STUDIES ON THE RICE BLAST PATHOGEN, RESISTANCE GENES, AND IMPLICATION FOR BREEDING FOR DURABLE BLAST RESISTANCE IN COLOMBIA

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Abstract. Rice blast disease caused by *Pyricularia grisea*, the anamorph of *Magnaporthe grisea*, is the main rice production constraint in Latin America. Development of resistant cultivars has been the preferred means of controlling this disease; however, blast resistance is defeated by the pathogen shortly after cultivar release, affecting both leaves and panicles of the plant and reducing yields severely. Major efforts are being made at CIAT to understand the high pathogen variation observed, often reported as the main cause of resistance breakdown. We have analyzed extensively the genetic structure of blast pathogen populations using MGR-DNA and rep-PCR fingerprinting techniques and studied the avirulence gene diversity using a set of rice differentials with known resistance genes. The blast pathogen in Colombia has been found to be mainly clonal exhibiting few genetic lineages. At present, there are three lineages predominating in the pathogen population and their frequencies depend upon the susceptibility and planted area of the commercial rice cultivars by farmers. In general, a single haplotype predominates within each lineage. These three genetic lineages exhibit broad spectrum of virulence and together defeat all known blast resistance genes. However, some resistance genes are effective against all members of a lineage, suggesting an association of avirulence genes and genetic groups in the pathogen. Avirulence genes vary in frequency in the pathogen population and some are highly frequent in several genetic lineages of the fungus. This suggests that these avirulence genes could play an important role in the pathogen or be associated with pathogenic fitness and then the corresponding resistance genes could be more relevant in breeding for durable resistance. Despite this high virulence diversity, breeders at CIAT have been able to develop durable blast resistant cultivars, indicating that combinations of these resistance genes may confer suitable and durable resistance to the pathogen. Evaluation and selection of breeding lines are routinely carried out under "hot spot" conditions favoring high pathogen pressure and diversity. Our studies are allowing us to identify and predict the durability of resistance gene combinations based on avirulence gene frequencies and the possible association of avirulence genes with pathogenic fitness. We have inferred the possible resistance genes present in our blast susceptible rice cultivars and initiated a backcrossing program to incorporate the desired resistance gene combinations into Latin American rice cultivars through marker assisted selection using mainly microsatellite and scar markers. Rice lines carrying the combination of the resistance genes Pi-1, Pi-2 and Pi-33 are then tested under controlled greenhouse conditions as well as our "hot spot" screening site using a spreader row technique to maintain a high and diverse population of the pathogen in the field. Resistant plants are then selected based on other desirable traits for their distribution to national programs in Latin America.

Introduction

Rice blast caused by *Pyricularia grisea* Sacc., the anamorph of *Magnaporthe grisea* (Hebert) Barr, is the main rice production constraint in the world. The fungus attacks leaves and panicles severely. Rice blast research has concentrated for many years on the identification of races of the pathogen and the incorporation of resistance genes to those races into commercial rice cultivars. However, blast resistance in Colombian commercial rice cultivars is lost in one to three years after cultivar release (Correa-Victoria and Martinez, 1994) with the exception of the commercial cultivars Oryzica Llanos 5 released in 1989 and the cultivar Fedearroz 50 released in 1998 (Table 1). Long-term studies are being conducted at the Centro Internacional de Agricultura Tropical, CIAT, to understand the great variability observed in the blast pathogen, often referred as the main cause of resistance breakdown. Diversity studies of *P. grisea* in Colombia were initiated in 1990. These studies have considered the diversity and frequency of avirulence genes as well as the spectrum of virulence of several hundred of blast isolates collected from different rice cultivars over the years. Isolates from the pathogen have been inoculated under greenhouse conditions on rice cultivars with known resistance genes, rice cultivars released in Colombia in the last 30 years, sources of durable blast resistance, a set of international differentials, and a set of near isogenic lines with reported resistance genes.

The molecular techniques RFLP using the MGR 586 DNA sequence (Levy *et al.*, 1993) and rep-PCR using the Pot-2 DNA sequence derived primers (George *et al.*, 1998) were used to determine the genetic structure of the same pathogen populations used for virulence studies. The complexity of the pathogen described as many races (Correa-Victoria and Zeigler, 1993a) has been simplified in just six genetic families, named SRL-1 to SRL-6 (Levy *et al.*, 1995) which are mainly compatible with indica type of rice, and a genetic lineage named A-7 (Correa-Victoria *et al.*, 1994) compatible mainly with japonica type (Figure 1). Studies on the relationship between spectrum of virulence and a genetic lineage of the pathogen indicate that the most important aspect of this interaction is the existence of resistance genes, which are effective in controlling all isolates of the same lineage. The rice project at CIAT as objective has been developing a breeding strategy for the development of durable blast resistance. This strategy is based on studies on the composition and frequency of avirulence genes of the pathogen, characterization of the genetic structure, identification and incorporation of resistance gene combinations into commercial rice cultivars

effective against populations of each genetic family, and the continuous evaluation and selection of breeding lines under a high disease pressure and pathogen diversity (Correa-Victoria and Zeigler, 1993a, 1993b, 1995).

Table 1 Rice cultivars released in Colombia, sources of resistance and year of resistance breakdown to *Pyricularia grisea*

Cultivar	Source of Resistance	Year of release	Resistance breakdown	Years of Resistance
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	C 46-15, Colombia 1, Tetep	1988	1989	1
Oryzica Llanos 5	IR 36, 5685, Colombia 1, Cica 9	1989	Not yet	> 13
Oryzica Caribe 8	Tetep, IR 665, Colombia 1, Cica 9	1993	1995	2
Fedearroz 50	IR 665, 5685, Colombia 1, Cica 9	1998	Not yet	> 4

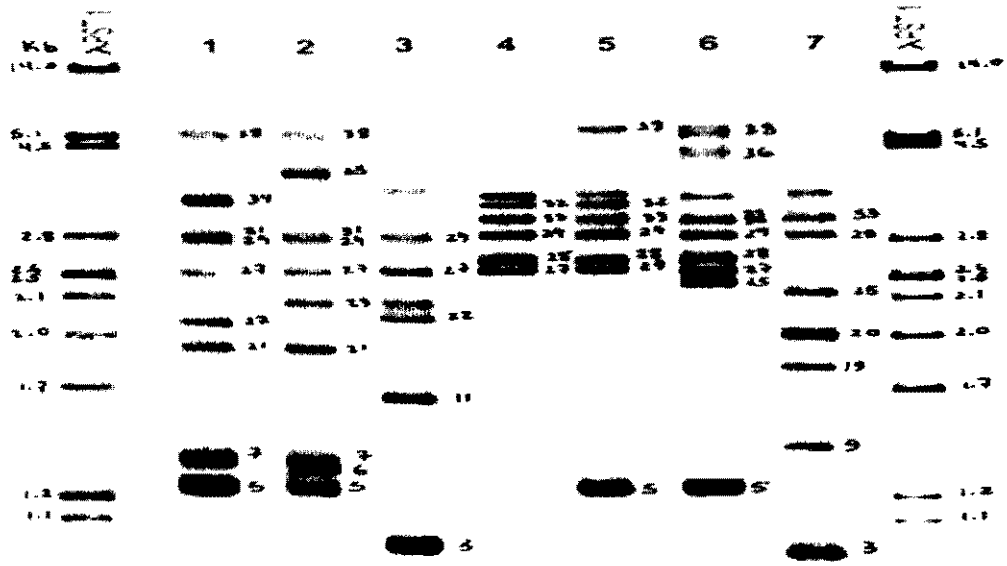
Characterization of virulence and genetic structure of *Pyricularia grisea* in Colombia

The CIAT's Rice Project develops its breeding activities on resistance to *P. grisea* under favored upland conditions in the experimental station "Santa Rosa" from FEDEARROZ in the Meta department, Colombia. This site is characterized for having high blast disease pressure and pathogen diversity. A high disease incidence and severity is maintained in the breeding plots during the entire crop cycle by using spreader rows, which are conformed of a mixture of commercial rice cultivars susceptible to the different genetic lineages of the pathogen. These rows are planted perpendicularly to the rice breeding lines being evaluated for resistance. Large amounts of fungal spores are produced on the spreader rows and then disseminated by the wind and rain onto the breeding lines, increasing the chances of a line to be exposed to the pathogen and reducing the possibility of escape to infection (Figure 2).

Under this condition of evaluation and selection, we have found that the resistance selected is more stable and durable than under conditions of less blast pressure. However, the durability of the resistance depends not only on the plant, but also on the pathogen dynamics and changes in virulence. Establishing a system to understand the pathogenic variability and dynamics is then essential for the development of a strategy to control the blast disease through genetic resistance.

Population studies of the blast fungus collected at this screening site during 12 years show the existence of more than 50 races of the pathogen, with virulence or compatibility with more than 13 resistance genes. Under greenhouse conditions, 21 days old plants are inoculated in three replications (10 plants per replication) by spraying a suspension of $5x10^5$ spores/milliliter, incubated for 15 days with high relative humidity, and evaluated for the lesion type developed and percentage of leaf area affected. Virulence frequency studies on 42 rice cultivars with different resistance genes were between 0.0 and 0.86 (Correa-Victoria and Zeigler, 1993a). Most isolates exhibit the lost of a large number of avirulence genes, but none is virulent on all the resistance genes (Table 2) suggesting the need to pyramid suitable gene combinations in order to develop a more effective resistance against the pathogen (Correa-Victoria *et al.*, 1994).

The molecular analysis of these blast populations suggests an asexual reproduction grouping the pathogen in just a few genetic families. The genetic structure is relatively simple despite of the great virulence diversity observed. The genetic similarity of isolates within a genetic lineage is more than 85%, while similarity among isolates of different lineages is between 37 and 85% (Levy *et al.*, 1993). The spectrum of virulence of isolates within a lineage is highly similar, differing in just a few virulence factors. Although different genetic families of the fungus share several avirulence genes, we have detected a high specific interaction between some avirulence genes in the pathogen and some resistance genes in the plant. This interaction is characterized by the conservation of some avirulence genes in each genetic family despite all the evolution process occurring in the fungus. This interaction is of much value from a breeding point of view for the development of blast resistant rice cultivars (Table 2). This specific interaction is the base for selecting progenitors to be included in a breeding program for durable blast resistance.



1. SRL-1
2. SRL-2
3. SRL-3
4. SRL-4
5. SRL-5
6. SRL-6
7. A-7

Figure 1 ADN fingerprinting of *Pyricularia* grisea determined by Pot 2-PCR (George *et al.*, 1998). Genetic lineages SRL-1 to SRL-6 and Altillanura 7 (A-7) from Colombia

The characterization of the genetic lineages, together with the virulence spectrum and frequency of the avirulence genes in the pathogen population should give us a better estimate of the potential durability of a resistance gene than the individual study of each one of these components. A resistance gene can be defeated by isolates from different genetic lineages, as it is the case of the genes Pi-t and Pi-k^s (Table 2). On the other hand, some resistance genes are effective controlling all the pathotypes of a single or several genetic families, even though they may be susceptible to the pathotypes of other different families. In this way, rice cultivars may have complementary resistance genes, which in combination in a cultivar confer resistance to the whole targeted pathogen population. The isogenic lines CT 13432-68, CT 13432-54, and CT 13432-55 which carry the resistance genes Pi-1, Pi-2, and Pi-33, respectively, have complementary resistance genes, which in combination or after pyramided in the isogenic line CT 13432-34 confer resistance to all the pathogen isolates belonging to the different genetic families of the fungus found in Colombia (Table 2).

The frequency of the different genetic lineages and avirulence genes depends on the resistance genes used in the commercial rice cultivars planted by farmers. The frequency of the genetic lineages change between years depending on the area planted with a particular cultivar and on the spectrum of virulence of the lineage. In a study on the compatibility frequency of the most virulent isolates from Colombia on 201 rice cultivars from Latin America (Correa-Victoria *et al.*, 2000), we observed that most cultivars were susceptible to the genetic lineage SRL-6 (80.6%) and SRL-5 (68.7%). The pattern observed with these two lineages should be the result of the narrow genetic base existing in the rice germplasm that has been used in Latin America for the development of the commercial rice cultivars. Lineage SRL-6 has been for many years the most frequent lineage in the blast population from Colombia. The lineages SRL-2 and SRL-4 have increased in frequency as the area planted with cultivars susceptible to them

has increased in the past few years. Isolates of these two lineages exhibit a broad spectrum of virulence on Colombian commercial cultivars and the isogenic lines. The frequency of lineages SRL-1 and SRL-5 have decreased due to a marked reduction in the area planted with susceptible cultivars to these lineages. These two lineages exhibit however a high compatibility with rice cultivars from Latin America. The frequency of lineage SRL-3 has been near zero during the past years due to the absence of susceptible cultivars and a narrow spectrum of virulence exhibited by this lineage. We have also observed a gain in virulence (lose of avirulence genes) for the most predominant lineages as can be observed in the subdivision of lineage SRL-6 in SRL-6B and lineage SRL-4 in Table 2. The early detection before having an increase in frequency, of pathotypes with a broad spectrum of virulence is of practical use for the identification of resistance genes that can be used in case that the resistance of a commercial cultivar is lost.

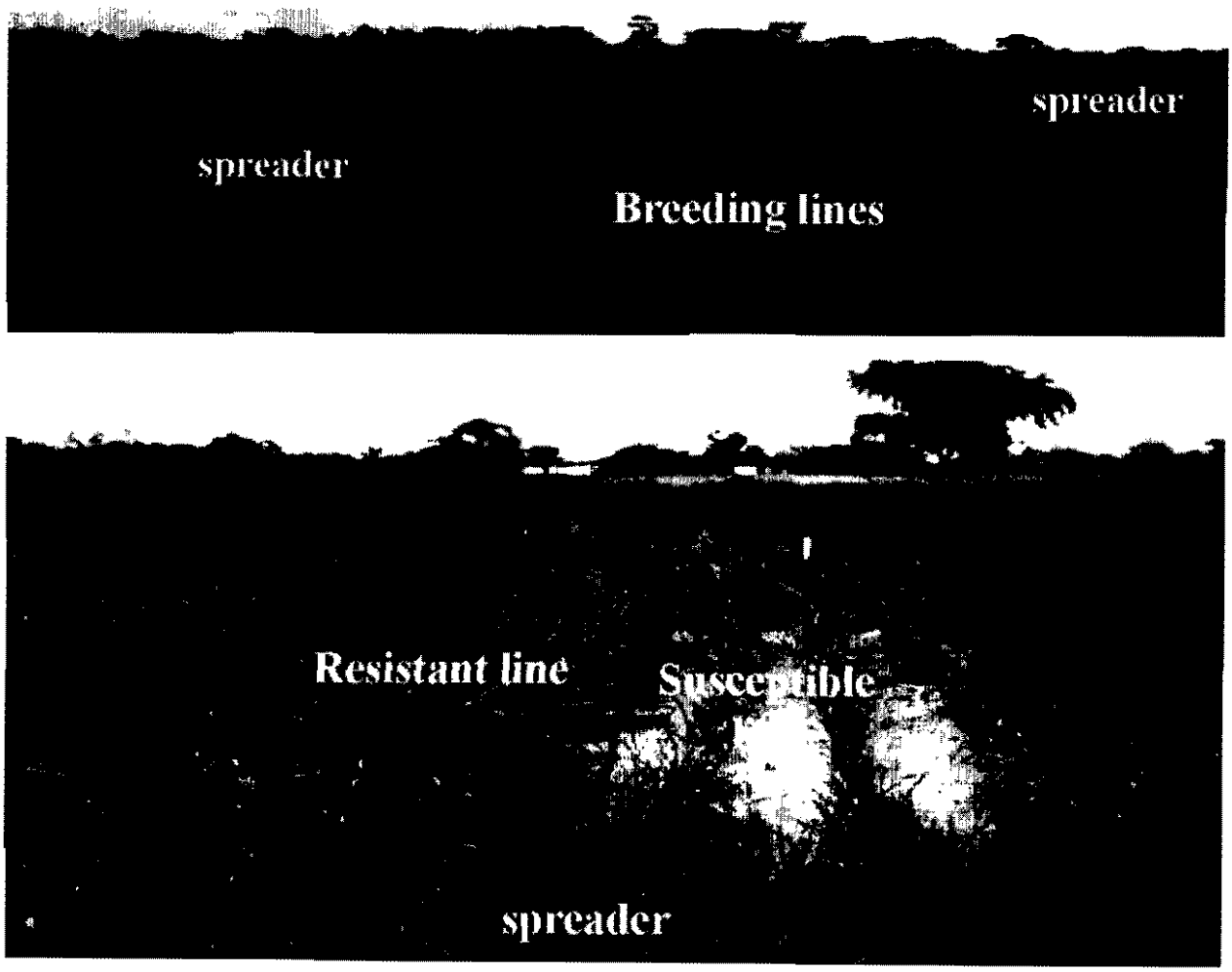


Figure 2 Experiment station of Santa Rosa for the evaluation of the resistance to *P. grisea* using spreader rows for the multiplication and dissemination of the blast pathogen maintaining a high disease pressure

the isogenic lines CT 13432-34, CT 13432-107, CT 13432-189, and CT 13432-246 (Table 2, Table 3, Figure 4) confers complete resistance to the blast populations present in Colombia, which are compatible with any single gene or the combination of two of them (Table 3, Figure 4). According to our studies, the avirulence genes avr-Pi-1 and avr-Pi-33 are highly conserved in the blast population from Colombia, suggesting that these genes have a lower frequency of mutation towards virulence and probably are important genes in the fitness of the fungus. On the other hand, the avirulence gene avr-Pi-2 is conserved only in lineage SRL-5, suggesting that this avirulence gene has a larger rate of mutation towards virulence and that it would be less durable by itself. This is confirmed by the fact that four of the six genetic lineages are compatible with the resistance gene Pi-2 (Table 2). Additionally, the resistance genes Pi-k^h, Pi-sh, and Pi-z can also be considered of great potential (Table 2) since in combination seem to confer resistance to the entire blast population studied.

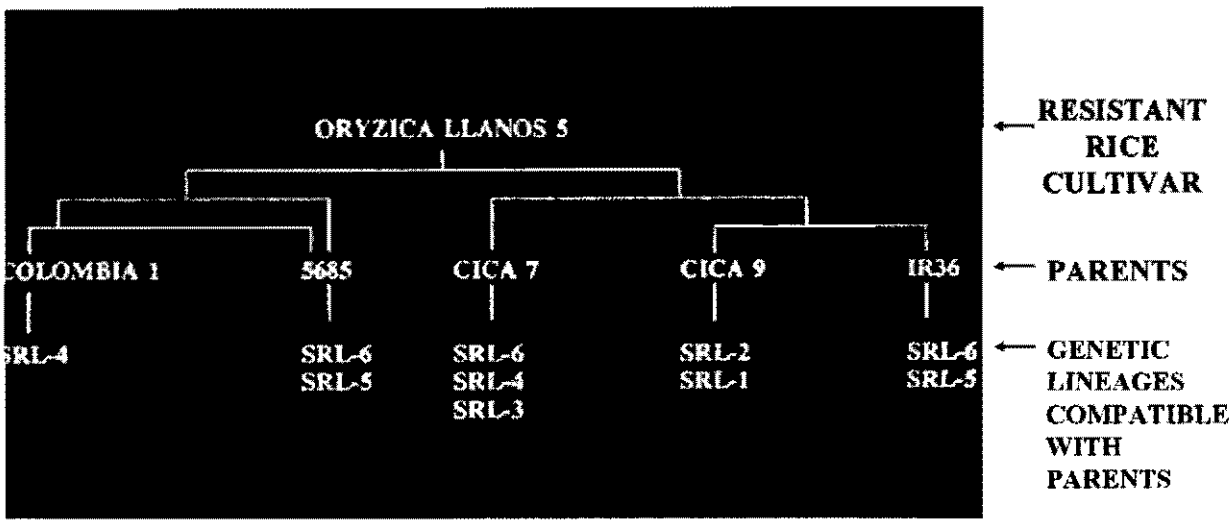


Figure 3 Genealogy of the rice cultivar Oryzica Llanos 5 with durable resistance to *P. grisea* and the complementary blast reaction of the progenitors to the different genetic lineages of the pathogen

The plant-pathogen interaction in the complex system rice-blast has been shown to follow the gene-for-gene hypothesis (Flor, 1971), where the resistance results from the genetic interaction between the resistance genes in the plant and the avirulence genes in the pathogen. The presence of only one of these corresponding genes in each organism (plant and pathogen) results in a resistant reaction. The mutation or lose of one of these genes in any of the two organisms is required for a susceptible reaction.

Table 3 Leaf and panicle reaction to *Pyricularia grisea* in isogenic lines with different combinations of the resistance genes Pi-1, Pi-2 and Pi-33

		Leaf blast		Neck blast Incidence (%)
Isogenic line	Resistance gene	BL4[1]	BL5[1]	
CT 13432-95	None	9	9	Dead
CT 13432-110	None	9	9	Dead
CT 13432-68	1	9	9	Dead
CT 13432-54	2	9	9	Dead
CT 13432-6	33	9	9	Dead
CT 13432-230	1 + 2	9	9	Dead
CT 13432-26	1 + 33	9	9	Dead
CT 13432-193	2 + 33	8	5	15
CT 13432-34	1 + 2 + 33	2	2	0
CT 13432-107	1 + 2 + 33	2	1	0
CT 13432-189	1 + 2 + 33	2	1	0
CT 13432-246	1 + 2 + 33	2	1	0

[1] Fourth and fifth evaluations of leaf blast (BL).

Many avirulence genes may act as "fitness" factors highly related to the survival capacity of the fungus (Leach *et al.*, 2001). It has been suggested that avirulence genes of high rate of mutation in the pathogen are probably less critical on the fitness processes than those that rarely mutate (Flor, 1971), and has been pointed out that the fitness of a pathogen is the factor or main force in the evolution and stability of a pathosystem in agriculture (1Van der Plank, 1968). In this way, it can be considered that the quality and durability of a resistance gene is a direct function of the effects imposed to the pathogen after losing the function of the corresponding avirulence gene to overcome the corresponding resistance gene (Leach *et al.*, 2001).

Two methods have been suggested to evaluate the effect on the fitness imposed by the mutation of an avirulence gene on a pathogen population (Leach *et al.*, 2001). First, to determine if there is a reduction of a virulence gene (avirulence gene mutated) in the absence of the corresponding resistance gene in the field. The hypothesis is that if the mutation does not confer a selective advantage in the pathogen, then the mutated gene will disappear from the population. Second, to determined directly if the inactivation of the avirulence gene has a direct effect on the fitness components of the pathogen. These studies require the validation of the laboratory results in the field. Positive answers to these two questions can be considered as evidence indicating that the effect of the avirulence genes on the pathogen can be used as an indicator to predict the durability of a resistance gene or the combination of several resistance genes (Leach *et al.*, 2001). In other words, those resistance genes imposing to the pathogen a high value or deleterious effect after losing the corresponding avirulence gene to breakdown the resistance of the gene, will probably be a durable resistance gene.

Our studies at CIAT have been focused on developing the capacity to predict the durability of the resistance genes with the objective of using them efficiently in our breeding program. Isogenic lines developed at IRRI and CIAT with different resistance genes and combinations have been useful to determine the frequency of different pathogen genotypes present during different crop cycles both in commercial fields as well as in the experiment station. Even though, there are many studies demonstrating that individual resistance genes may confer durable resistance, our studies indicate that it is not the case for the control of rice blast in Colombia. It can be observed in Table 3 that for the eight possible genotypes using three resistance genes, the pathogen has developed probably seven genotypes, except the one losing the function of the three avirulence genes corresponding to the three resistance genes Pi-1, Pi-2, and Pi-33, combination which exhibits a complete blast resistance (Figure 4). The results suggest that the pathogen can lose the function of any of the three avirulence genes, or the combination of any two of them, but not the three avirulence genes (Table 2). It is possible that after losing one or two of the avirulence genes the other gene confers the needed fitness component to survive. This capacity would be lost in the case of losing the three avirulence genes. In this case, it is necessary that in order to predict the durability of the resistance by the use of these genes, the combination of the three genes should be used and not only one or two of them.

Table 4 Possible resistance genes present in commercial rice cultivars from Colombia inferred from inoculations with *Pyricularia grisea* isolates carrying the corresponding avirulence genes

	Resistance gene									
Rice cultivar	Pi-1	Pi-2	Pi-33	Pi-z	Pi-z^t	Pi-ta[2]	Pi-sh	Pi-k^h	Pi-k	Pi-b
Oryzica 2	X[1]	X				X	X	X	X	X
Oryzica 3						X			X	
Cica 8	X					X			X	X
Cica 9		X				X				
IR 22						X	X		X	
Linea 2		X								
Oryzica Llanos 4		X					X		X	
Oryzica Caribe 8		X					X		X	
Oryzica Yacu 9		X								
Oryzica Llanos 5		X	X	X	X	X	X		X	X
Fedearroz 50		X	X	X	X	X	X		X	X

1. X = Presence of resistance gene

It is important to note that even for isolates with broad spectrum of virulence (many avirulence genes lost) as it is the case of isolate 1 of lineage L6B (SRL-6) in Table 2, this isolate has lost the avirulence genes for the resistance genes Pi-1 and Pi-2, but has conserved the avirulence gene for Pi-33. Similarly, isolate 4 identified as L4 (SRL-4), which

has lost the avirulence genes for Pi-2 and Pi-33, has conserved the avirulence gene for Pi-1, and isolate 9 identified with lineage L5 (SRL-5) has lost the avirulence genes avr-1 and avr-33, but has conserved avr-2. In addition, it can be noted that the combination of the resistance genes Pi-k^h and Pi-z exhibits a similar exclusion and resistance to all the genetic lineages used in this study (Table 2).

Isogenic lines with individual resistance genes are also useful for the identification of avirulence genes present in different isolates of the blast pathogen, which can be used to predict which resistance genes could be present in a rice cultivar. The characterization of the avirulence genes in several hundred isolates of the fungus in Colombia has allowed us to infer the possible resistance genes present in the commercial cultivars of rice in Colombia (Table 4) after inoculating them with those isolates in the greenhouse. The rice cultivars Oryzica Llanos 5 and Fedearroz 50 that have exhibited a durable blast resistance (Table 1) carry the greatest number and similar resistance genes (Table 4). These two cultivars seem to carry the resistance genes Pi-2 and Pi-33 but not the gene Pi-1. The durability of the resistance of these two cultivars is probably due to the action of these two genes plus the action of the other genes shown in Table 2, and probably the presence of other unidentified genes.

With the objective to predict a future breakdown of the durable resistance exhibited by the cultivars Oryzica Llanos 5 and Fedearroz 50, we have been collecting leaf and panicle samples of single lesions occasionally developing on these two cultivars. These samples have been analyzed in order to advance a breeding program by identifying and incorporating resistance genes against the genetic lineages found to be in an evolution process to breakdown the resistance of these cultivars. The results of the molecular analysis of the isolates collected from these two cultivars in the last few years indicate that more than 90% belong to lineage SRL-4 and a few to lineage SRL-6. These isolates however, do not re-infect the two cultivars in greenhouse inoculations and do not develop typical lesions of the disease. Occasionally, some of these SRL-4 isolates induce under nutritional stress the formation of small non-sporulating lesions, or in a few cases typical blast lesions. However, these results suggest that lineage SRL-4 is in the process of evolution with higher probabilities than the lineages SRL-5 and SRL-6 of breaking down the resistance of the cultivars Oryzica Llanos 5 and Fedearroz 50. This observation is happening despite the fact that lineage SRL-6 has predominated in the entire pathogen population for many years. Our question of why lineage SRL-4 is found in more frequency than the other two lineages on these two cultivars, and why it is evolving with potentiality of breaking down their resistance, can be logically deduced from the data presented in Table 2. As it can be observed, isolate 4 in Table 2 exhibits the most recent evolution of lineage SRL-4 with virulence towards all the resistance genes present in the cultivars Oryzica Llanos 5 and Fedearroz 50 according to Table 4. This lineage however has not lost the avirulence gene to the resistance gene Pi-1, and it does not need to lose it, as this resistance gene is not present in any of the two cultivars (Table 4). On the other hand, those isolates with broader spectrum of virulence within lineages SRL-6 (isolate 1, Table 2) and SRL-5 (isolate 9, Table 2) would have to mutate or lose the avirulence genes to the resistance genes Pi-33 and Pi-2, respectively, which are present in the cultivars Oryzica Llanos 5 and Fedearroz 50. These two lineages have already lost the avirulence gene to Pi-1, and therefore to breakdown the resistance of the two cultivars would need to lose the three avirulence genes avr-Pi-1, avr-Pi-2, and avr-Pi-33. According to our previous discussion, losing the three avirulence genes would have a deleterious effect on the pathogen.

The lineage SRL-4 has lost the avirulence genes for the resistance genes Pi-ta^2, Pi-k, and Pi-b (Table 2), which are present in those cultivars with durable resistance (Table 4). This lineage has not lost the avirulence gene for the resistance gene Pi-k^h, which is not present in the cultivars Oryzica Llanos 5 and Fedearroz 50. Therefore, this gene together with Pi-1, could be used in a breeding program to be incorporated in the two cultivars complementing their durable resistance, and moving ahead to the evolution that is apparently going on in this lineage of the pathogen that would lead them to the breakdown of the durable resistance present in the two commercial cultivars. Our results also suggest that the two cultivars with durable resistance might carry other unknown resistance genes that need to be identified. We are in collaboration with Kansas State University working on the dissection of all the resistance genes present in the cultivar Oryzica Llanos 5.

With the objective to develop rice cultivars with durable blast resistance to *P. grisea* for other Latin American countries, we have initiated a backcross program to introduce the resistance genes Pi-1, Pi-2, and Pi-33 in 14 commercial rice varieties from the region (Table 5). These rice cultivars are still economically important for many farmers but they are blast susceptible. The backcrossing procedure is described in Figure 5 and the incorporation of the resistance genes Pi-1, Pi-2, and Pi-33 is followed through the use of micro satellites (McCouch *et al.*, 2001) associated with the resistance genes, greenhouse inoculations with the appropriate isolates carrying the

corresponding avirulence genes, and the evaluation and selection of resistant lines in the field under high pressure of the disease and diversity of the pathogen (Figure 2). Populations and selected lines with the three resistance genes will be distributed to the different countries in Latin America for the evaluation and selection of rice lines incorporating both, the blast resistance as well as other desired agronomic traits.

Table 5 Latin American rice varieties used for the incorporación of the resistance genes Pi-1, Pi-2, and Pi-33 through molecular markers, inoculations with *Pyricularia grisea* isolates, and field evaluations

Rice variety	Country
Fedearroz 2000	Colombia
Colombia XX1	Colombia
Oryzica 1	Colombia
Fedearroz 50	Colombia
Epagri 108	Brazil (irrigated)
Irga 409	Brazil (irrigated)
Primavera	Brazil (upland)
Bonanza	Brazil (upland)
El Paso 144	Uruguay, Argentina
Cimarron	Venezuela
Capirona	Peru
Panamá 1048	Panama
CR 1113	Costa Rica
J 104	Cuba

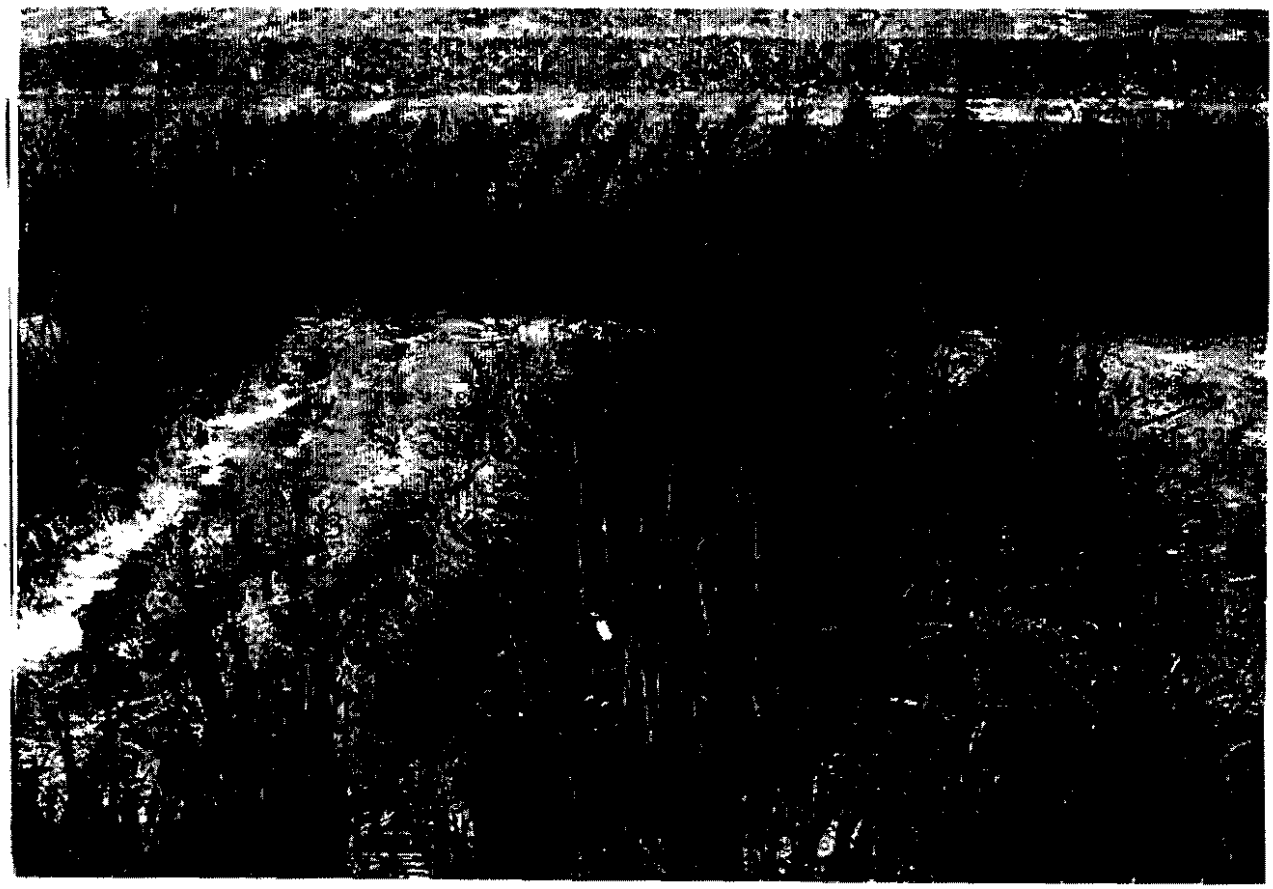


Figure 4 Complete resistance to *Pyricularia grisea* in the isogenic line CT 13432-34 conferred by the combination of the resistance genes Pi-1, Pi-2, and Pi-33

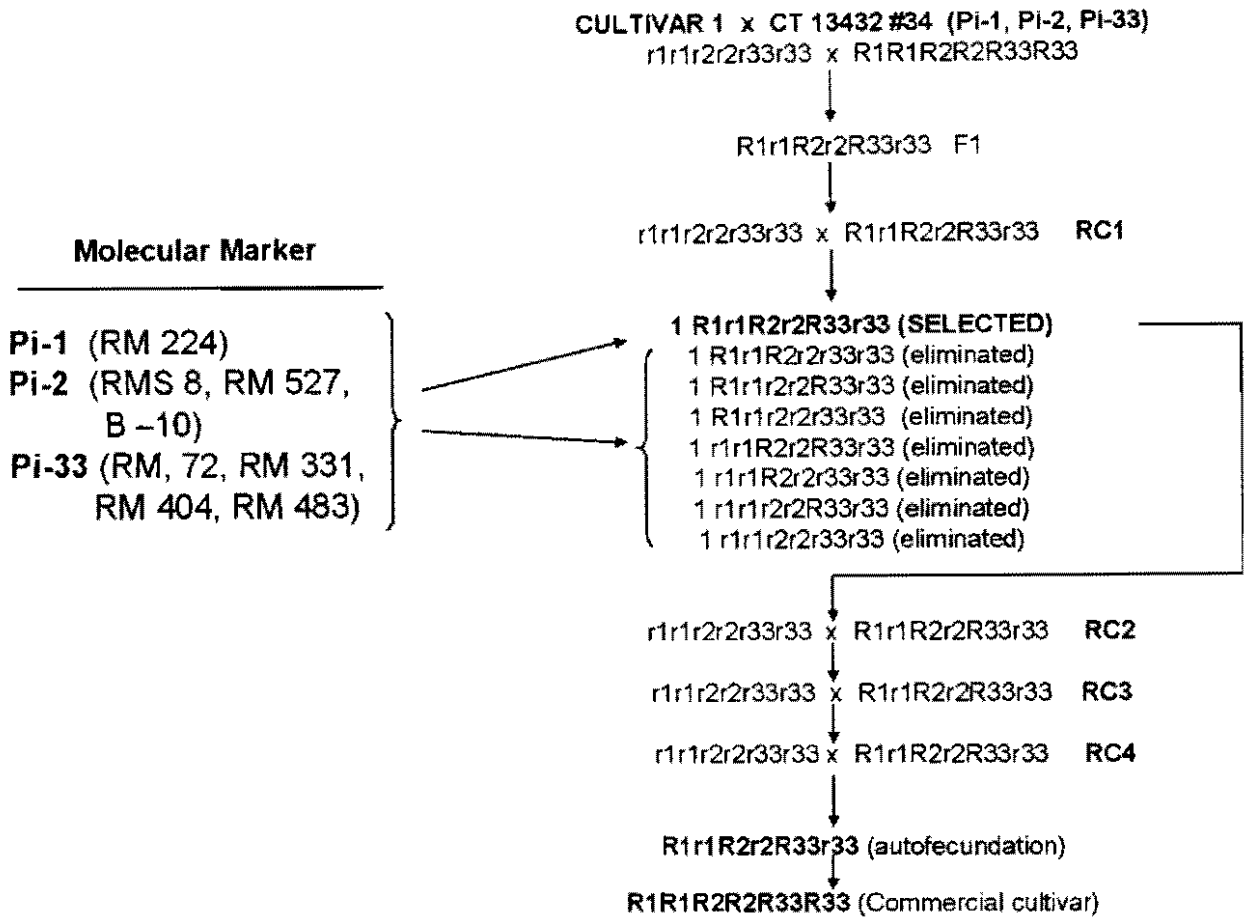


Figure 5 Backcross procedure for the introgression of the resistance genes Pi-1, Pi-2, and Pi-33 to *P. grisea* in rice varieties from Latin America

Conclusions

- The genetic structure of *P.* grisea in Colombia ifs formed by few genetic lineages whose frequency depend on the resistance genes in the planted cultivars
- The use of isogenic lines with different resistance genes for determining the frequency of avirulence genes in the pathogen allow us to identify relevant combinations of resistance genes for the control of rice blast
- The rice blast pathogen in Colombia exhibits virulence to all known resistance genes. Durable resistance then can only be developed through combinations of resistance genes
- Based on the relative contribution of the avirulence genes to fitness of *P. grisea*, plant genotypes can be designed and generated carrying the most effective combinations of resistance genes
- A pathogen such as *P. grisea* which is mainly clonal, do not seem to be able in tolerating a continuous increase of mutations in its avirulence genes even in the case that those genes have minimal contributions to fitness
- The combination of the resistance genes Pi-1, Pi-2, and Pi-33 confers resistance to the blast populations in Colombia. The use of molecular markers and greenhouse inoculations are useful for following the incorporation of resistance genes in breeding populations
- Rice populations developed in breeding programs with the objective of accumulating several blast resistance genes should be evaluated and selected using field methodologies that maintain a high disease pressure and pathogen diversity.

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