lineage					
	SRL-1	SRL-2	SRL-3	SRL-4	SRL-5	SRL-6
IR36	R	R	R	R	S	S
CICA 7	R	R	S	S	R	S
CICA 9	S	S	R	R	R	R
5685	R	R	R	R	S	S
Colombia 1	R	R	R	S	R	R

R = All isolates tested showed incompatible reaction; S = some isolates showed incompatible reactions and others were compatible.

TABLE VII. Virulence frequencies (%) on five near isogenic lines inoculated with *Pyricularia grisea* lineages found in Colombia.

Pathogen lineage	Isogenic line (resistance gene)				
	C 101 LAC (Pi-1)	C 101 A51 (Pi-2)	C 104 PKT (Pi-3)	C 101 PKT (Pi-4a)	C 105 TTP (Pi-4b)
SRL-1		100			
SRL-2		100		25	
SRL-3					
SRL-4			100	100	
SRL-5	86		100	100	100
SRL-6		21	42	91	97